AN ABSTRACT OF THE THESIS OF

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Title: LIFE TABLE ANALYSIS OF DOUGLAS-FIR BEETLE

(DENDROCTONUS PSEUDOTSUGAE HOPK.) POPULATIONS

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The dynamics of Douglas-fir beetle (Dendroctonus pseudotsugae

Hopk.) populations in windthrown, old growth Douglas-fir trees

(Pseudotsugae menziesii (Mirb.) Franco) were investigated on the

Marys Peak watershed near Corvallis, Oregon from 1963 to 1966.

Sampling techniques were designed to measure population

densities of the various stages of the beetle, namely eggs, four larval

instars, fall callow adults, spring callow adults and emerging adults,

in individual windthrown trees. It was not possible to measure popula-

tion densities of beetles from time of emergence to time of attacking

new host.

Attacking female beetles preferred to attack shaded windthrow

or the shaded portions of windthrow in comparison to exposed logs.

Except in those cases where exposure is a factor, females attack a

windthrown log in a random fashion. The intensity of attack for a

given year is a function of the total number of female beetles, and

the total amount of available host material. Shaded logs will be

attacked much more heavily than exposed logs.

Special studies were carried out to provide estimates of mortality due to intraspecific competition. Life tables were constructed for the major age intervals of the life cycle of the Douglas-fir beetle from the time of attack till adult emergence. Where possible, mortality within a specific age interval was assigned to a factor.

The life tables were analyzed in several ways. Although the data in the life tables did not represent complete generation survival, the analyses demonstrated that the critical-age interval was the larval stage and that intraspecific competition during the first, second and third larval instars was the key factor. This factor (intraspecific competition) acts in a density-dependent fashion and is capable of completely compensating for changes in host density.

Predation mortality caused by Medetera aldrichii Wheeler (Diptera: Dolichopodidae) and Enoclerus sphegeus Fab. (Coleoptera: Cleridae) became an important factor in the fourth instar, pupal and early callow adult stage. Predation occurred in a density-dependent manner. Medetera aldrichii are more numerous and more responsive to host density than Enoclerus sphegeus, hence, more effective.

It is concluded that Douglas-fir beetle populations are regulated by density-related processes within blowdown host material from time of attack to time of emergence. The availability of blowdown host material is the result of density-independent events, i.e. weather.

Life Table Analysis of Douglas-fir Beetle
(Dendroctonus pseudotsugae Hopk.) Populations

by

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LIFE TABLE ANALYSIS OF DOUGLAS-FIR BEETLE

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I. INTRODUCTION

A basic goal of ecology is to explain the distribution and

abundance of animals. Knowledge of the population dynamics of an

animal species may result in accurate predictions of where that animal

species may occur and in what numbers. Milne (1957) defined population

dynamics as

> "that branch of ecology which investigates (1) the
> causation of changes of total numbers in a given place
> (i.e. - population changes) and (2) the mechanisms of
> natural control of populations."

Many theories have been advanced to explain the distribution

and abundance of animals. According to Clark et al. (1967), the main

theoretical contributions can be considered in four groups: (1) those

of workers who think that density-related processes, termed 'density-

dependent', play a key role in the determination of population numbers

by operating as regulating mechanisms; (2) those of workers who regard

density-dependent processes as playing little or no role in determina-

tion of animal abundance. In this case, weather or climate is con-

sidered to be the important factor; (3) those of workers who advocate a

combination of the first two theories - i.e. density-related processes

regulate populations within a broader framework of density-independent

events; (4) those of workers who emphasize the influence of the genetic

factor in the determination of population numbers.

Various approaches to the study of natural populations of

organisms have been employed by ecologists. The use of ecological life

tables is a quantitative approach that has received considerable
attention, particularly in the study of insect populations in recent
years. It should be emphasized that life tables are not an end in
themselves, but should merely serve as a tool in the analysis and
interpretation of the dynamics of natural populations.

Life tables were first used where they formed the basis of
actuarial studies for human populations. Several variations of the
basic idea as applied to human populations can be found in the
literature of the 1930's and 1940's. The first reasonably complete
life tables in the field of forest entomology were developed by
Morris and Miller (1954) for the spruce budworm, and since then,
many examples appear in the literature indicating a wide acceptance
of the method. There are two major problems that can limit the use
of life tables for ecological work: (1) the development of suitable
techniques for measurement of populations and (2) the identification
and assessment of the various factors that influence populations.

The Douglas-fir beetle, Dendroctonus pseudotsugae Hopkins,
is the most destructive insect enemy of its major host, Douglas-fir,
Pseudotsugae menziesii (Mirb.) Franco. Outbreaks of the beetle in
coastal stands of Douglas-fir differ from those in interior stands.
Normally, an outbreak in standing timber in coastal forests is
preceded by catastrophic windfall in which the beetle can breed,
develop and increase rapidly in numbers. This type of outbreak, how-
ever, dies very quickly. In interior stands, the beetle appears to
be more aggressive and normally infests uninjured timber. Outbreaks

in these stands subside slowly.

On October 12, 1962 (Columbus Day), a storm described as the most severe in recorded history struck the Pacific Northwest. Wind velocities reached an estimated 170 miles per hour in the Oregon Coast Range. Surveys co-ordinated by the U.S. Forest Service showed that 11.19 billion board feet of timber, primarily Douglas-fir, was blown down in Oregon and Washington. Thus, the potential existed for an extremely severe outbreak of the Douglas-fir beetle and the opportunity for population studies of the Douglas-fir beetle was recognized. These studies started in the spring of 1963 and continued for a four-year period by forest entomologists from Oregon State University.

The major objectives of the study were as follows:

1. Development of sampling techniques for populations of the Douglas-fir beetle.

2. Construction of life tables for four consecutive generations of the Douglas-fir beetle.

3. Analysis of life tables;

    (a) determination of critical stages of population increase or decrease in the life cycle of the Douglas-fir beetle.

    (b) identification of major mortality factors and characterization of their variability relative to population density.

II.   THE BIONOMICS OF THE DOUGLAS-FIR BEETLE

AND ASSOCIATED ORGANISMS

Douglas-fir Beetle

The adult Douglas-fir beetle was originally described by
Hopkins (1901) who later published a full description of the adult,
larval and pupal stages (1909a and 1909b).   Swaine (1918) also provided
a description of the adult beetles that closely resembled Hopkins'.
Prior to 1901, Hopkins (1900) collected the Douglas-fir beetle through-
out Oregon, Washington and Idaho but identified it as
Dendroctonus similis and D. rufipennis.   Several other collectors
during the late 1800's had also obtained adult specimens of the
Douglas-fir beetle and identified them as a species of Dendroctonus,
usually similis, rufipennis or simplex, or Dendroctonus n. sp.

Hopkins' monograph (1909a) was a major contribution to the
knowledge of the genus Dendroctonus and remained as the only comprehen-
sive work until Wood (1963) published his revision of the genus.
Hopkins originally assigned 24 species to the genus which Wood, based
on characteristics of the adult, reduced to 14 species.   Thomas (1965)
published a key separating the larvae of the genus Dendroctonus and
his observations on the immature stages agreed with the conclusions
on synonomy made by Wood (1963).

Many descriptions of the various life stages and seasonal
history of the Douglas-fir beetle are available (Hopkins 1909b, Bedard
1950, Keen 1952, McCowan and Rudinsky 1954, Evenden and Wright 1955,

Walters 1956 and Wood 1963) and the following description is
summarized from these authors:

Adults

Mature beetles - hard brown or black integument, frequently
with reddish brown elytra, cylindrical, about 1/5 inch long (6 mm).
Callow or immature adults - white or light yellow at first but
become progressively darker.

Eggs

White, shiny, slightly oblong, rounded at both ends, about
1/25 inch long (1.2 mm).

Larvae

Four instars, pink or white color with light brown head
capsule, wrinkled, legless, subcylindrical type, mature larvae have an
average head capsule width of 1.2 mm (range 1.0 - 1.5 mm) and an
average length of 5.0 mm (range 3.4 - 6.4 mm).

Pupae

White, becoming light brown as they transform into beetle,
general form and size of the adult.

The Douglas-fir beetle has a one-year life cycle with two
broods per generation. The beetle overwinters in the callow adult
stage, emerges from infested logs in April and May and establishes
first brood (called spring brood) in new host material. A small
portion of these adults re-emerge during the summer and establish a
second brood (called summer brood), after which the adults usually die.

Opinions in the literature as to the size and importance of spring and summer broods vary widely. Summer broods and subsequent over-wintering larvae are considered rare in the Corvallis area. Some spring attacking females undoubtedly do re-emerge following oviposition of the first brood, but the incidence is low and difficult to detect.

Upon emergence, virgin female beetles seek a suitable host and bore through the outer bark. Rudinsky (1966) stated that the dispersal flight of the Douglas-fir beetle is oriented toward fresh windthrown and cut trees, when these are present in the stand. The beetle is attracted by volatile terpenes which are released by such material. This type of attraction is known as "host" or "primary" attraction, and more females than males respond to these resinous substances of the host. On entering the host, virgin females produce a secondary and stronger attractant to which more males than females respond and resulting in mass concentration of beetles around the center of primary attraction.

The attack on a standing tree usually begins in the upper midbole area and progresses upward and downward from that point. In windthrown material, at least when the bark is relatively thick, the beetles attack all sides over most of the length of the log. The duration and intensity of attack is quite variable and probably depends upon the number of beetles in the area, host characteristics (such as resistance), and local climatic and edaphic factors.

The egg galleries are constructed in the phloem region of the inner bark. They are in continual contact with the cambium and may

very lightly score or stain the wood. The egg galleries are straight, unforked, opposed to gravity and parallel to the grain of the wood. Mating occurs within the gallery and egg laying commences after approximately one inch of gallery has been constructed. After the gallery has been extended a few inches, the male may pack the lower areas with frass thereby closing the entrance hole, or he may leave the gallery. Ventilation holes or turning niches are placed at irregular intervals, or they may be entirely absent. Egg galleries range from 6 to 30 inches in length with the average being approximately 12 inches.

Egg grooves which extend from an inch to several inches and contain the egg niches are constructed by the female on alternate sides of the gallery. The number of eggs laid per groove or even per niche varies considerably. The total number of eggs laid per gallery may range from 50 to 300, depending mainly on gallery length. The eggs are deposited in a single row in contact with one another and oriented with the long axis perpendicular to the egg gallery. This habit of orienting the egg is peculiar to the genus and is presumably associated with the fact that the larvae construct individual mines. The eggs are held in position by a rather thick layer or partition of coarse, fibrous frass that separates them from the egg gallery.

The egg stage lasts 7 to 21 days, depending mainly on the temperature. The larvae construct mines at approximately right angles to the egg gallery and are in continual contact with the cambium area. The mines increase gradually in width as the larvae grow larger and

together they tend to form a fan-shaped pattern. The beetle requires 60 to 120 days to develop from egg to callow adult in the field. The larvae pass through four instars. Near the end of larval development, a pupal chamber may be excavated in the cambium area at the end of the larval mines, or more frequently, the late instar larvae bore into the phloem some distance before pupating. Overwintering generally occurs in the callow adult stage or occasionally as fourth instar larvae depending upon the time of establishment of the brood and the seasonal temperatures. In spring, mature beetles bore through the bark and fly to fresh host material. Spring flight commences in April or May, as soon as the maximum air temperatures reach 58 to 60°F. The major portion of the flight period extends through May and June with only sporadic flight thereafter. Very little is known about the flight period; such questions as how far can a Douglas-fir beetle fly or what distances are involved when the beetles respond to attraction (either primary or secondary) have yet to be answered.

The sex ratio is 1:1 if measured before the beetles emerge from the bark in the spring. In freshly attacked trees, females outnumber males three to two. However, this should not be unexpected since many males do not stay with females throughout the entire egg gallery construction period. Furthermore, a female can make more than one attack without requiring additional fertilization. Vité and Rudinsky (1957) demonstrated that a sex ratio of four males to five females would, in any case, secure complete fertilization because of the bigamous or polygamous behaviour of the males.

According to Keen (1952), Johnson (1960) and Wood (1963) the preferred host of Douglas-fir beetle is Douglas-fir, (Pseudotsugae menziesii (Mirb.) Franco), but western larch, (Larix occidentalis Nutt.), bigcone Douglas-fir (Pseudotsugae macrocarpa (Vasey) Mayr.) and western hemlock (Tsuga heterophylla (Rafn.) Sarg.) are less commonly attacked with broods produced in some instances. The Douglas-fir beetle is found throughout the range of the major host tree, Douglas-fir, in the Rocky Mountain region from northern Mexico into Canada and in the Pacific Coast region from central California northward through Oregon and Washington to Vancouver Island.

Epidemics of the Douglas-fir beetle usually develop from some abnormal disturbance in the forest. For example, according to Orr (1963), over three billion board feet of standing timber was killed following a nine billion board foot blowdown in Oregon and Washington in the early 1950's. LeJeune, McMullen and Atkins (1961) stated that in the interior of British Columbia, infestations of Douglas-fir beetle can often be traced to logging disturbance. Johnson (1960) stated that severe outbreaks may also follow fire or drought. Beetle outbreaks have influenced forest management and logging plans throughout the Douglas-fir region in that road systems have been rapidly expanded in order to facilitate salvage programs. Also, the tree mortality caused by beetle outbreaks has resulted in a greatly increased fire hazard.

The Douglas-fir beetle prefers windthrown, felled trees, slash

over eight inches diameter, or weakened standing trees, but will also
infest living, healthy trees singly or in groups of a few to a hundred
or more. If standing trees are successfully attacked, they will be
killed as a result of the girdling effects of the larval feeding mines
plus introduced fungi. Evenden and Wright (1955) stated that death
may be hastened by the action of various fungi which are introduced
into the tree by attacking beetles and clog the sap conducting systems.
Bedard (1950) said that the most important fungus is bluestain fungus,
Ceratostomella pseudotsugae Rumold. It is claimed that this fungus
can girdle and kill the tree, even though the attacking beetles may
fail to develop successful broods. Damage to blowdown or felled
timber directly by the Douglas-fir beetle is, of course, negligible.

Natural control factors will be discussed in the following
chapter. Various methods of direct control have been proposed (Keen
1952, Evenden and Wright 1955, Gibson 1957, and LeJeune et al. 1961).
These methods include:

1. Peel infested logs – burn bark

2. Submerge infested logs in water

3. Insecticides – ethylene dibromide, aldrin, heptachlor
   have been recommended

Unfortunately, all these methods are expensive and not considered
practical in Pacific Coast forests.

Probably the best approach to Douglas-fir beetle control is
in the direction of prevention. This can be accomplished by prompt
salvage of windthrown and standing infested trees, proper disposal of

logs and slash, giving cutting priority to overmature stands, and avoiding or preventing mechanical damage to remaining trees during logging operations.

Associated Organisms

This section reviews pertinent information concerning other organisms associated with the Douglas-fir beetle. These include predators and parasites, mites, nematodes, diseases, fungi, buprestids, cerambycids and other scolytids. Kline and Rudinsky (1964) list 13 known species of predators and parasites.

Class Insecta

      Coleoptera: Cleridae – *Enoclerus sphegeus* Fab.

                      – *Enoclerus lecontei* Wolc.

                      – *Thanasimus undatulus* Say

          Ostomatidae – *Temnochila virescens chlorodia* Mann.

   Diptera: Dolochopodidae – *Medetera aldrichii* Wh.

                      – *Medetera* sp. (near *nigripes* Lev.)

                      – *Medetera* sp. (near *oregonensis* Van Duzee)

         Lonchaeidae – *Lonchaea* sp. (near *corticis* Taylor)

                      – *Lonchaea* sp. (near *watsoni* Curran)

  Hymenoptera: Braconidae – *Coeloides brunneri* Vier.

        Pteromalidae – *Roptrocerus eccoptogasteri* Ratz.

                      – *Cecidostiba burkei* Crawford

                      – *Cecidostiba dendroctoni* Ashm.

The following are listed by Kline and Rudinsky (1964) as being commensals or possible predators and parasites of the Douglas-fir beetle.

Class Insecta

      Coleoptera: Ostomatidae - _Tenebroides_ sp.

                  Histeridae - undetermined sp.

             Staphylinidae - undetermined sp.

               Othniidae - undetermined sp.

          Tenebrionidae - _Corticeus_ sp.

           Melandryidae - _Rushia_ sp.

            Colydiaidae - _Lasconotus_ sp.

     Hemiptera: Anthocoridae - _Lyctocoris_ sp.

       Diptera: Scenopinidae - undetermined sp.

            Stratiomyidae - undetermined sp.

               Itonididae - undetermined sp.

               Empididae - undetermined sp.

Class Arachnida: Order Pseudoscorpionida

Our attention in terms of describing life cycles need be directed towards only a few of these insects since the others were not found in the course of the study or were not present in numbers sufficient to justify further consideration. A fuller description of the importance of parasites and predators in relation to Douglas-fir beetle is presented in the following chapter.

The most abundant predator found was _Medetera aldrichii_ Wheeler

Theses by Johnsey (1964) and Fitzgerald (1968) and publications by Kline and Rudinsky (1964) and Johnsey, Nagel and Rudinsky (1965) present information on this insect. While all *Medetera* involved in my study were named *aldrichii*, it should be understood that several other species were probably involved, with *aldrichii* being the most numerous among those in the complex.

Several species of *Medetera* larvae are reported to be predaceous on the immature stages of various scolytid bark beetles. Dyte (1959) states that records from throughout the world indicate that larvae of *Medetera* live under the bark of trees and logs preying on the larvae and pupae of Scolytidae and other beetles. Bedard (1933) was the first to report *M. aldrichii* preying on Douglas-fir beetle broods.

Briefly, the seasonal history of *M. aldrichii* is as follows: adult females lay eggs throughout the summer months, in small clusters of two or three beneath bark scales and in bark crevices. First instar larvae penetrate the bark and attack Douglas-fir beetle brood. It normally overwinters beneath the bark in the third (last) instar, and pupation occurs in the spring. Emergence of adults occurs through Douglas-fir beetle emergence holes.

The second-most abundant predator found was *Enoclerus sphegeus* Fab. A thesis by Cowan (1965) and publications by Cowan and Nagel (1965) and Kline and Rudinsky (1964) review the literature and present the results of various studies of this insect. This species is one of

the most abundant and widespread predators in western North America. The larvae commonly prey on larvae, pupae, and callow adults of many species of Scolytidae, primarily Dendroctonus and Ips.

Cowan and Nagel (1965) report that E. sphegeus has a two-year life cycle as determined from studies in western Oregon, whereas Reid (1957) reports a one-year life cycle for E. sphegeus preying on Ips species infesting lodgepole pine in the Rocky Mountain region of Canada. Eggs are laid in clusters under scales of the outer bark and first instar larvae enter the cambial region through Douglas-fir beetle entrance holes. Larvae have two instars and complete development by late summer. It overwinters as a prepupal larva, then according to Kline and Rudinsky (1964) pupation occurs and adults of E. sphegeus emerge fairly soon after the emergence of Douglas-fir beetle in April or May. Cowan and Nagel (1965), however, found no evidence of emergence in the spring stating that emergence of adult E. sphegeus did not occur until August or September, and that these adults then overwintered for the second year. Adults of E. sphegeus are predaceous on adult Douglas-fir beetles.

Other predators found throughout the four-year study were Enoclerus lecontei Wolc., and Thanasimus undatulus Say, both members of the Cleridae family and Temnochila virescens chlorodia Mann. from the Ostomatidae family. Numerically, none of these could be considered important at least in relation to M. aldrichii and E. sphegeus. Their habits and life cycles are similar to those of E. sphegeus.

Many _Lonchaea_ larvae (probably _Lonchaea furnissi_ McAlpine) were found under the bark associated with Douglas-fir beetle brood. Johnsey et al. (1965) stated that larvae of _L. furnissi_ did not attack and kill the bark beetle in any stage, so it was ruled out as a predator.

Various species of mites are reported to be predaceous on eggs and early instar larvae. Rust (1933) reported very high Douglas-fir beetle egg mortality that he accredited to mites and Walters and Campbell (1955) found that 30% of the Douglas-fir beetle eggs were destroyed by five species of mites.

Nematodes are found to infest Douglas-fir beetle adults (Massey 1956, Khan 1957 and 1960, Atkins 1959 and Furniss 1967). Their presence is said to result in reduced egg-laying capacity of female beetles. They may also influence flight although not necessarily in an adverse fashion. At least six species have been reported.

Pathogenic diseases caused by bacteria, viruses or fungi, are evidently rare in Douglas-fir beetle. Johnson (1960) reports that various investigators on different occasions have sent apparently diseased Douglas-fir beetle individuals to experts but nothing was found.

Bluestain fungus, _Ceratostomella pseudotsugae_, the spores of which are transported by adult Douglas-fir beetles, could have a deleterious influence on Douglas-fir beetle brood development and survival. As previously mentioned, according to Evenden and Wright

(1955) and Bedard (1950), bluestain can kill trees or hasten death of trees by interfering with the sap conducting systems. Johnson (1960) states that if bluestain develops and spreads faster than the larvae are able to mine, it may cause beetle mortality by reducing the nutritive value of the inner phloem.

Various species of roundheaded borers (Cerambycidae), flatheaded borers (Buprestidae) and Scolytidae are frequently found associated with the Douglas-fir beetle in blowdown logs. However, these species normally utilize different portions of the log than the Douglas-fir beetle. Some of these species are reported by McCowan and Rudinsky (1954) and Schmitz and Rudinsky (1968) to be:

Roundheaded borers   - _Tetropium velutimum_ Lec.
(Cerambycidae)
                        - _Leptura obliterata_ Hald.

Flatheaded borers   - _Buprestis rusticorum_ (Kirby)
(Buprestidae)
                        - _Buprestis aurulenta_ L.

                        - _Melanophila drummondi_ Kby.

Scolytidae   - _Dryocetes pseudotsugae_ Sw.

                        - _Pseudohylesinus_ sp.

                        - _Scolytus unispinosus_

Ambrosia beetles   - _Trypodendron lineatum_ Olivier

III. MORTALITY FACTORS THAT INFLUENCE DOUGLAS-FIR BEETLE POPULATIONS

The action and influence of the various mortality factors
(i.e. natural control factors) that act on Douglas-fir beetle popula-
tions are described in this chapter. Factors whose effects may be
measured quantitatively are: natural enemies, competition, heat,
excessive moisture, overwintering mortality, sex ratio imbalance, and
salvage by man. The effects of other factors such as disease, adult
migration (dispersal), failure of adults to find suitable host
material, pitched-out attacks and failure of females to be mated can-
not be measured at present. All these factors are not necessarily
subtractive mortality factors, for example, a sex ratio imbalance in
favour of females could influence populations in the plus direction.

At this point, some general comments regarding the measurement
of the effects of mortality factors would be pertinent. Owing to the
very nature of bark beetle habits and habitat, it is virtually
impossible to directly measure mortality and attribute it to a
specific cause. Instead, the only reasonable alternative is to study
each factor separately and/or various combinations of factors in an
effort to determine their individual roles in the overall situation.
This procedure results in the overlapping of mortality rates such that
they total more than 100%. Because several factors operate simul-
taneously, they generally have a modifying or damping influence on
each other (catastrophic events excluded). Consequently, when each
factor involved is isolated and allowed to operate without restraint

its effect will be greater than when it is operating in conjunction

with other factors. Thus at some point, a decision must be made as

to which factor or group of factors will receive credit for how much

mortality. For example, mortality from natural enemies and excessive

heat can occur during the larval period. All mortality within the

area influenced by the heat could be assigned to heat mortality even

though a significant proportion of the total mortality may have

actually been caused by predators. However, it is impossible to

measure this predation mortality unless measurements are made

virtually every day. Furthermore, in this particular example, all

bark beetle larvae within the affected zone would die from the

excessive heat irrespective of predators. Therefore, there seems to

be ample justification for assigning the mortality to the one factor

(excessive heat). However, the mortality can be partitioned depend-

ing on the number of predators, species, and length of time that they

are present. Mortality determined in this fashion is not measured

directly but represents a potential amount of mortality arrived at

experimentally. Mortality due to factors such as heat, moisture,

overwintering mortality and salvage can be measured directly in most

cases since they occur separately and are catastrophic in nature.

Other factors such as natural enemies, and competition, frequently

occur simultaneously throughout the larvae period and partitioning the

mortality due to each factor is difficult and may be unrealistic.

Natural Enemies

As previously mentioned (pages 11 and 12), 18 identified and at least seven unidentified species of insects are reported to be predaceous or parasitic on the Douglas-fir beetle. Of these, only two species were numerous enough throughout this study to warrant attention. These were Enoclerus sphegeus (Coleoptera: Cleridae), and Medetera aldrichii sp. (Diptera: Dolichopodidae), both predators, the life cycles of which were described in the previous chapter. Parasitism by Coeloides brunneri appeared to be incidental throughout the course of the study.

The importance of predators and parasites in regulating the abundance of populations of Douglas-fir beetle has not been determined. Attempts have been made to assess the role of individual species. Cowan and Nagel (1965) concluded that Douglas-fir beetle survival at the prey- and predator-density levels they studied, depended to a large extent on gallery and progeny density, and was relatively unaffected by the presence of E. sphegeus larvae. Other predators studied by Cowan and Nagel (1965) were E. lecontei, E. schaefferi, E. eximius, Enoclerus sp. and Thanasimus undatulus. The numbers of those species that occurred in conjunction with Douglas-fir beetle broods were so low however, that they are considered to be of no importance in controlling the Douglas-fir beetle.

Predaceous larvae of the dipteran genus Medetera Fisch. have frequently been reported as preying on larvae and pupae of scolytid

bark beetles (Dyte 1959). Bedard (1933) first reported M. aldrichii

preying on Douglas-fir beetle broods. Kline and Rudinsky (1964) state

that larvae of this insect are very abundant under the bark of trees

infested by D. pseudotsugae and that it was the most numerous of all

the predators. Johnsey et al. (1965) presented data that demonstrated

the capability of third instar Medetera larvae to kill various stages

of Douglas-fir beetle. McGhehey and Nagel (1966) reported that

M. aldrichii increased numerically in response to a recently increased

Douglas-fir beetle population. Fitzgerald (1968) concluded that

Medetera aldrichii was effective in significantly reducing surviving

host populations beyond that ascribable to non-Medetera related

mortality factors. Furthermore, evidence indicated a functional

response by Medetera larvae, i.e. predator killed more prey at high

than at low density levels. Thus all the evidence points to

Medetera aldrichii as being a potentially effective predator capable

of operating in a density-dependent fashion.

Ryan and Rudinsky (1962), described Coeloides brunneri Vierech

(Hymenoptera: Braconidae) as being one of the most abundant and effec-

tive insect parasites of the Douglas-fir beetle. However, it was

demonstrated that the percentage of host larvae parasitized at any

given height in a tree is influenced by the percentage of the tree

circumference which has an outer bark thickness less than the mean

parasite ovipositor length. Therefore, C. brunneri can only parasitize

Douglas-fir beetle larvae that are inhabiting thin-barked trees or

portions thereof. Furthermore, the incidence of parasitism attribut-
able to C. brunneri in this study was very low and cannot be considered
to be an important factor. The reason seems clear, namely the pre-
dominance of thick bark on old growth Douglas-fir blowdown that were
studied.

The overall influence of predation and parasitism on Douglas-
fir beetle populations is difficult to assess. For example, McMullen
and Atkins (1961), in their studies of the Douglas-fir beetle in
British Columbia, concluded that a great proportion of brood mortality
could not be attributed to obvious factors, such as parasitism and
predation, but was believed to be the result of intraspecific
competition. Rudinsky (1962) stated that increases and collapses in
bark beetle populations could not be attributed to the failure or
increase of biotic factors. Parasites and predators played a sub-
ordinate role; at most they slowed down the gradation and during the
collapse they may have accelerated it. Rudinsky (1962) stated further
that although biotic factors (particularly predators) are not
considered generally decisive factors in the collapse of a beetle
outbreak, they are, nevertheless, considered important, and in a few
instances they may have effected collapse.

Competition

Competition for food and/or space is an important factor which
can limit the rate of multiplication of insects, particularly bark

beetles (Scolytidae). Competition has been defined by Milne (1961),

> "as the endeavour of two (or more) animals to gain
> the same particular thing, or to gain the measure each
> wants from the supply of a thing, when that supply is
> not sufficient for both (or all)."

Competition may occur within a species (intraspecific) or among several species (interspecific).

Douglas-fir beetle larvae develop in the inner bark or phloem region of the tree. When these larvae are so numerous that their food requirements exceed the available phloem, starvation and subsequent death result. This is known as intraspecific competition since only the Douglas-fir beetle is involved. Competition can occur among members from the same parent gallery or among members of different galleries.

It has been shown by McMullen and Atkins (1961) that competition effects are noticed when the attack density is higher than three to four per square foot of bark surface. Attack densities of less than three per square foot are seldom encountered in the field, thus some degree of competition usually occurs. Competition can occur at any overall population level, i.e. it can occur in years of endemic or epidemic populations since competition is a function of beetle density and available host material. In the normal situation, there seems to be a relatively variable amount of blowdown available every year. Some of these logs are apparently more attractive than others, and receive a higher number of attacks. Outbreaks of the beetle occur when there is a large amount of blowdown available to endemic populations of

beetles. Very little competition occurs in this situation and apparently biotic factors are unable to check the insect, resulting in a rapid buildup of populations. Subsequently, high population densities invade normal or small amounts of host material which result in extreme competition, poor survival and a population decrease.

There is a close relationship between percent mortality of beetle broods and beetle density. McMullen and Atkins (1961) and Schmitz and Rudinsky (1968) showed that when competition was the only factor involved, mortality of beetle broods increased as beetle density increased. The significance of this is that competition would appear to be a powerful density-dependent factor that can regulate beetle populations. However, a complicating factor arises, mainly because of predation. We are concerned not only with the effects of competition and predation but also with their interaction since one may modify or intensify the other.

Excessive Pitch

This is a somewhat rare phenomenon in windthrown trees but commonly occurs when healthy, standing Douglas-fir trees are attacked by Douglas-fir beetle (Belluschi, Johnson and Heikkenen 1965). In windthrown trees that are still partially rooted, excessive pitch may occur in small, localized situations within a log, usually in the lower portion of the tree or sometimes most of the entire tree seems to be characterized by excessive pitch. In any case, early stages of beetle development are affected. In extremely excessive pitch

conditions, adult beetles attempting to construct egg galleries will be killed. With less pitchy conditions, the egg galleries may be constructed but the eggs either fail to hatch or the larvae die in first or second instar. Death from pitch may result from mechanical reasons, such as drowning or inability to move in the sticky media or pitch may have toxic effects.

Excessive Heat

Temperatures under the bark of blowdown trees that are directly exposed to the sun's rays can reach 140° to 150°F in extreme situations, which is more than sufficient to kill Douglas-fir beetle larvae, pupae and callow adults. Rudinsky (1962) states that temperatures, 50°C to 55°C, (122°F to 131°F) are lethal within a short time, higher humidity prolonging and lower humidity decreasing the time necessary to effect death. Normally, the highest ambient temperatures are reached in July and August, in western Oregon, which coincides primarily with larval development although pupae and early callow adults may also be affected.

Mortality can be a direct result of the extreme heat or from the excessive dryness of the food material, but is most likely the result of the interaction of these two factors.

Excessive Moisture

This is also a relatively rare factor which is generally associated with a condition known as "sour cambium" which describes a

particular condition of the inner bark of woody vegetation. Such inner bark is greatly discolored and fermenting and tends to have a high moisture content and a low starch and protein content. According to Rudinsky (1962), this condition is found in trees that either have been dead for more than one year or have been recently windthrown. Several "sour cambium" windthrown trees were encountered during the course of the study. In all cases, the inner bark of such trees was darker colored and more moist and stringy than the inner bark of the more commonly encountered "normal" trees. In addition, the "sour cambium" condition was usually confined to the upper bole portions of downed logs.

The causes of "sour cambium" are unknown but one of the symptoms is excessive moisture. For example, the moisture content of inner bark from a "sour cambium" tree was 192% (on a dry weight basis) compared to a moisture content of 129% for inner bark from a nearby normal tree (both blowdowns). Other symptoms of "sour cambium" are that the inner bark is greatly discolored (usually bright reddish brown compared to a light brown or yellow brown inner bark on normal trees). There is also a lower protein and starch content associated with "sour cambium".

Very low survival of Douglas-fir beetle brood occurs in trees with the "sour cambium" condition. Mortality may be a result of drowning or suffocating due to a moisture saturated environment. It has also been suggested that increased mortality in presence of "sour cambium" may be due to poor nutrition or to production of alcohols that

are toxic to Douglas-fir beetle brood.

Overwintering Mortality

The major portion of overwintering mortality is probably due
to lethal low temperatures or fluctuation of temperatures. The sudden
onset of cold in the fall with little preconditioning to low tempera-
tures would be disastrous, as would warm days followed by cold nights
in the spring. Johnson, Wright and Orr (1961) found that there was
significant overwintering mortality of Douglas-fir beetles due to
drowning in work carried out in windthrown trees in western Washington.
Moisture and cold-hardiness are related. Increased mortality occurs
to beetles inhabiting moist phloem as compared to those in dry outer
bark. Thus the virtually constant rainfall that occurs in the Coastal
Mountains of western Oregon throughout most of the winter could play
an important role by maintaining virtually saturated bark conditions.
Johnson and Pettinger (1961) presented data comparing overwintering
survival of larvae and adult Douglas-fir beetles under a variety of
conditions. Fifty-four percent of adult Douglas-fir beetles over-
wintered successfully for three months in loose bark on the forest
floor, 40% survived in forest litter and 84% survived in undisturbed
bark of windthrown trees. Survival of larvae subjected to over-
wintering in similar materials and on the same sites was of the same
order of magnitude as for adult beetles. Surviving pupae did not
develop into adults.

Salvage

Concentrated efforts were made by the U.S. Forest Service throughout the years of the study to salvage most of the blowdown Douglas-fir on the Marys Peak watershed. Since salvage operations are a continual process, Douglas-fir beetle mortality due to this factor could occur at any stage of development. Of course, for salvage to be a mortality factor, infested blowdown must be removed from the woods before emergence of the adults occurs. Salvage logging is recommended by Lejeune et al. (1961) as a means of controlling Douglas-fir beetle populations. However, they point out that if sanitation logging is practised, then standing trees may be attacked; thus small amounts of slash should be available from year to year to absorb beetle populations.

Sex Ratio Imbalance

The sex ratio of emerging beetle populations was determined each year in order to discover if any serious imbalances occurred. The methods tested by Jantz and Johnsey (1964) of examining by touch the elytral declivity to determine sex and checking periodically by microscopic examination were employed.

For various reasons, the following probable mortality factors cannot be measured quantitatively, therefore, any effect on Douglas-fir beetle populations can only be speculative.

Disease

There are no diseases known to be associated with the Douglas-fir beetle.

Migration, Dispersal, Failure of Adults to Find Host,
Pitched Out Attacks, Failure of Females to be Mated, Adult Predation

These are a set of potential mortality factors, (not necessarily subtractive) that have a common characteristic; namely, all involve the time period that includes emergence, flight and attacking a new host, i.e. adult beetle. A lack of suitable sampling methods, in addition to a scarcity of biological and behavioural knowledge prevents an adequate assessment of these factors. However, for a given area, it may be possible to estimate the total population size of emerging adults and the total population size of attacking adult beetles. Any difference between the two can be attributed to one or more of the previously mentioned factors. For example, if the size of the attacking population is larger than that of the emerging population then the increase must be due to immigrating beetles. This, in turn, does not deny that the other factors are also probably operating at the same time. However, one could get as many beetles immigrating as there are emigrating and although sizeable shifts would occur in the population they would not be detected. Finally, a decrease in the size of the attacking population, compared to the size of the emerged population implies that the combined effect of all of the mortality factors

outweighs that of immigration of beetles into the area. For the present, this time period in the life cycle of the Douglas-fir beetle must be treated in a rather superficial fashion. If changes occur in population size during this period which are vital to a complete understanding of the population dynamics of the Douglas-fir beetle, then additional research will be required in order to clarify the picture.

IV. SAMPLING METHODS

If we are going to follow insect population densities and attempt to explain these densities in terms of various environmental factors, then we must measure populations. It should be obvious that, in most forest insect population studies, it would be impractical if not impossible to count all members of the population, therefore, we turn to sampling.

The principles of population sampling are universal and are adequately treated in text books. However, the application of these principles has led to great diversity in techniques because of great diversity in the life cycle and habitats of different insect species and in the particular objectives of different field studies. That is, there is no one method that is best.

Sampling design has been described as a combination of art and science. It takes skill and judgement along with the application of theory, knowledge and science to develop good sampling techniques.

Some important definitions in the vocabulary of the sampler are:

Universe – a collection of objects of interest, usually defined in forest entomological work as the habitat where the insect lives.

Population – consists of all possible values of a variable, usually

defined as all insects of a certain species living in the

universe as defined – can also be attributes of the

insects, thus we have many simultaneous populations in a

universe.

Sampling – a sample is a part of a population or a portion taken as

representative of the whole. Information from the sample

is used to make inferences about the population. For this

reason, it is particularly important to define the popula-

tion under discussion and to obtain a representative

sample from the defined population. All extremes in the

population should be represented in the sample. To

obtain a representative sample, the principle of random-

ness is generally applied when drawing the sample items.

Essentially, any sample selected by a chance mechanism

with known chances of selection is called a random

sample. By definition, a random sample is free from

selection bias.

One of the major objectives of this study was the development

of sampling methods to provide accurate population measurements for

successive stages of the Douglas-fir beetle. This section of the

dissertation reports on studies undertaken to investigate the

procedure necessary to draw bark samples from a population of infested

blowdown Douglas-fir trees in such a manner that the estimates of the

mean beetle density for each stage of the life cycle and their respective variances will be representative and precise.

One of the earliest papers in the literature related to the topic of sampling forest insects was by De Gryse (1934) who reviewed the population work on forest insects up to 1934. Prebble (1943), Stark (1952), Henson (1954), Morris and Reeks (1954) and Morris (1955) described sampling techniques for various stages of defoliating forest insects. Somewhat later, Morris (1960), drawing on his extensive sampling experience with spruce budworm, *Choristoneura fumiferana* (Clem.) in New Brunswick, published a general review of forest insect sampling.

A series of papers by Ives (1955), Ives and Turnock (1959), and Turnock (1960) described sampling techniques for egg, cocoon and adult populations of larch sawfly, *Pristiphora erichsonii* (Hartig). Lyons (1964) presented methods for sampling all stages of the two pine saw-flies, *Neodiprion sertifer* and *N. swainei*. Howse and Dimond (1965) described methods for sampling gall populations of the pine leaf adelgid, *Pineus pinifoliae* (Fitch) and Cheng and LeRoux (1966a) reported methods for sampling all stages of the Birch Leaf Miner, *Fenusa pusilla*.

Thus most of the work on forest insect sampling deals primarily with those species of insects or stages thereof that are found in the foliage of trees or in the ground. Sampling infested trees for bark beetle populations is a difficult and tedious process. The mechanics

of removing bark samples and counting the organisms that are present
is both time consuming and costly. Consequently, less attention has
been paid to sampling designs for this group of insects. Knight
(1959 and 1960) described methods that he used to measure populations
of the Black Hills beetle (Dendroctonus ponderosae Hopk.) and the
Engelmann spruce beetle (Dendroctonus engelmanni Hopk.). Furniss
(1962a and 1962b) discussed sampling methods and a special tool for
removing bark samples for populations of Douglas-fir beetle,
D. pseudotsugae, in both standing and windthrown Douglas-fir trees.
Carlson and Cole (1965) described a technique for sampling populations
of the mountain pine beetle, D. monticolae Hopk., in lodgepole pine.
DeMars (1966), as part of a Ph.D. thesis, presented a method for
sampling populations of western pine beetle, D. brevicomis LeConte.

Several ecological textbooks with good sections on sampling are
available. The most useful ones are Allee et al. (1949), Andrewartha
and Birch (1954), MacFadyen (1957), Odum (1963), Graham (1963) and
Southwood (1966). Examples of texts dealing with the mathematical
and statistical principles of sampling are Snedecor (1956), Steel and
Torrie (1960), Stuart (1962) and Cochran (1963).

Egg Sampling

Douglas-fir beetle egg galleries are constructed in the phloem
region of the inner bark, parallel to the grain of the wood. Adult
beetles mate in the gallery and egg laying commences after approx-
imately one-half to one inch of gallery has been constructed. Total

egg gallery lengths vary primarily from 6 to 30 inches with the
majority being 8 to 16 inches long. Egg grooves varying from an inch
to several inches encompassing the egg niches are constructed by the
female on alternate sides of the gallery. The number of eggs in any
one groove or any one niche varies considerably. The total number of
eggs per gallery may range from 50 to 300. The duration of the egg
stage varies greatly under field conditions ranging from 7 to 21 days.

Egg gallery inch was chosen as the unit of measurement or basic
sample unit because it satisfied most of the criteria listed by Morris
(1955). Two alternative sample units were considered. One was the
whole gallery, the other was some unit of bark area. Both of these
were for various reasons considered unsuitable. Considerable
variation exists in the length of whole galleries, and therefore also
in the number of eggs per gallery. There is also a timing factor that
would make either the gallery or bark area sample units difficult to
use. It is virtually impossible to obtain whole galleries with
unhatched eggs throughout the length. For example, by the time the
eighth or ninth inch of an egg gallery has been constructed, eggs
in the first two or three inches have hatched.

The advantages of egg gallery inch as a sample unit are:
the ease with which units can be easily and quickly delineated, the
resolution of the egg hatch timing problem and the ready conversion
of eggs per gallery inch to eggs per unit area of bark.

Data were collected from infested windthrown Douglas-fir trees
on the Marys Peak watershed of the Siuslaw National Forest (Figures 1
and 2). Preliminary egg sampling was conducted in the spring of 1965
when a total of 252 egg gallery inches were examined from seven trees.
Following this preliminary work, 916 egg gallery inches were
examined from ten trees during May and June of 1966. The trees used
for sampling in both years were of all sizes and represented many
edaphic conditions.

Sample trees were divided lengthwise into approximately equal
thirds, then each third was stratified circumferentially into top and
sides, providing nine zones in each log. The bottom of the log was dis-
regarded since this portion was usually in contact with the ground and
not easily available for sampling. Twelve to fifteen inches of egg
galleries were exposed and measured in each zone. An individual egg
gallery was divided into consecutive inch sections and the number of
eggs in each inch was recorded.

A frequency distribution of the counts of eggs per gallery
inch was formed for each year's data (Tables 1 and 2). A graph of the
1965 frequency distribution appeared to be similar to the 1966
distribution (Figure 3). Both are slightly skewed to the right. The
expected frequencies for the normal, Poisson and negative binomial
distributions were calculated. The observed and calculated expected
frequencies were compared using the Chi square goodness-of-fit test.
Highly significant differences existed at the .1% level between the
observed and expected frequencies for the Poisson and negative binomial

Figure 1. Map showing location of the Marys Peak watershed

20

Burnt
Woods

Blodgett

Wren

Corvallis

99
W

20

Willamette River

20

Philomath

34

Rock Cr.

Marys
Peak

Griffith Cr.

Marys River

N

99
W

34

Alsea
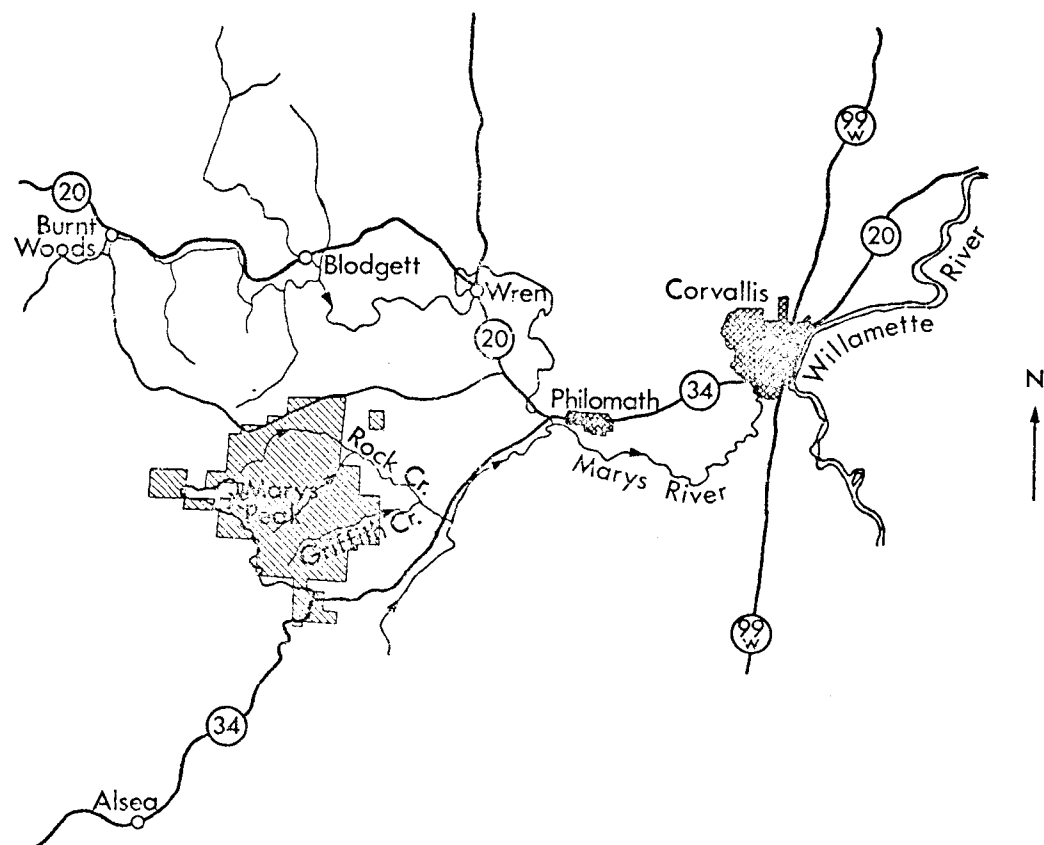
LEGEND

National Forest
(Marys Peak District)

Major Highways — 34 —
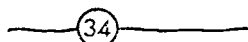
Rivers and Streams

Scale
0 1 2 3 4

Miles

Figure 2. Detailed map of the Marys Peak watershed

LEGEND

Watershed Boundary - - - - - -

Marys Peak X

Roads

Creeks

National Forest Land

City of Corvallis

Woods Creek Road

Old Peak Road

KP Cabin

East Trail

Rock Creek Road

Miller's Ridge Road

Griffith Ridge Road

Rock Creek

Franklin Ridge Road

Marys Peak Road

34

34

N

0   ½   1
Scale in Miles
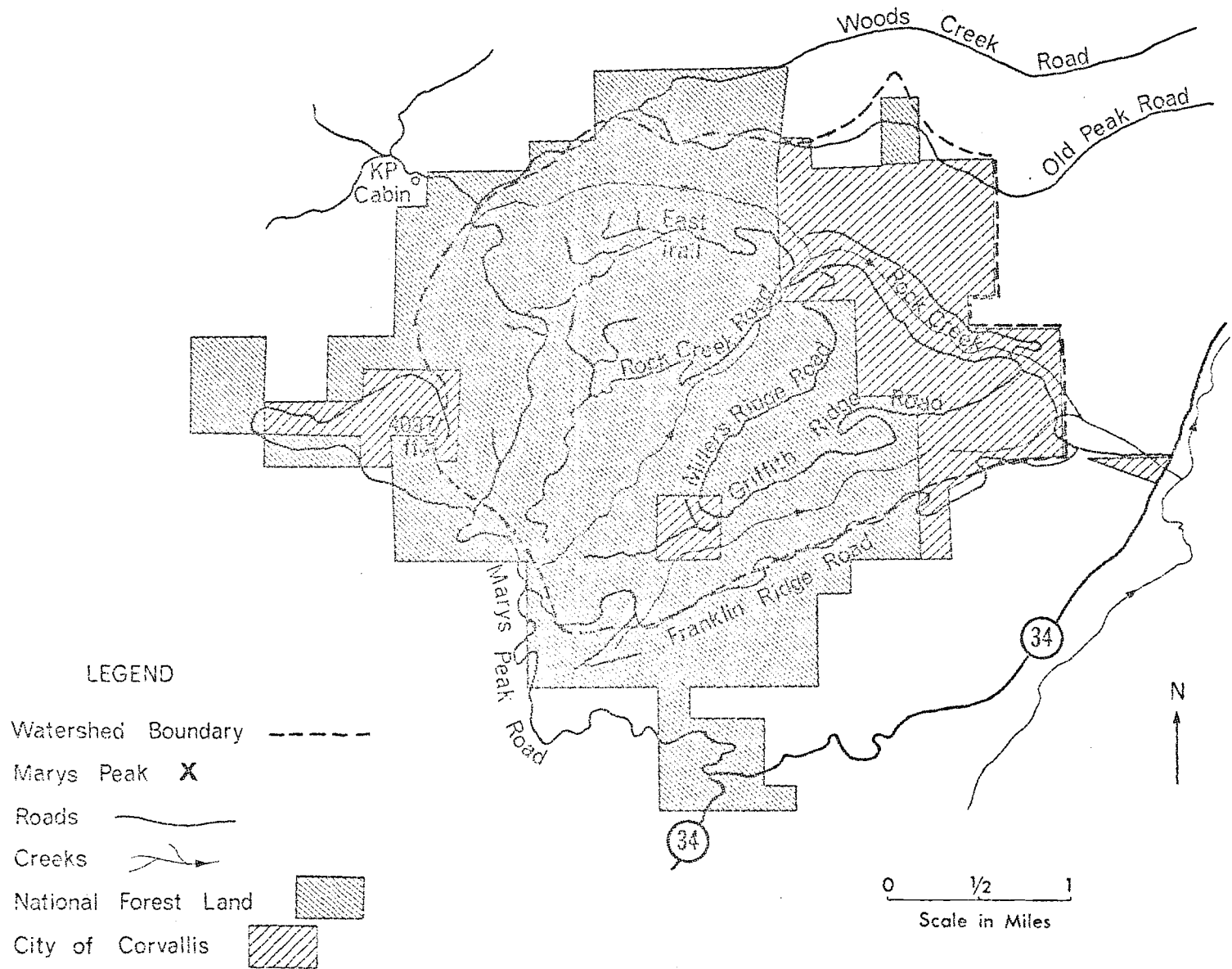
Table 1. Frequency distribution of 1965 egg data.

Class interval	Observed frequency	Expected frequency (based on normal distribution)	$\dfrac{(O-E)^2}{E}$
0	17	11.26	2.93
1- 2	9	12.12	.80
3- 4	25	19.81	1.36
5- 6	24	28.12	.60
7- 8	29	34.80	.97
9-10	32	37.47	.80
11-12	39	35.23	.40
13-14	32	28.53	.42
15-16	22	20.31	.14
17-18	12	12.50	.00
19-20	6	6.75	.08
21-22	3	3.18	.01
23-24	2	1.92	.01
	sum = 252	sum = 252	CHI SQUARE = 8.52

where class interval = no. of eggs per inch of parent gallery
Frequency = no. of observations that fall into that class (X)
Chi Square = 8.52 with 10 degrees of freedom
(n-1-2 = 13-1-2 = 10 d.f.)
not significant, range 50% - 70%

Thus the observed frequency would appear to be the same as the expected frequency. Expected frequency calculated on basis of normal distribution.

Table 2. Frequency distribution of 1966 egg data.

Class interval	Observed frequency	Expected frequency (based on normal distribution)	$\frac{(O-E)^2}{E}$
0	38	27.4	4.10
1- 2	34	35.1	.03
3- 4	63	62.8	.00
5- 6	88	95.8	.64
7- 8	126	126.1	.00
9-10	122	142.2	2.87
11-12	165	137.5	5.50
13-14	119	113.9	.23
15-16	77	81.3	.23
17-18	43	49.6	.88
19-20	20	26.0	1.38
21-22	12	11.8	.00
23-24	4)	)	)
	)	)	)
25-26	1)	)	)
	)	)	)
27-28	3) 9	) 6.5	) .96
	)	)	)
29-30	0)	)	)
	)	)	)
31	1)	)	)
	sum = 916	sum = 916.0	CHI SQUARE = 16.82

where class interval = no. of eggs per inch of parent gallery
Frequency = no. of observations that fall into that class (X)
Chi Square = 16.82 with 10 degrees of freedom
(n-1-2 = 13-1-2 = 10 d.f.)

Table 2. (continued)

not significant, range 5% - 10%

Thus the observed frequency would appear to be the same as the expected frequency. Expected frequency calculated on basis of normal distribution.
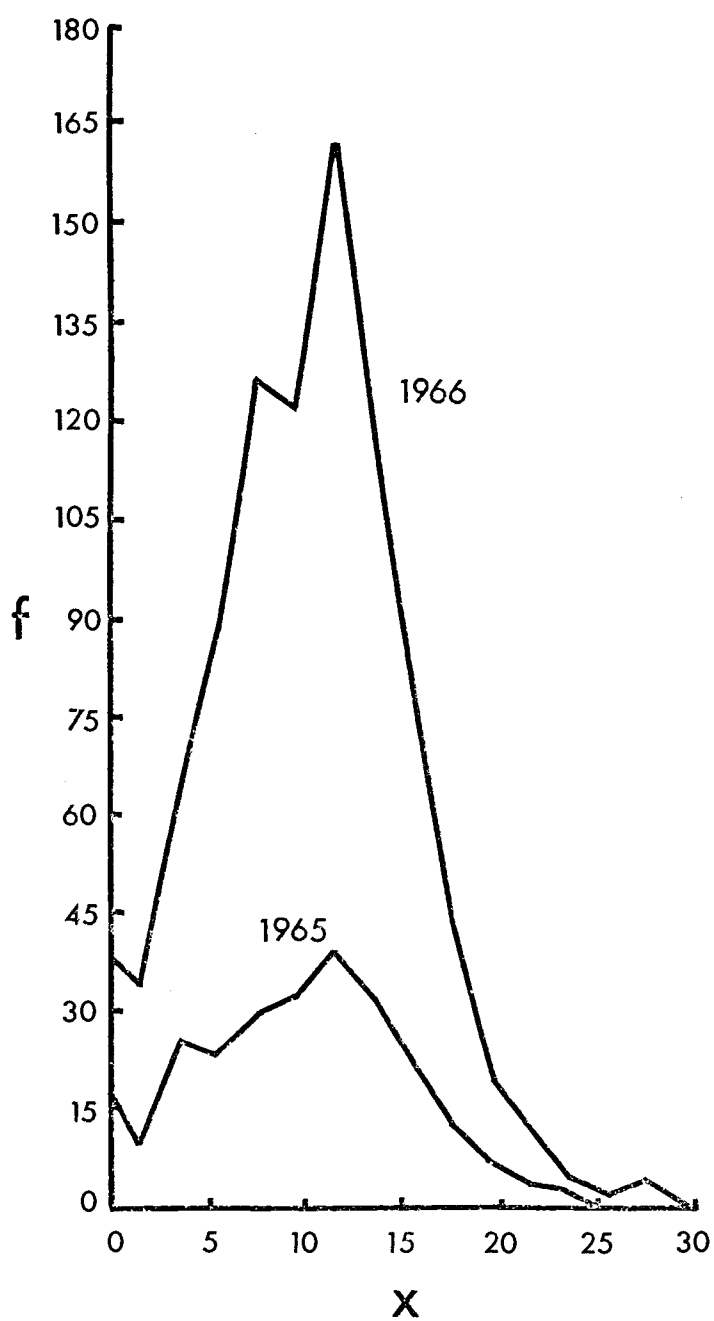
Figure 3.   Frequency distribution of 1965 and 1966 Douglas-fir beetle
egg counts

distributions. The expected frequency based on the normal distribu-
tion was not significant for the 1965 data at a probability range
of 50% to 70% and at the 5% to 10% range for the 1966 data. From
this, it was concluded that the egg counts per gallery inch conformed
to the normal distribution. Since the statistical distribution of egg
counts was normal, the necessity of transforming data in order to
stabilize variance was eliminated.

The analysis of variance of all the ten trees sampled in 1966
was performed (Table 3). With the data available, it was possible to
check for significant differences in egg densities among trees, among
the three levels, among the top and sides (Quadrants) and the various
interactions of these factors. The only significant difference detected
was among egg densities from tree to tree.

Analysis of the average number of eggs per gallery inch showed
that the first inch was responsible for much of the within gallery
variance. Disregarding the first inch would decrease variation but
would result in egg density estimates that were too high.

Graphs, plotting the average number of eggs over the inch of
gallery, were prepared for each tree. Examples illustrated are trees
66-4, 66-6, and 66-8 (Figures 4, 5 and 6 respectively) and the com-
bined data for trees 66-4, 6 and 8 (Figure 7). A line representing
the average number of eggs per gallery inch for that tree was placed
on each graph. This mean intersected the line representing the average
number of eggs for each gallery inch at either the sixth or seventh
gallery inch in each tree. This relationship was tested further on egg

Table 3. Analysis of variance of Douglas-fir beetle egg densities
performed on the 1966 sample trees.

Source	d.f.	SS	MS	F	Reqd. F 5%	1%
Trees	9	916.14	101.7933	10.8413**	2.15	2.94
Levels	2	17.80	8.9000	>1.00		
Quadrants	2	44.27	22.1350	2.3574	3.26	5.25
Trees x Levels	18	297.98	16.5544	1.7631	1.90	2.49
Trees x Quad.	18	343.83	19.1017	2.0344*	1.90	2.49
Levels x Quad.	4	60.79	15.1975	1.6186	2.63	3.89
Error	36	338.02	9.3094			
Total	89	2,018.83				

Each source of variance was tested against the second-order interaction
(Trees x Levels x Quadrants). In no instance, however, was any
significant variance associated with levels or level interactions.
Accordingly, levels were accepted merely as replicates and the sums
of squares were pooled to obtain a stronger error term as shown below

Table 3. (Concluded)

Source	d.f.	SS	MS	F	Reqd. F 5%	1%
Trees	9	916.14	101.7933	8.5470**	2.02	2.70
Levels	2	17.80	8.9000	>1.0000		
Quadrants	2	44.27	22.1350	1.8586	3.15	4.98
Trees x Levels	18	297.98	16.5544	1.3900	1.78	2.26
Trees x Quad.	18	343.83	19.1017	1.6039	1.78	2.26
Levels x Quad.	4	60.79	15.1975	1.2760	2.52	3.65
Trees x Levels x Quad.	36	338.02	9.3894	>1.0000		
All except trees, quads. and their interaction	60	714.59	11.9098			

* Significant at 95% level
** Significant at 99% level
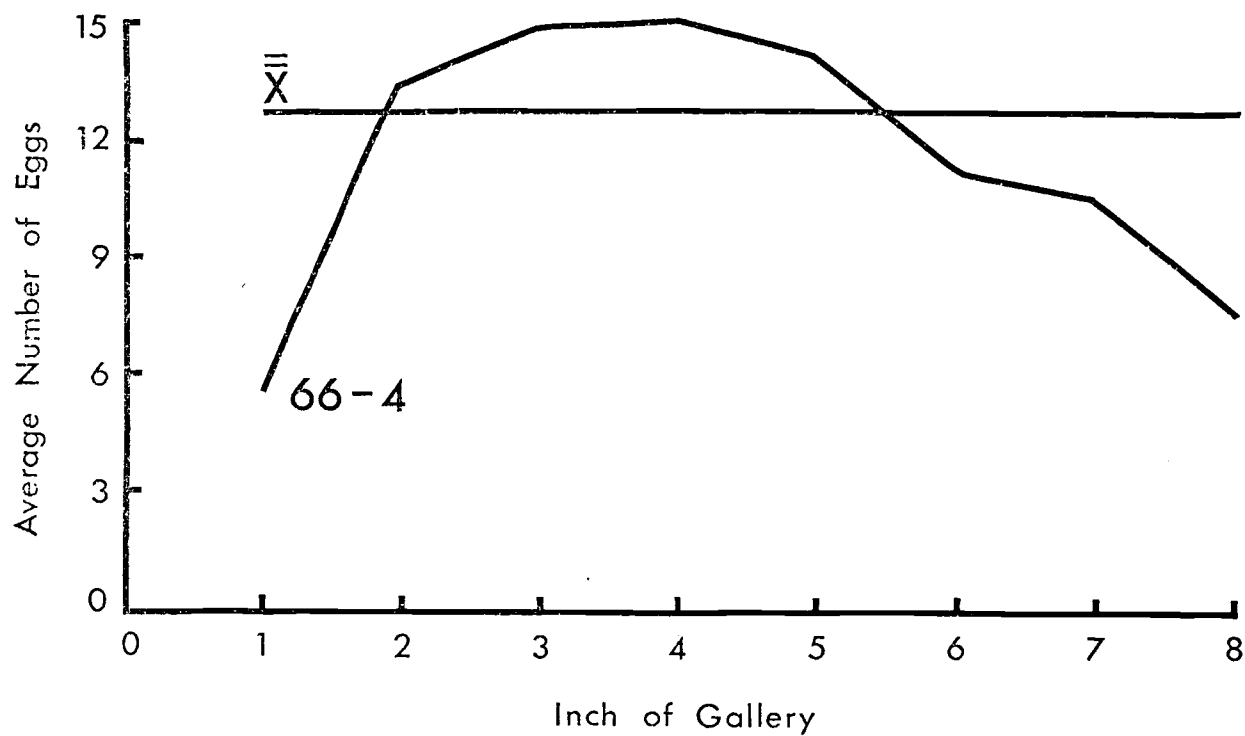
Figure 4. Egg sampling data for tree 66-4. Average number of eggs per gallery inch is plotted against gallery inch. Mean number of eggs per gallery inch for tree 66-4 = 13.0 ($\bar{\bar{X}}$)
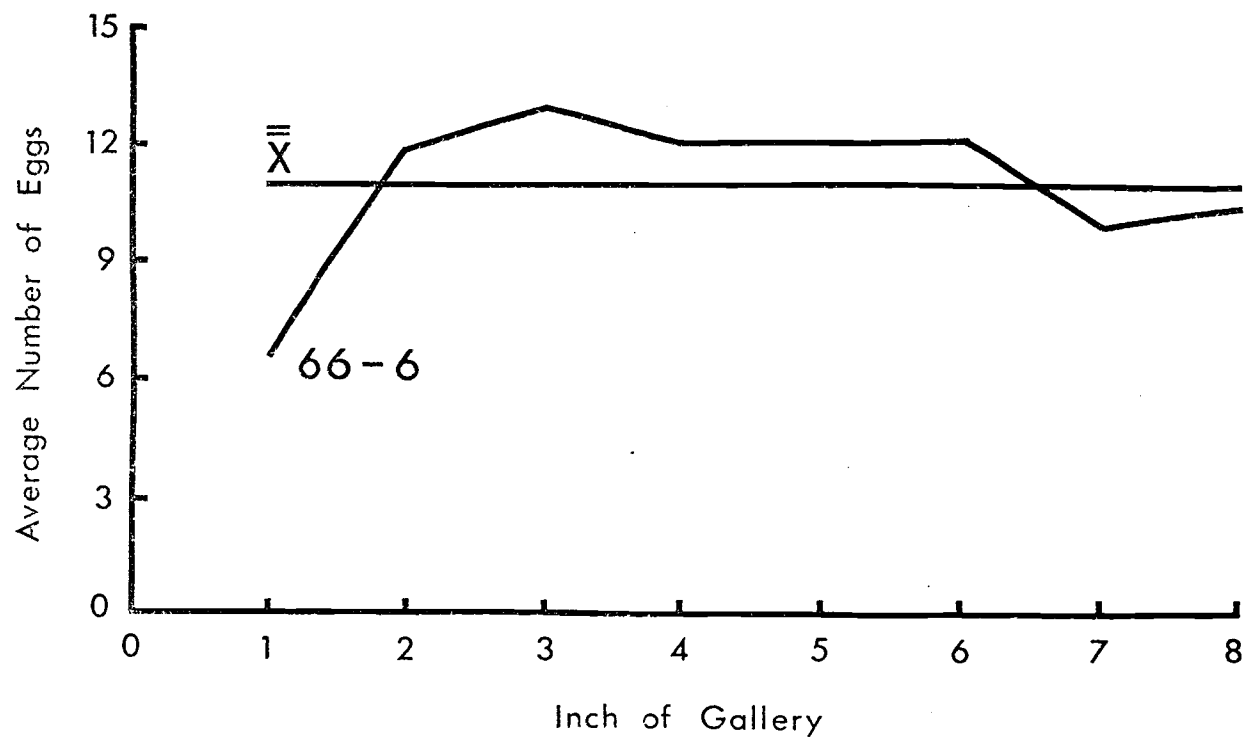
Figure 5.   Egg sampling data for tree 66-6.   Average number of eggs per gallery inch is plotted against gallery inch.   Mean number of eggs per gallery inch for tree 66-6 = 11.0 ($\overline{\overline{X}}$)
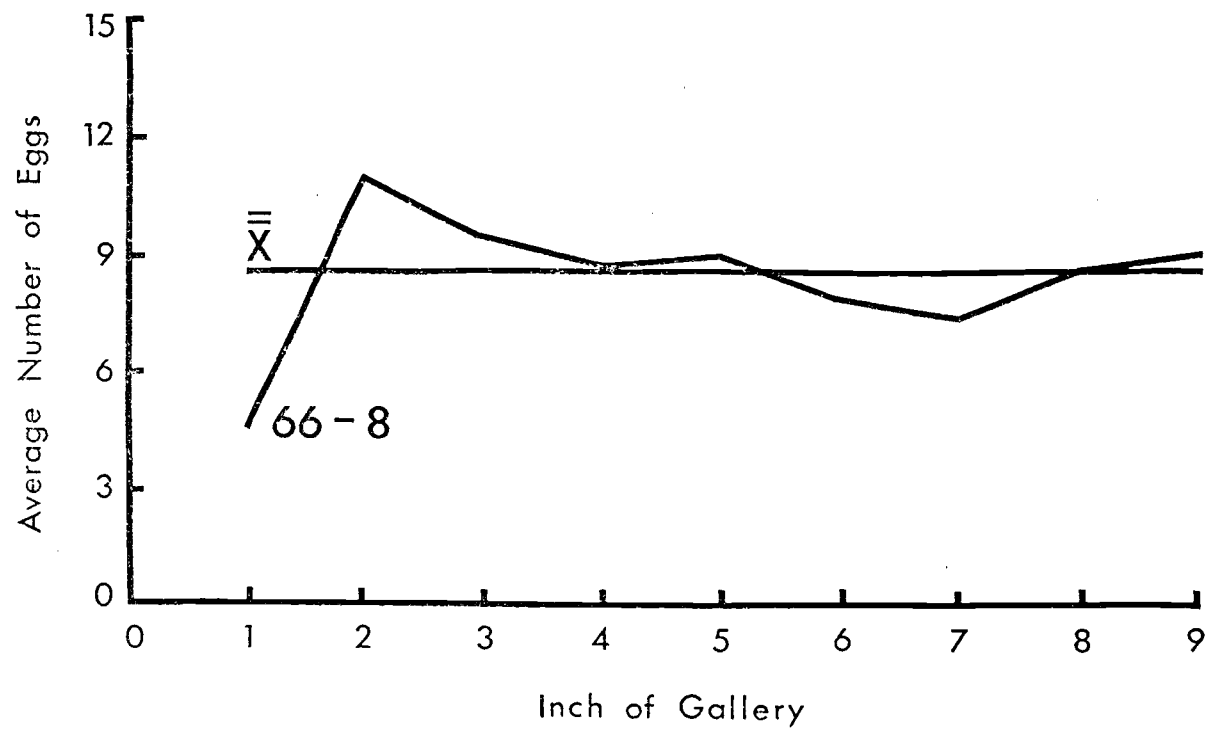
Figure 6. Egg sampling data for tree 66-8. Average number of eggs per gallery inch
is plotted against gallery inch. Mean number of eggs per gallery inch for
tree 66-8 = 8.4 ($\bar{\bar{X}}$)
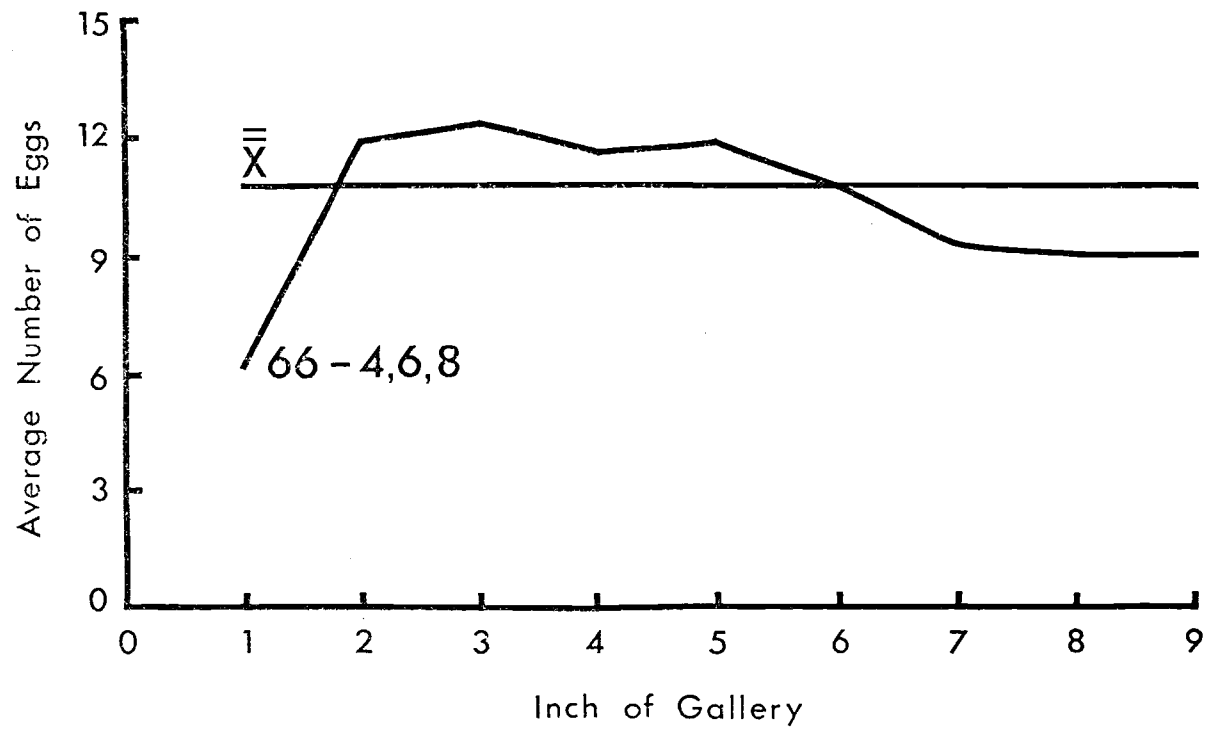
Figure 7. Egg sampling data combined for trees 66-4, 6 and 8. Average number of eggs per gallery inch is plotted against gallery inch. Mean number of eggs per gallery inch for trees 66-4, 6 and 8 = 10.8 ($\bar{\bar{X}}$)

data contained in a thesis by R.F. Schmitz (1965) (Figure 8) and in a publication by W.D. Bedard (1933) (Figure 9). The same pattern held for both of these cases, although Bedard was working with the inland form of Douglas-fir.

Using the sixth and seventh gallery inches as a sample unit, mean eggs per gallery inch were calculated for seven of the 1966 trees and one of the 1965 trees. Either the sixth or seventh inch used separately proved to be a poor estimator, but when combined they appeared to closely approximate the mean number of eggs per gallery inch for each tree computed from whole gallery inches (Table 4). A "t" test between whole gallery inch means per tree and sixth plus seventh inch means per tree showed no significant differences. In six of the eight trees, the variance was reduced by using sixth plus seventh inch means, it increased slightly in one tree and increased considerably in the remaining tree (Table 4).

Sample sizes that would be necessary to meet a standard error of 10% of the mean using the sixth and seventh gallery inches as a sample unit were calculated (Table 5). As an average, approximately 50 sixth and seventh inch counts in equal proportions would be required for reliable estimates of the mean egg number per gallery inch for each tree. This average sample size is about one-half required by the whole gallery inch method of sampling.

The next question to be answered was to determine if enough sixth and seventh gallery inches could be obtained from any given
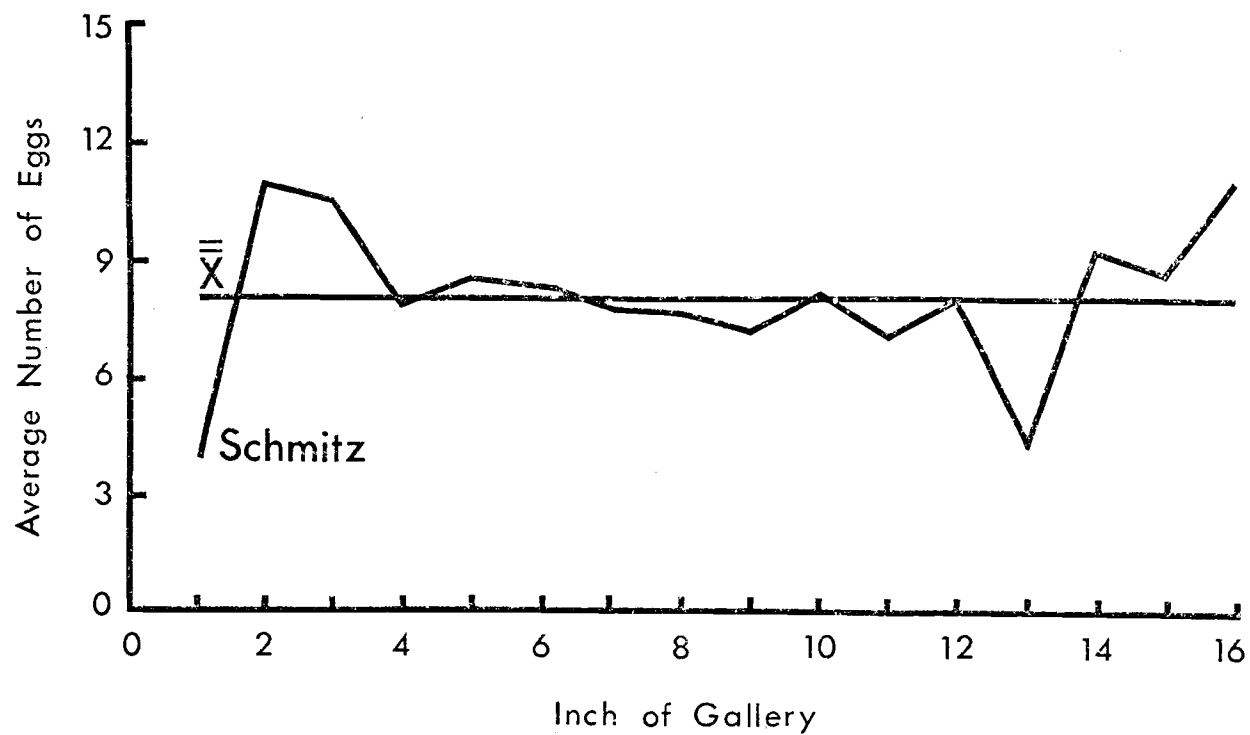
Figure 8. Egg sampling data from Schmitz (1965). Average number of eggs per gallery inch is plotted against gallery inch. Mean number of eggs per gallery inch for these data = 8.0 ($\overline{\overline{X}}$)
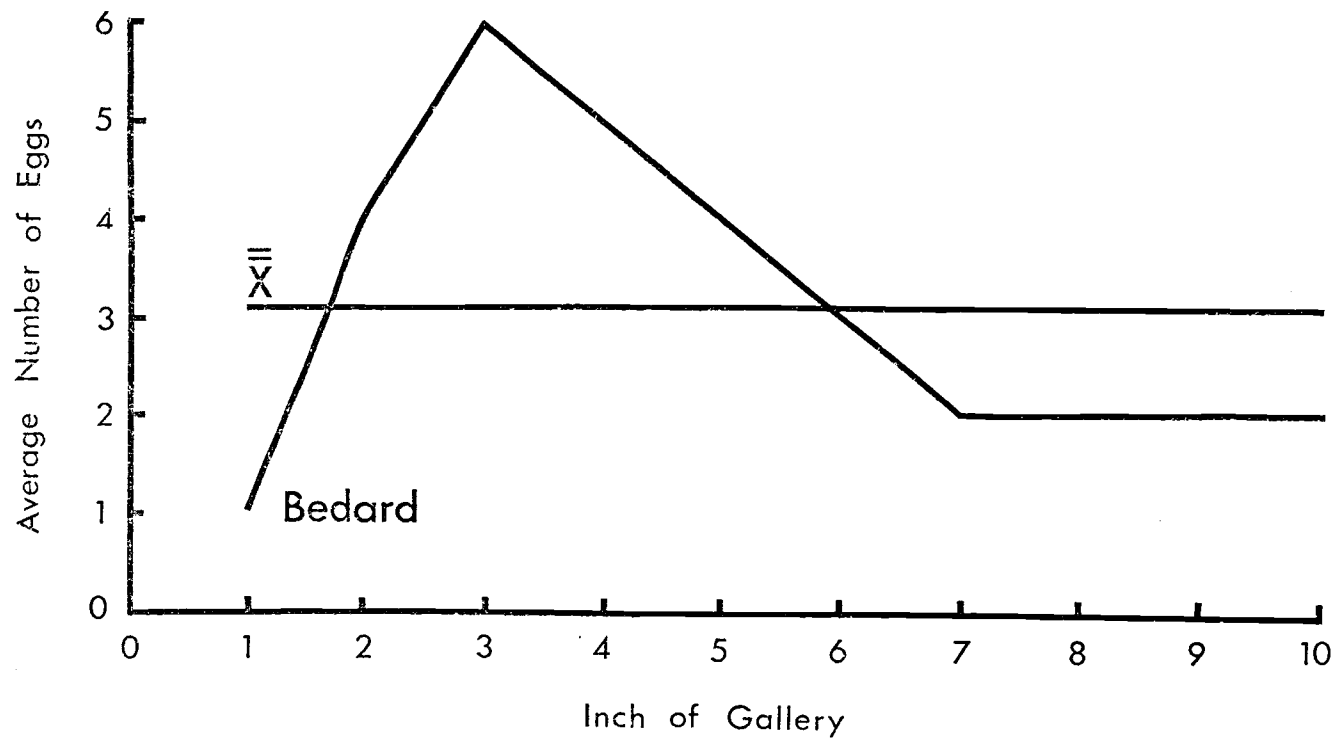
Figure 9. Egg sampling data from Bedard (1933). Average number of eggs per gallery inch is plotted against gallery inch. Mean number of eggs per gallery inch for these data = 3.1 ($\overline{\overline{X}}$)

Table 4. Comparison of mean egg densities
and variances as determined by
two methods

Tree	$\bar{X}$	$\bar{X}_{67}$	s^2	s^2_{67}
66 – 2	10.14	11.00	28.908	16.333
3	8.16	8.64	19.881	8.855
4	13.05	12.10	31.357	41.620
5	9.54	10.88	16.600	15.570
6	11.04	11.94	14.515	19.400
7	9.05	9.60	24.973	4.250
8	8.41	8.30	16.504	14.842
65 – 7	13.92	14.77	28.596	14.500

$\bar{X}$ = mean egg density for the tree as determined by whole gallery egg counts

$\bar{X}_{67}$ = mean egg density for the tree as estimated from sixth and seventh gallery inch egg counts

s^2 = variance associated with whole gallery egg counts

s^2_{67} = variance associated with sixth and seventh gallery inch egg counts

Table 5. Comparison of sample size necessary to achieve an error no greater than 10% of the mean for two egg density methods

Tree	Sample size – inches (whole gallery method)	Sample size – inches (6 and 7 inch method)
66 – 2	112	54
3	119	45
4	74	114
5	73	53
6	48	54
7	122	19
8	93	86
65 – 7	59	27
	Sum = 700	Sum = 452
	$\bar{x}$ = 87.5	$\bar{x}$ = 56.5

tree. Gallery length measurements were made on 207 randomly selected complete galleries from five trees. These gallery lengths from the five trees averaged 8.4" long with individual gallery lengths ranging from 3.0" to 17.0". Seventy percent of all galleries were 7.0" or longer.

In contrast, 41 randomly selected complete galleries from two other trees had an average length of 4.0" with a range of 2.0" to 7.0". Only one of the 41 galleries was at least 7.0" long.

A sampling technique for eggs can now be suggested based on the preceding information. The analysis of variance showed that no significant differences existed within zones of blowdown logs, thus the sample does not have to be stratified. Furthermore, in order to save time the entire sample can be taken at any desired location within the log. Where possible, the sample unit should be the combination of sixth and seventh gallery inches since this unit provides greater accuracy with a smaller sample size. This sampling method can be used for trees that have egg galleries 7.0" or longer. Some trees will have to be sampled by the whole gallery method since in these trees, egg galleries rarely or never attain lengths of 7.0" or more. Whichever method is used, preliminary estimates of the mean egg density per gallery inch and variance will have to be obtained for each tree. Sample size can then be calculated for each tree using the sample size equation.

Since it is desirable to express population densities of all stages of the Douglas-fir beetle in terms of numbers per area of bark

surface, it is necessary to convert egg densities expressed as number of eggs per gallery inch to number of eggs per square foot.

Theoretically, all one must do is multiply the total number of parent gallery inches found on each square foot of bark surface by the number of eggs per gallery inch for that tree. The validity of this conversion was tested by removing square foot bark samples from trees for which egg densities had previously been determined. It was found that this conversion consistently gave overestimations. This problem was solved when it was found that eggs were not laid in the last two or three inches of a parent gallery. When these non-egg containing portions of the galleries were eliminated from the total gallery inches, the conversion proved to be quite accurate.

Larval Sampling

The Douglas-fir beetle passes through four larval instars after hatching. Estimates of population density are required for each instar. Since the developing larvae leave a record of their presence in the bark surface, it is not necessary to time the sampling so that the live forms are present. Larval samples for all instars can be obtained any time after early September.

The data gathering methods for larval counts were similar to those described for egg sampling. Ten or more infested windthrown Douglas-fir trees on the Marys Peak watershed were selected each year for the four-year period of the study. These trees were of all sizes,

ranging from 21" to 68" d.b.h. and representing many edaphic conditions (Appendix I, Tables 21, 22, 23 and 24). Sample trees were divided lengthwise into thirds, then each third was stratified circumferentially into top and sides, providing nine zones in each tree. The basic method was to remove one randomly located square foot bark sample from each zone at periodic intervals.

In 1963, this sampling procedure was repeated for five trees at two week intervals starting in June and continuing until October. Another five trees, in 1963, were sampled by removing one square foot samples from the top and two sides at ten foot intervals throughout the length of the tree. One-quarter square foot samples, i.e. 6" x 6", were also collected in 1963.

In 1964, the sample procedure was modified so that square foot samples were taken from the trees every three weeks starting in July and continuing until October, while in 1965 and 1966, square foot samples were taken monthly starting in August and continuing until November. In addition, two square foot samples, i.e. 1' x 2', were obtained in 1964.

Throughout this phase of the work and other phases yet to be described, the basic sample unit has been one square foot of bark area, i.e. 1' x 1'. It is generally agreed that the basic sample unit should be a natural part of the habitat used by the insect. For instance, in the case of a foliage insect on conifers, a branch or combination of branches would be a natural part of the habitat. However, for bark

beetles, this becomes a little more difficult to define. Certainly, any portion of the bark is a part of the habitat but the question of size and shape is arbitrary. In the case of the Douglas-fir beetle the universe and habitat are synonomous and is defined as all the blowdown Douglas-fir trees that are attacked by the beetle.

Various sized bark samples, i.e. one-quarter, one and two square foot, were compared using the coefficient of variation as defined by Steel and Torrie (1960), as a measure of efficiency.

C.V. = $s/\bar{x}$ x 100 where C.V. = coefficient of

variation, s = sample standard deviation and $\bar{x}$ = sample mean. Figure 10 shows the coefficient of variation plotted against the size of sample unit. It is apparent that the C.V. decreases as the sample unit size increases. It is also generally true that for any given sample unit size the C.V. decreases as the population density increases. Thus, the greatest gain in precision occurs when we go from a one square foot sample unit to a two square foot sample unit at low population densities. Furthermore, when we compare the total amount of bark area that must be sampled by two square foot units to achieve a set error no greater than 10% of the mean, we find that it is necessary to sample less total bark area using two square foot samples than one square foot samples. Thus all the evidence indicates that the best basic unit is the two square foot sample.

However, we are interested not only in drawing a sample from the infested blowdown that accurately reflects the population density
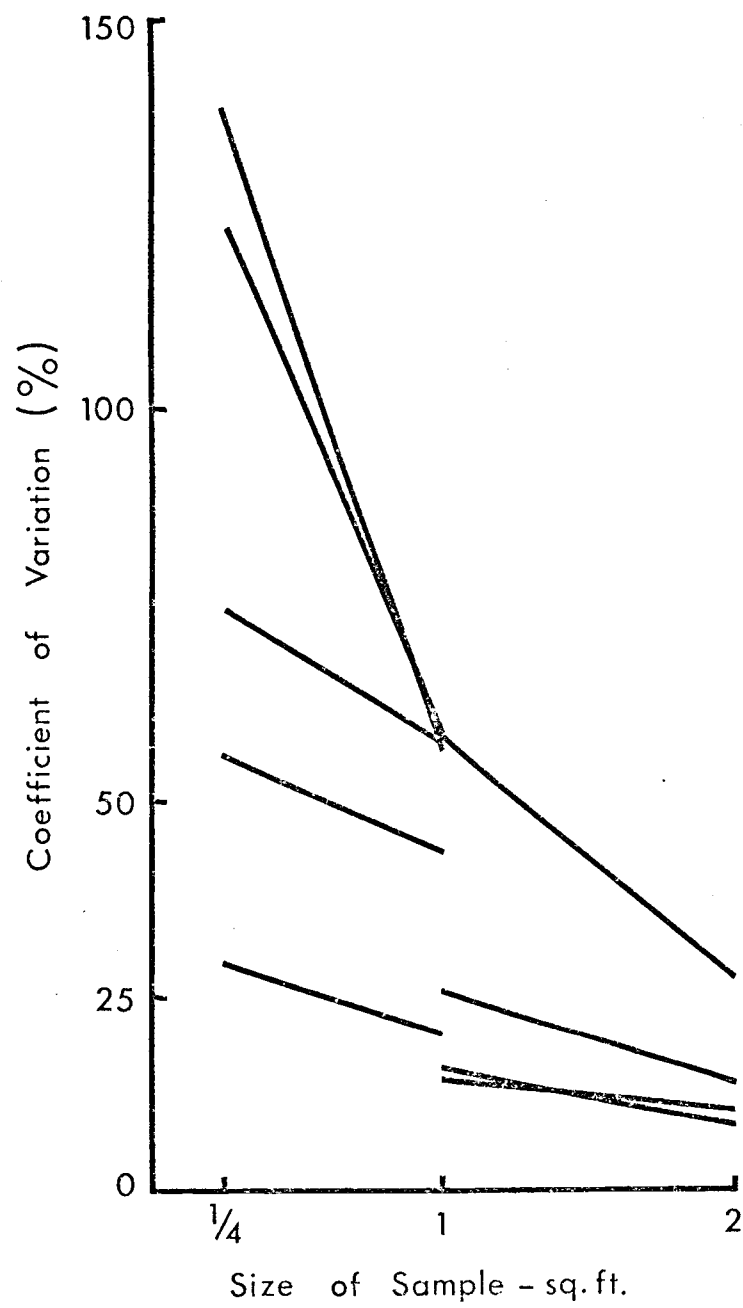
Figure 10. Efficiency of three different sized sample units

in that log, but also in drawing serial samples throughout all stages

of development of the bark beetle. Therefore, to maintain a once every

two, three or four week sampling schedule throughout the season using

two square foot bark samples would result in considerable oversampling.

For this reason, one square foot samples were used since only one-half

as much work is necessary while still generally meeting precision

requirements.

The possible influence of sample shape, i.e. square, rectangular

or circular, was not considered of sufficient importance to warrant

study. Consequently, only square one foot samples (1 foot x 1 foot)

were used.

Frequency distributions of the first and fourth instar larval

counts per square foot for each tree that was sampled were formed.

These frequency distributions were not normal but were generally

skewed considerably to the right. The relationship between the means

and variances varied proportionally which usually indicates a

contagious distribution. Attempts to fit theoretical distributions,

such as negative binomial and Poisson, to the observed distributions

were not successful. However, a logarithmic transformation of the

form $y = \log_{10} (x+1)$ removed some of the dependence between mean and

variance.

An analysis of variance was performed on all sample trees using

both raw data and transformed data for each year in order to determine

which intertree variables were significant. Very similar results were

found for both raw and transformed data. These results showed that

significant differences existed in population densities of first and

fourth instar larvae from tree to tree, among levels within trees

(levels are upper third, middle third and lower third of a sample tree)

and in the interaction of trees x levels. Quadrants, which were the

left, upper and right sides of a sample tree and any interactions

involving quadrants were not significant except for trees classified

as exposed (Chapter V).

The comments of Southwood (1966, p. 11) concerning transforma-

tion are very interesting:

> "The use of transformations can lead to problems when
> comparing means, which may be based on different trans-
> formations, in constructing life tables."

In other words, a transformation of the type $y = \log_{10} (x+1)$ may be

more suitable for transforming first instar larval counts than another

type of transformation such as square root. However, the reverse could

be true for fourth instar larvae or other stages and comparing mean

densities based on different transformations is not valid. Thus, as

Southwood (1966) suggests,

> "There is indeed much to commend the use of the
> arithmetic mean (i.e. that based on the untransformed
> data) in population studies."

In any case, the analysis of variance of both untransformed and

transformed data gave virtually identical results, thus arithmetic

means were used in subsequent analyses including the construction of

life tables.

Three formulae were used to calculate the number of square foot bark samples that it was necessary to examine from each infested blowdown log. In all cases the desired standard error of the mean was set at 10% of the mean. The number of samples required on a simple random basis was prohibitively large. The negative binomial sample size formula reduced the number of samples required to one-third that of the simple random method but was still quite high. The third formula, based on stratified random sampling with optimum allocation with equal sampling costs among strata, proved satisfactory. Using the stratified random technique, three equal-sized stratum were recognized in each study tree based on the analysis of variance; lower, middle and upper. Stratification minimizes the variance within strata and maximizes it between strata, providing that reasons for stratification exist. The primary reason for lengthwise stratification in this study involves varying attack densities of the beetle along the tree length. Attack densities and consequently larval densities in the lower one-third of the blowdown trees are normally lower compared to the middle or upper thirds. No stratum appears to represent consistently a median of the population in the tree.

Figure 11 depicts a relationship between the coefficient of variation and the number of samples required to satisfy an accuracy level where the standard error is 10% or 20% of the mean. For stratified random sampling with optimum allocation with equal sampling costs, the C.V. $= \sum s_h / \sum \bar{x}_h \times 100$. In essence, this graph is the
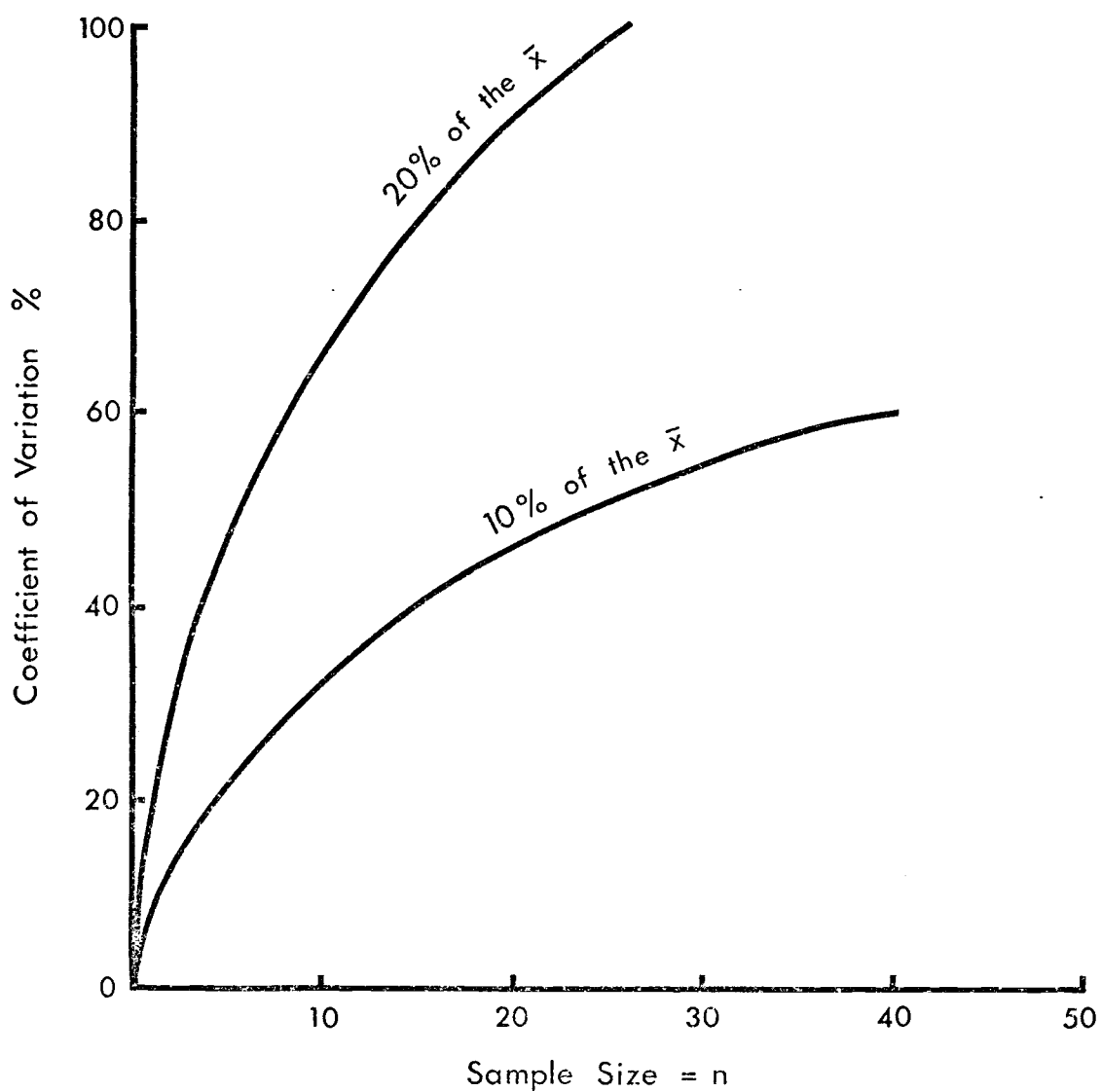
Figure 11. Relationship between the coefficient
of variation and the number of samples
required to satisfy an accuracy level where
the standard error is 10 or 20% of the
mean

nucleus of the larval sampling method. Estimates of the variance

and mean can be obtained for any infested trees by preliminary

sampling. Calculating the ratio of the sum of the strata standard

deviations to the sum of the strata means automatically provides the

number of samples required for the desired level of accuracy.

Table 6 compares the number of samples actually taken with the

number of samples required for a level of accuracy of 10% of the mean

for first instars. Of a total of 33 trees, 19 or 58% had the required

number of samples taken. Twenty-seven of the trees (82%) required 30

or less samples which is considered to be the maximum that can be

handled from any given tree.

Table 7 contains the same data concerning number of samples as

Table 6, except these are for fourth instars. Of 34 trees, 17 or 50%

had the required number of samples taken and 26 (76%) required 30 or

less samples.

If a 20% standard error of the mean is considered acceptable

then all but one tree would require 30 or fewer samples. Furthermore,

all but three trees would have been oversampled under these terms of

reference. Lyons (1964) recommends trying to keep standard errors in

the vicinity of 10 to 15% of the mean for this type of work. Southwood

(1966) states that,

> "For many purposes an error of 10% of the mean is
> a reasonable standard."

Thus, for sampling larval instars of Douglas-fir beetle in most

windthrown trees, approximately 25 to 30 one square foot bark samples

Table 6. Number of samples taken from each tree compared with the required number of samples for first instar larvae calculated by stratified random sampling formula (with optimum allocation with equal sampling costs).

Tree	Number of samples taken	Required number of samples	Tree	Number of samples taken	Required number of samples
1966 - 1	12	20	1965 - 3	12	9
2	12	33	6	12	27
3	12	5	8	12	12
4	12	13	9	8	9
5	12	25	10	9	7
6	12	10	11	9	3
7	12	11	12	8	6
8	12	5	14	6	5
9	12	21	15	9	5
10	12	25			
1964 - 1	17	9	1963 - 1	25	35
3	20	12	3	15	33
5	15	12	4	20	99
7	10	7	6	17	21
8	14	8	7	16	32
10	14	7	10	15	39
11	14	19	11	9	27

Stratified random sampling formula (with optimum allocation with equal sampling costs among strata), from Freese (1962)

$$ n = \frac{(\sum_{h=1}^{L} N_h s_h)^2}{N^2 D^2 + \sum_{h=1}^{L} N_h S^2_h} $$

(Symbols defined in Table 7)

Table 7. Number of samples taken from each tree compared with the required number of samples for fourth instar larvae calculated by stratified random sampling formula (with optimum allocation with equal sampling costs).

Tree	Number of samples taken	Required number of samples	Tree	Number of samples taken	Required number of samples
1966 - 1	12	12	1965 - 3	18	49
2	12	53	6	18	17
3	12	6	8	12	40
4	12	15	9	8	6
5	12	21	10	16	10
6	12	8	11	9	6
7	12	13	12	12	30
8	12	12	14	6	15
9	12	151	15	9	8
10	12	94			
1964 - 1	18	18	1963 - 1	16	21
3	15	10	3	13	19
5	18	9	6	17	27
7	12	12	7	12	23
8	15	11	8	11	23
10	12	13	10	15	36
11	12	92	11	10	42
			12	11	4

Where n = required number of samples

L = number of strata

S_h^2 = variance within each stratum

N_h = total size (number of units) of stratum h(h=1, ..., L)

N = total number of units in all strata

$$(N = \sum_{h=1}^{L} N_h)$$

D = desired size of standard error of the mean

are sufficient to estimate the larval densities with a fair degree of precision. These 25 to 30 one square foot bark samples can be sampled randomly on a proportional or optimum allocation basis from each stratum within the tree (lower, middle and upper third). This procedure applies to windthrown trees that are not completely exposed, i.e. shaded or partially shaded. For blowdown trees that are completely exposed, for example, lying in a clear cut area, it is necessary to double the number of samples required because there is a difference from side to side of the downed tree (Chapter V).

Adult Sampling

The remaining stages of the Douglas-fir beetle life cycle that could be sampled were various phases of the adult form, i.e. callow adults in the fall, callow adults in the spring and adults that emerged successfully. Data for adult beetles were obtained for the same trees sampled for eggs and larvae by removing square foot bark samples from each of the nine zones in each windthrown tree on two different occasions in the fall. These data were virtually identical (except densities were somewhat lower) to that obtained for fourth instar larvae. This sample was repeated in the spring, usually in March, to obtain density estimates of overwintering survivors. Again, these data were similar, i.e. in terms of frequency distribution and contagion to that obtained for fourth instar larvae and callow adults in the fall. The final stage that could be sampled was the emerging adults. Data were

obtained for 1964, 1965 and 1966 generation sample trees by actually capturing beetles in traps as they emerged. Fine wire mesh traps were used in 1964 and tanglefoot coated plastic traps were employed in 1965 and 1966. Generally, two or three sets of traps (18 or 27 individual traps) were placed on each sample tree. Emergence data for the 1963 generation was estimated from the number of emergence holes counted on square foot units. Subsequent work (in 1964, 1965 and 1966) showed that the number of emergence holes overestimated the number of beetles that actually emerged. Thus, the 1963 emergence data were corrected on that basis.

Frequency distributions of the emerged adult counts per square foot for each tree were formed. These distributions were sharply skewed and had a high preponderance of negative values and a low mean density. Plotting variances against the appropriate means did not provide a clear indication that the variances were dependent upon the mean. Negative binomial "k" values and Morisita's index (Southwood 1966) were calculated and both indicated that the distributions were contagious. Calculations of expected values based on the negative binomial distribution were almost identical to the observed values. Thus, it was assumed that the distribution of emerged adults per square foot of bark surface was of the negative binomial form.

Analyses of variance were performed on untransformed and transformed ($y = \log_{10} [x+1]$) data looking for significant sources of variation among trees, levels (upper, middle and lower thirds),

quadrants (top and both sides) and the various interactions. The only

significant result was the interaction of trees x levels which was

significant at the 95% level for the untransformed data and at the

99% level for the transformed data. Previous comments concerning

transformation of larval counts are also applicable for adult counts

and subsequent analyses were performed using the raw data.

The required number of samples based on the simple random

sampling formula were prohibitively large. The required number based

on the negative binomial formula was reduced to about one-quarter of

those needed on a simple random basis. Stratified random sampling

(based on optimum allocation with equal sampling costs) reduced the

required number of samples to a reasonable level provided one is willing

to accept a precision that is between 10 and 20% of the mean. Table 8

illustrates an example of this point.

In summary of this chapter on sampling methods, it is note-

worthy that the method used from 1963 to 1966 was largely a result

of available manpower, money, time and other practical considerations

in both the field and laboratory. In other words, it was decided that

a certain amount of work could be done each year and this was carried

out in a way considered best adapted to solving the problem. Thus a

full-scale intensive study to design sampling methods and incorporate

the best methods into the field work was not attempted. Basically,

much of these sampling data were not analyzed until the completion of

the field work in the spring of 1967. At best, it was hoped that these

Table 8. Comparison of three sample size formulae used to calculate the number of samples required to achieve a standard error of the mean of 10 and 20% for emerging adults.

Tree	n (Simple random) 10%	20%	n (Negative binomial) 10%	20%	n (Stratified random) 10%	20%	Actual number of samples
66 - 1	1010	252	289	72	85	23	27
2	1590	398	397	99	33	9	18
3	1365	341	340	85	54	15	18
4	638	161	160	40	52	14	27
6	720	180	191	48	50	13	27
7	5186	1297	1295	324	204	67	27
8	1424	386	356	89	4	1	21

Simple random sample formula (Cochran 1963)

$$n = \frac{t^2 s^2}{d^2}$$

where n = required number of samples

d = chosen margin of error

s^2 = population variance

t = tabular value of "t" for d.f. and p = .05

Negative binomial sample formula (Southwood 1966)

$$n = \frac{\frac{1}{\bar{x}} + \frac{1}{k}}{D^2}$$

where n = required number of samples

$\bar{x}$ = mean per sample

k = dispersion parameter of the negative binomial

D = required level of accuracy

Stratified Random Sampling Formula (with optimum allocation with equal sampling costs among strata) - Table 6

data would provide relatively reliable population density estimates for life tables for this study and would serve as the basis for the design of methods for future work. In the opening section of this chapter, sampling design was described as a combination of art and science. It takes skill and judgement along with the application of theory, knowledge and science to develop good sampling techniques. It is impossible to state categorically which of the above attributes and factors deserve most of the credit, but it would seem that the methods that emerged through sheer necessity and practical consideration over a four-year period with some modifications from year to year were generally satisfactory.

V. ATTACK PATTERNS OF DOUGLAS-FIR BEETLE IN BLOWDOWN LOGS

Coastal Douglas-fir forests of western North America experience a considerable, but variable, amount of windthrow each year. The quantity of windthrow in any particular year is due to prevailing weather conditions throughout the fall and winter seasons, i.e. amount of rainfall, frequency of storms, wind velocity, etc.

Female Douglas-fir beetles attack windthrown Douglas-fir trees usually in the spring following the occurrence of the blowdown. The first females that attack a blowdown are termed "pioneer" beetles and they are attracted to windthrow by volatile terpenes emitted from the host material. This process of host attraction is called primary attraction. It is not known whether "pioneer" beetles are simply early emerging members of the population or if they possess a keenly developed ability to detect and follow terpenes to their source. In any case, after the initial attack has occurred, a secondary attraction is established which results in mass attack by other adult Douglas-fir beetles. The source of secondary attraction is a pheromone produced by virgin female beetles after they have attacked and commenced gallery construction in blowdown logs. The pheromone attracts both male and female beetles although males generally outnumber females.

Occasionally, after boring into the phloem, attacking females will construct a short irregular gallery and bore back to the exterior of the bark or leave through the entrance hole. Attacks of this type are termed "aborted" and the specific reasons for their occurrence are unknown. Aborted attacks may be the only type of attack to occur in

some trees, or they may occur intermingled with successful attacks or may be completely absent. Successful attacks are defined as those attacks resulting in the construction of a parent gallery and oviposition of eggs. The incidence of aborted attacks to successful attacks is an interesting problem in itself. However, when describing attack patterns, there is no need to differentiate between the two types, since the behavioural and environmental factors that govern the attack process are probably the same, regardless of the end result. Therefore, an attack is defined as an entrance hole of a gallery, irrespective of whether the gallery was eventually successful or aborted.

The data used to describe attack patterns were obtained by a sampling procedure described in greater detail in Chapter IV, but, in brief, consisted of removing square foot bark samples from representative portions of blowdown trees and counting the number of entrance holes. Understanding the attack patterns of the Douglas-fir beetle in blowdown logs and realizing how these patterns are related to environmental and other factors, may facilitate the design of more efficient sampling techniques. In addition, this knowledge provides insight into the behaviour and habits of the adult beetle.

Annual Attack Rate and Attack Rate Per Tree

In general, the annual attack rate is determined for any given year by the total bark area of blowdown available for attack and the total number of female beetles that attack the blowdown. For example, the attack rate will be low if there is much blowdown and few beetles.

The attack rate will increase if the same number of beetles are present but there is less blowdown. Thus, it is the amount of blowdown relative to the number of beetles that is most important in establishing the annual attack rate. Undoubtedly there is an upper limit to the attack rate since an area of bark cannot receive an unlimited number of attacks. The maximum number of attacks recorded during this study was 14 per square foot of bark surface over a small part of one blowdown tree. The highest recorded attack rate for a tree was 7.4 per square foot, and the highest recorded annual attack rate was 3.6 per square foot, therefore, it is believed that the upper limit for overall attack rate is rarely reached under natural conditions.

Attack rates were determined for the study area, Marys Peak watershed, for a four-year period by sampling blowdown trees each year. The total amount of blowdown on the watershed each year was estimated from records of timber salvage sales by the U.S. Forest Service (Appendix II). Thus an estimate of the total number of female Douglas-fir beetles that attacked blowdown each year in the watershed can be obtained by multiplying the total amount of blowdown attacked, by the attack rate. The following table (Table 9) provides a summary of the pertinent data.

The total number of female beetles that attacked blowdown each year on the watershed (Table 9) are probably slightly overestimated since a single female beetle could be responsible for more than one attack. However, these figures undoubtedly reflect population trends from year to year quite accurately.

Table 9. Attack data for Marys Peak watershed, 1963-1966.

	1963	1964	1965	1966
Number of sample trees	10	9	11	10
Attack rate (female beetles per square foot of bark surface)	.587[1]	2.833	3.588	3.504
Total amount of blowdown attacked (square feet of bark surface)	4,441,343[2]	1,713,570	1,128,951	33,640
Total number of female beetles that attacked blowdown	2,607,068	4,700,322	3,999,873	120,532

[1] The number of entrance holes per sample unit for successful galleries was not recorded in 1963. Therefore, in order to obtain an attack rate, the number of parent galleries per square foot was multiplied by a correction factor of .60 and this product was added to the number of aborted galleries per square foot. The correction factor of .60 was obtained by determining the ratio between the number of entrance holes for successful galleries per square foot and the number of successful galleries per square foot for the 1964, 1965 and 1966 data. In other words, .6 or 60% of the successful galleries had entrance holes located on the same sample unit.

[2] In 1963 there was 8,882,686 square feet of bark surface but only 50% of the total was attacked. All blowdown in 1964, 1965 and 1966 was attacked.

The total number of attacks received by each sample tree was estimated by random sampling from defined strata within each blowdown tree. Attack rates in each strata were weighted according to the strata size and an estimate of total attacks for the tree was obtained.

An analysis of variance showed that no significant differences existed among the attack rates for 1964, 1965 and 1966, whereas the attack rate for 1963 was significantly different from the other three years. Consequently, the attack rate data for 1964, 1965 and 1966 were pooled for further analysis.

Scatter diagrams, analysis of variance and regression techniques were used to determine if relationships existed between the attack rate and such variables as tree size, tree age, stand exposure, elevation, root condition, top condition, direction of slope where blowdown was located and direction tree was lying. The only significant relationship detected by these analyses was between attack rate and stand exposure. Blowdown trees in closed stands are attacked at the highest rate, windthrow in exposed areas receive the lowest rate of attack and trees in stands with open exposures are the recipients of an intermediate attack rate (Table 10).

Regressions between attack rate per tree and tree size (bark area) were not significant. Figure 12 shows this relationship for trees grouped by year and Figure 13 for trees grouped by exposure class. Thus, when considered on an attack rate per tree basis, larger trees are neither more nor less attractive than smaller trees. The end result, however, is that larger trees attract a greater total number of

Table 10. Attack rates in blowdown trees classified by stand exposure
(pooled data from 1964, 1965 and 1966).

	Closed stand[1]	Open stand[2]	Clear cut (exposed) stands[3]
Attack rate	4.322 per sq. ft.	2.978 per sq. ft.	1.782 per sq. ft.

[1] Closed stand is defined as one with 75% to 100% crown closure –
blowdown trees in such a stand are completely shaded all day.

[2] Open stand is defined as one with 25% to 75% crown closure – blow-
down trees in such a stand are partially shaded throughout the day.

[3] Clear Cut (exposed) stand is defined as one with 0 to 25% crown
closure – blowdown trees in such a stand receive no shade all day.
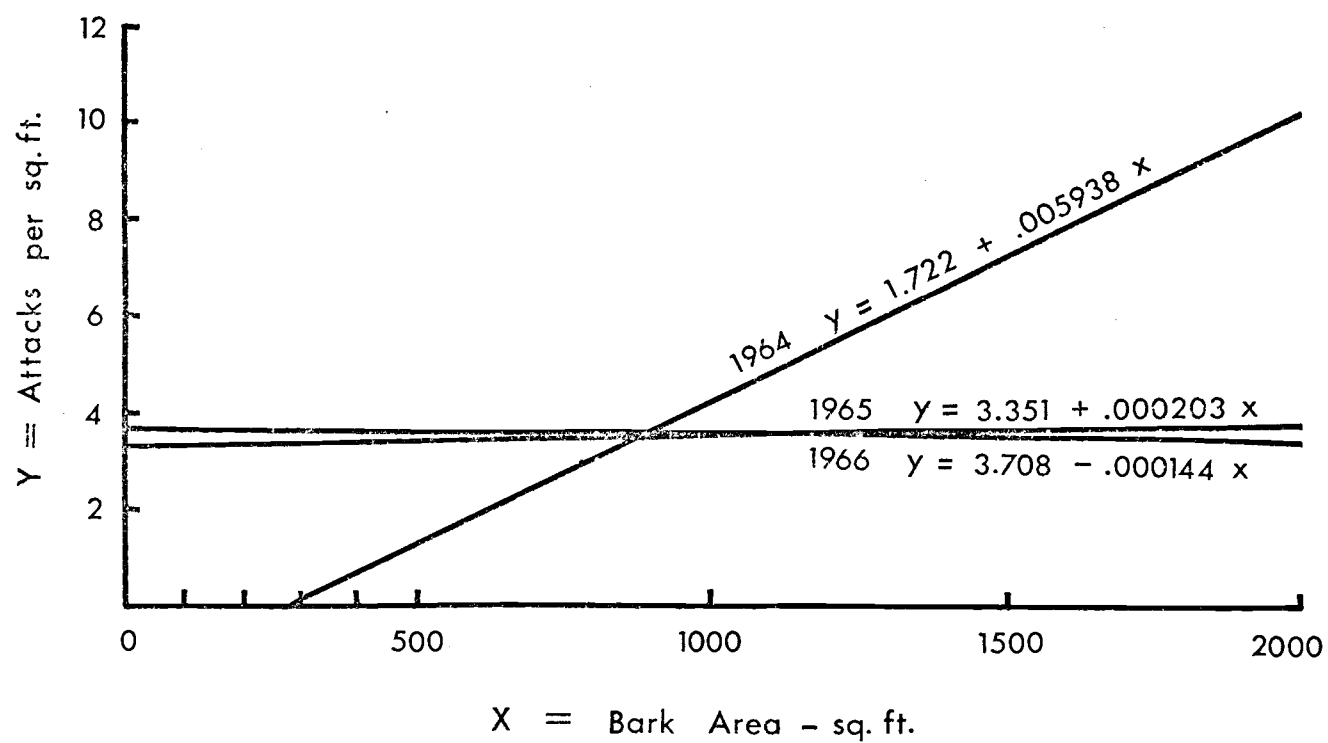
Figure 12. Relationship between attack rate per tree and tree size for each year
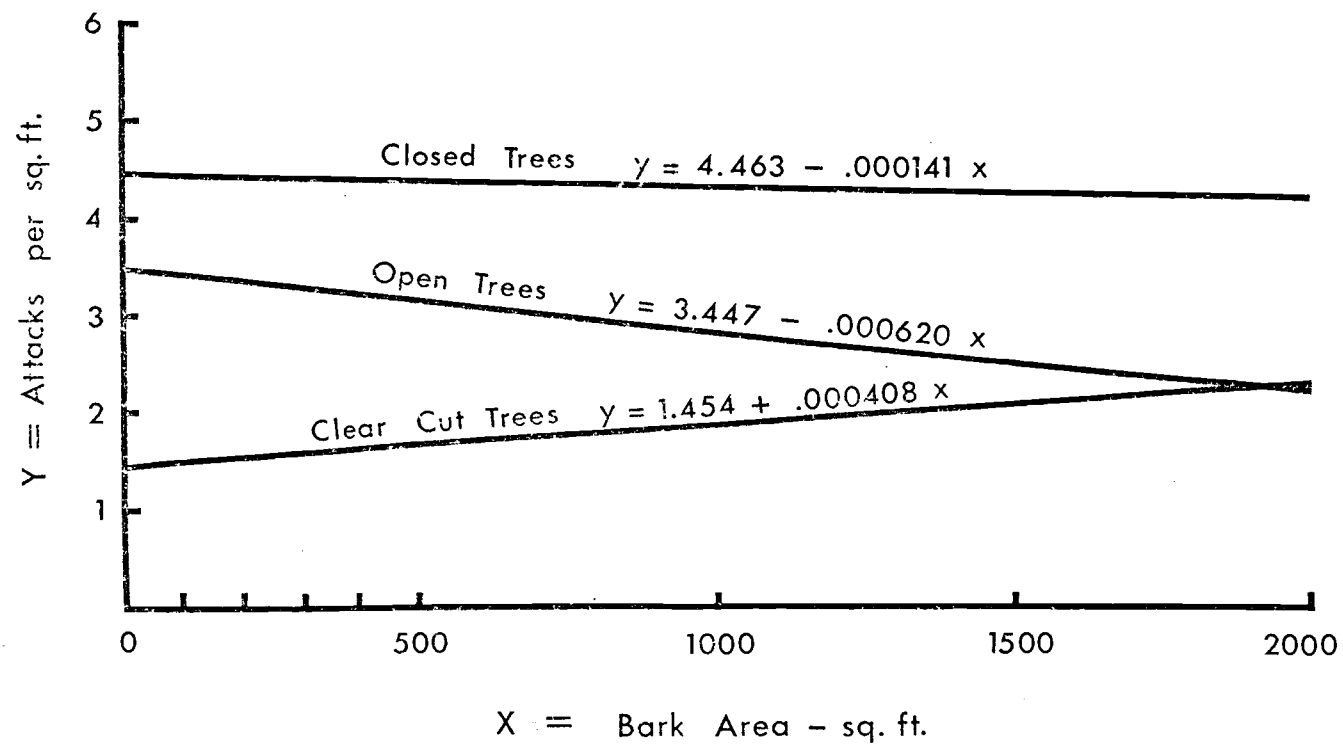
Figure 13.   Relationship between attack rate per tree and tree size
         for each exposure class

beetles than smaller trees.

Attack Rate Patterns Within Blowdown Trees

An analysis of variance performed on the within tree attack

rate data (Table 11) produced the results contained in Table 12.

Closed and open trees showed the same pattern in that trees, levels and

the interaction of T x L were highly significant sources of variation.

Clear cut trees differed with all sources of variation other than trees

being significant or highly significant. Generally, attack rates in

the upper, middle or lower portions of the blowdown log, i.e. levels,

were the greatest source of variation followed by trees except for

clear cut trees where quadrants was the greatest source of variation

followed by levels.

Again, these data demonstrate the effect of exposure on attack

rates. Attack rates per tree are highest for closed trees, lowest for

clear cut trees and intermediate for open trees. Furthermore, the

sides of a blowdown log can be oriented with regard to exposure. Thus,

for closed and open trees there is no difference in attack rates

between the top or sides of the tree. Trees lying in completely open

exposures (clear cut category) exhibit a marked difference between the

shaded side of the log and the exposed and top sides. The attack rate

within a blowdown tree (attacks per square foot of bark surface) tends

to increase from the lower level (butt end) to the upper level (top

end). This increase is only apparent however, and not real, since, due

to log taper, bark area per linear foot actually decreases as we move

Table 11. Mean attack rates within trees grouped by exposure class.

| | "Closed" trees (12 trees in this category) | | | |
	Top	Shaded	Exposed	$\bar{X}$
Upper	4.84	4.27	4.73	4.62
Middle	6.72	4.28	4.56	4.85
Lower	3.59	3.54	3.15	3.42
$\bar{X} =$	4.72	4.03	4.15	

| | "Open" trees (13 trees in this category) | | | |
	Top	Shaded	Exposed	$\bar{X}$
Upper	3.97	3.27	3.37	3.54
Middle	3.20	3.43	3.21	3.28
Lower	1.88	2.48	2.00	2.12
$\bar{X} =$	3.01	3.06	2.86	

| | "Clear cut" trees (5 trees in this category) | | | |
	Top	Shaded	Exposed	$\bar{X}$
Upper	1.92	4.14	1.93	2.66
Middle	.87	2.26	1.63	1.58
Lower	.43	2.19	.67	1.10
$\bar{X} =$	1.07	2.86	1.41	

Table 12. Summary of results of analysis of variance of within tree attack rate data.

Source of variation	Tree Exposure		
	Clear cut	Open	Closed
Trees	NS	HS**	HS**
Levels (upper, middle, lower)	HS**	HS**	HS**
Quadrants (top, shaded, exposed)	HS**	NS	NS
T x L	HS**	HS**	HS**
T x Q	HS**	NS	NS
L x Q	S*	NS	NS

NS – not significant at p > .05

* S – significant at p = .05

** HS – highly significant at p = .01

towards the top of the tree. In other words, 50 beetles attacking a ten foot section in the lower level would produce a much lower attack rate per square foot of bark surface than the same 50 beetles attacking a ten foot section in the upper level. The increase in the attack rate is of the same magnitude as the decrease in bark area. Thus, if we consider an attack rate based on attacks per linear foot of log, we find that they remain relatively constant throughout the length of the log. This, in turn, is evidence that female beetles attack a log in a random fashion and except in those cases where exposure is a factor, all parts of a blowdown log have an equal probability of being attacked.

VI. INTRASPECIFIC COMPETITION

Throughout the course of this study considerable attention was focussed on the role of intraspecific competition as a factor in the population dynamics of the Douglas-fir beetle. This attention was warranted because observations and results of other researchers had indicated that a large and variable amount of mortality, which occurred particularly in the larval instars, was due to intraspecific competition. Various writers have pointed out that competition acts in a manner directly related to density, which in turn, implies the possibility that mortality due to competition could be a "key factor" (Chapter VIII).

McCowan and Rudinsky (1954) working with the Douglas-fir beetle in the coastal forests of Oregon observed that when the density of successful attacks was more than eight per square foot of bark surface, a large number of larvae died apparently as a result of food shortage brought on by overcrowded conditions. McMullen and Atkins (1961), after studying the effects of intraspecific competition on brood production by the Douglas-fir beetle in the interior of British Columbia, stated that

> "If attack density is a reflection of population levels,
> as the population increases the attack density will
> increase with a consequent reduction in progeny produc-
> tion. The effect of competition thus acts as a regulating
> feature to keep the population in check."

In their work they showed that the important effects are felt at the higher attack densities, i.e. above four per square foot. They noted that several effects of intraspecific competition were evident; as

crowding increased the parents abandoned the egg galleries more rapidly, the egg galleries were shorter, fewer eggs were laid, and mortality during the larval and pupal stages was higher.

Schmitz and Rudinsky (1968) studied the effects of competition on survival in western Oregon of the Douglas-fir beetle in windthrown trees. Their results showed that brood survival decreased with increases in attack density, total length of egg gallery and number of larval mines per square foot. They concluded that

1. Interspecific competition was not a factor in natural control of the Douglas-fir beetle in the studies described.

2. Intraspecific competition was an important natural control of the Douglas-fir beetle, and its effect must be considered in any prediction of population trend.

The effects of intraspecific competition on brood survival of other species of bark beetle has been described in the literature. For example, Rudinsky (1962) in a general review dealing with the ecology of Scolytidae states that

"Inter- and intraspecific competition for food and space increases the developmental time, and causes as well, extensive mortality and reduced size and reproductive ability in the surviving individuals."

and

"Competition, both interspecific and intraspecific, has been found to contribute significantly to the decline of bark beetle populations."

Miller and Keen (1960) in their summary of 50 years of research on the biology and control of the western pine beetle, (Dendroctonus brevicomis Lec.), noted that the effects of intraspecific competition, in terms of brood survival, varied from year to year and was apparently directly related to the number of attacks. Reid (1963), working with the mountain pine beetle (Dendroctonus monticolae Hopkins) in the East Kootenay region of British Columbia, found that brood survival per inch of egg gallery decreased with increasing density, indicating that competition within and between galleries had commenced at the lowest density.

In a general review article dealing with intraspecific competition and the regulation of insect numbers, Klomp (1964) states that

"Among plant-feeding insects, competition has been said to occur regularly between bark beetles. Competition between beetle larvae has been described in Agrilus, Blastophagus, Ips and Dendroctonus. In some cases the mortality of the larvae is caused by food shortage, probably always after a deterioration of the food plant. Sometimes mortality can be attributed to the disturbance of pupating larvae or pupae by moving larvae. Notwithstanding the density-governed reactions described above, the dispersal of adults is most likely to be responsible for regulation in these species."

Thus intraspecific competition seemed unquestionably to be an important factor in the population dynamics of the Douglas-fir beetle. For the purposes of this study, it was necessary to try to determine how much mortality in each of the stages or age intervals of the Douglas-fir beetle should be attributed to intraspecific competition. As Klomp (1964) has pointed out, the only realistic means of expressing

the deleterious effects of competition are in quantitative terms of rates of mortality, reproduction and emigration. Furthermore, the type of relationship between the rates of mortality, reproduction and emigration on the one hand, and density on the other, should be determined in order to help provide an explanation of the process of regulation. Therefore, the remainder of this chapter presents the methods that were used to determine the amount of mortality caused by intraspecific competition in each of four larval instars of the Douglas-fir beetle and the results obtained.

Methods

The methods used for studying the effects of intraspecific competition on brood survival of Douglas-fir beetle primarily employed the principle of predator-parasite exclusion cages. In March and April of each year prior to attack by adult beetles and predators, cages were placed on three of the 1966 and three of the 1965 blowdown Douglas-fir trees that were later sampled to obtain life table data. Generally, three cages were built on each tree, one cage in each of the lower, middle and upper portions of the bole. Each cage was approximately six feet long and completely encompassed the circumference of the log. The caged portions were covered with fine-mesh, nylon plastic window screening in order to exclude all species of windthrow-inhabiting insects. The unprotected portions of each of these blowdown trees were then attacked by adult Douglas-fir beetles and their predators in late

April and early May. Pairs of mature adult beetles, collected before emerging from infested trees and from laboratory rearing experiments were then placed inside the cages. The numbers placed in the cages were approximately that of the natural attack density adjacent to each cage.

This field method was supplemented by data from laboratory experiments in which Douglas-fir beetle broods were reared in slabs under controlled environmental conditions. The rearing method described by Johnson (1962) was used.

In October and November of each year, when the beetle broods had developed to the callow adult stage, the cages were removed and six square foot (12" x 12") bark sections were sampled in each of the caged sections. Six more square foot bark samples were removed from each caged portion in March of the following year. Counts were then made on a per square foot basis of first, second, third and fourth instar larval galleries and the number of callow adults. Similar counts were made for laboratory reared beetle broods in slabs.

Survival rates for each instar for each square foot of bark sampled were determined by calculating the percentage of each instar that lived to the following instar or stage. For example,

N_1 = number of first instar larvae per square foot

N_2 = number of second instar larvae per square foot

N_3 = number of third instar larvae per square foot

N_4 = number of fourth instar larvae per square foot

N_5 = number of fall callows per square foot

Therefore, the survival rate of first instar larvae which are effected only by competition is determined as follows:

$$S_{1-c} = \frac{N_2}{N_1} \times 100 \text{ where}$$

S_{1-c} = survival rate of first instar larvae which are effected by competition only, and N_2 and N_1 are defined above.

Similarly, S_{2-c}, S_{3-c} and S_{4-c} are calculated as follows:

$$S_{2-c} = \frac{N_3}{N_2} \times 100$$

$$S_{3-c} = \frac{N_4}{N_3} \times 100$$

$$S_{4-c} = \frac{N_5}{N_4} \times 100$$

where S_{2-c}, S_{3-c} and S_{4-c} are the survival rates of second, third, and fourth instar larvae effected by competition respectively. It should be noted that S_{4-c} actually reflects the survival rate of fourth instar larvae and pupae. It is difficult to get a fix on the population density during the pupal stage, thus the next stage, i.e. fall callow adults, are sampled and the survival rate combines fourth instar and pupal mortality.

Results

The next step was to plot the survival rate for each instar against the number entering the stages for which the respective

(corresponding) survival rate was calculated, i.e. each S_{1-c} is plotted against each respective N_1 with N_{1-c} on the Y axis and N_1 on the X axis.

The scatter diagrams indicated a possible linear relationship between survival rate of a given instar and the number of larvae that were alive at the start of that instar. Therefore, linear regressions were calculated for S_{1-c} and N_1, S_{2-c} and N_2, S_{3-c} and N_3, and S_{4-c} and N_4 for each experimental tree and the laboratory data. These results are summarized in Table 13.

Each set of regression coefficients (b values) were tested for homogeneity using the analysis of covariance. The results of these tests are summarized in Table 14 and show that with the exception of the fourth instar there is no difference in survival rates among trees for each instar.

Thus the data for each instar were combined to form linear regressions relating survival to density, one regression for each instar. It is believed that the significant variation among b values for the fourth instar are more likely a result of sampling error than the fact that a real difference exists in fourth instar survival rates from tree to tree, particularly in view of the fairly conclusive results for the first, second and third instars. The linear regressions of the form $Y = a + b X$ for each instar that were formed from combining all data for each instar are as follows:

First instar $Y = 93.55 - .14449 X$ (Figure 14)

Second instar $Y = 92.34 - .23284 X$ (Figure 16)

Table 13. Summary of statistics of linear regressions calculated for density and survival.

| Data source | Linear regression for S_{1-c} and N_1 (S_{1-c} = Y, N_1 = X) | | | | |
	a	b	r	Significance of regression	n
Laboratory rearing	97.53	− .09303	.4997	NS	9
Field trees 66- 3 (fall)	88.67	− .10309	.4651	NS	12
66- 3 (spring)	91.55	− .15846	.6721	NS	6
66- 2	90.39	− .17777	.4849	NS	13
66- 5	79.31	− .08320	.6520	*	11
65- 4	84.70	− .08412	.3503	NS	13
65-17	101.73	− .12105	.5520	*	15

| Data source | Linear regression for S_{2-c} and N_2 (S_{2-c} = Y, N_2 = X) | | | | |
	a	b	r	Significance of regression	n
Laboratory rearing	102.21	− .19015	.9461	**	10
Field trees 66- 3 (fall)	99.07	− .25916	.4969	NS	12
66- 3 (spring)	88.96	− .23493	.3304	NS	5
66- 2	100.91	− .40052	.6987	**	13
66- 5	82.58	− .13662	.4171	NS	10
65- 4	96.63	− .36166	.6799	**	16
65-16	114.29	− .69559	.9228	*	5
65-17	83.16	− .13752	.3184	NS	16

Continued...

Table 13. (Concluded)

| Data source | Linear regression for S_{3-c} and N_3 (S_{3-c} = Y, N_3 = X) | | | | |
	a	b	r	Significance of regression	n
Laboratory rearing	101.28	- .37144	.8021	**	10
Field trees 66- 2	107.15	- .67599	.3931	NS	23
66- 3 (fall)	118.57	- .62219	.7337	**	12
66- 3 (spring)	177.89	-1.74008	.9050	**	6
66- 5	86.76	- .07832	.0877	NS	15
65- 4	33.63	- .28047	.2915	NS	15
65-16	122.97	- .99498	.4907	NS	9
65-17	114.95	- .61482	.5542	**	23

| Data source | Linear regression for S_{4-c} and N_4 (S_{4-c} = Y, N_4 = X) | | | | |
	a	b	r	Significance of regression	n
Laboratory rearing	114.34	- .70564	.8596	**	10
Field trees 66- 2	41.40	- .20985	.4782	NS	14
66- 3 (fall)	28.27	- .04057	.0412	NS	12
66- 5	44.32	- .11613	.1233	NS	14
65- 4	70.32	-1.53030	.5845	*	15
65-16	103.05	-1.32212	.9322	**	15
65-17	30.01	- .30277	.4104	*	24

** significant at p = .01

* significant at p = .05

NS not significant p > .05

Table 14. Test for homogeneity among regression coefficients using analysis of covariance.

	Regression between			
Source	S_{1-c} and N_1	S_{2-c} and N_2	S_{3-c} and N_3	S_{4-c} and N_4
	F	F	F	F
Regression due to b	20.23**	35.26**	21.07**	18.96**
Variation among b's	$.32^{NS}$	1.25^{NS}	1.22^{NS}	4.75**

** significant at p = .01

NS not significant (p > .05)

Third instar   Y = 100.95 - .41416 X   (Figure 18)

Fourth instar   Y = 58.61 - .49195 X   (Figure 20)

These regressions are illustrated graphically in Figures 14, 16, 18 and 20 with a composite of the four regressions in Figure 22.

Each of these regressions was significant at a level of p = .01 when the hypothesis of β = 0 was tested. These regressions were then used to estimate the amount of mortality that occurred in each instar due to competition for each tree that was sampled for life table data. This is illustrated by an example using actual data from the study. The first instar linear regression between survival rate and density was Y = 93.55 - .14449 X. In this case, Y equals the expected number of larvae that live to enter the second instar after competition has taken its effect on the first instar larvae, thus we can set $Y = N_{2-c}$ and $X = N_1$. Thus, this equation enables us to calculate the number of larvae that will live to second instar if intraspecific competition is the only factor affecting the population, providing we know the density of first instars. It is now an easy step to produce a set of competition curves, each of which represents the relationship between the numbers of any given instar and the numbers of the next instar. These curves are represented in graphical form in the following figures: 15, 17, 19 and 21 with a composite graph of the four curves in Figure 23.

The relationship between N_1 and N_{2-c} is:

$$N_{2-c} = S_{1-c} \, N_1$$
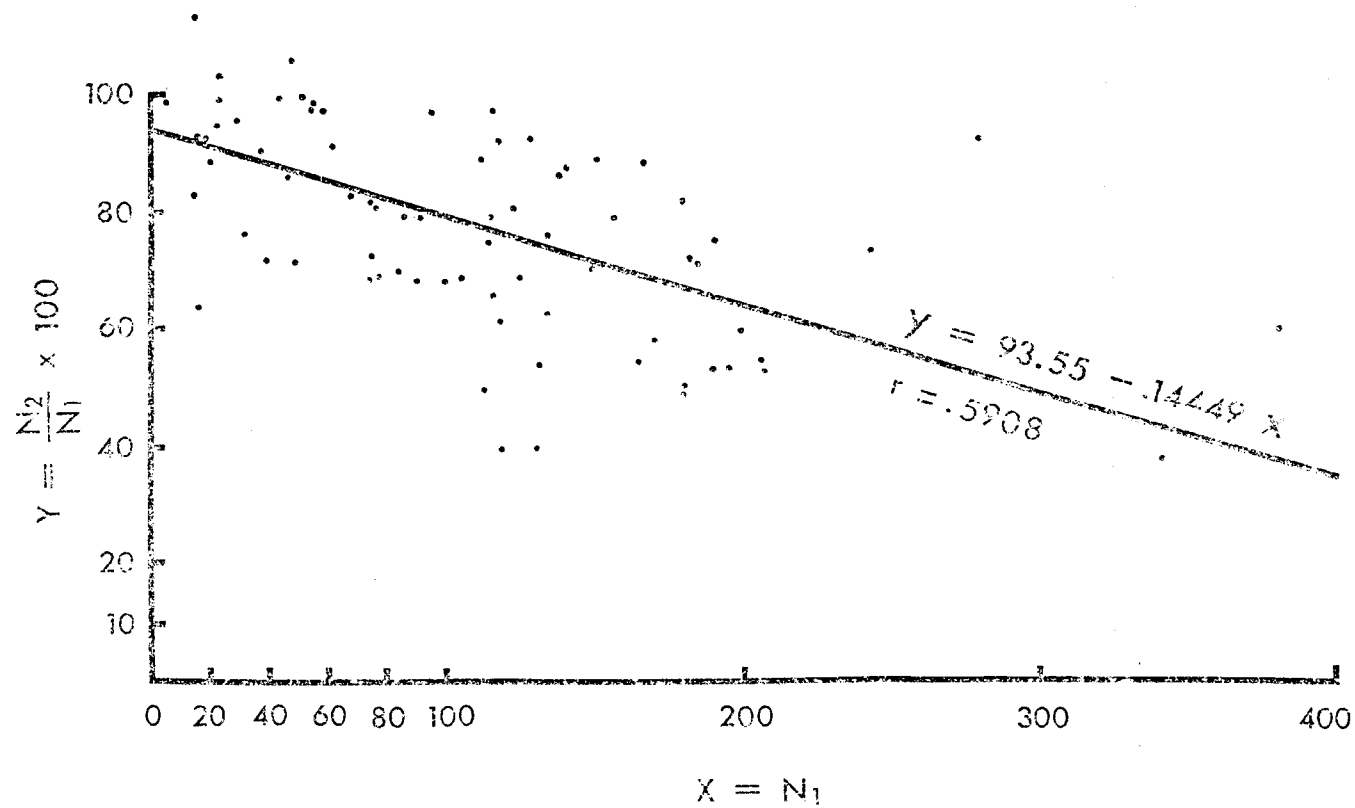
Figure 14. Relationship between survival of first instar larvae (affected only by competition) and density of first instar larvae
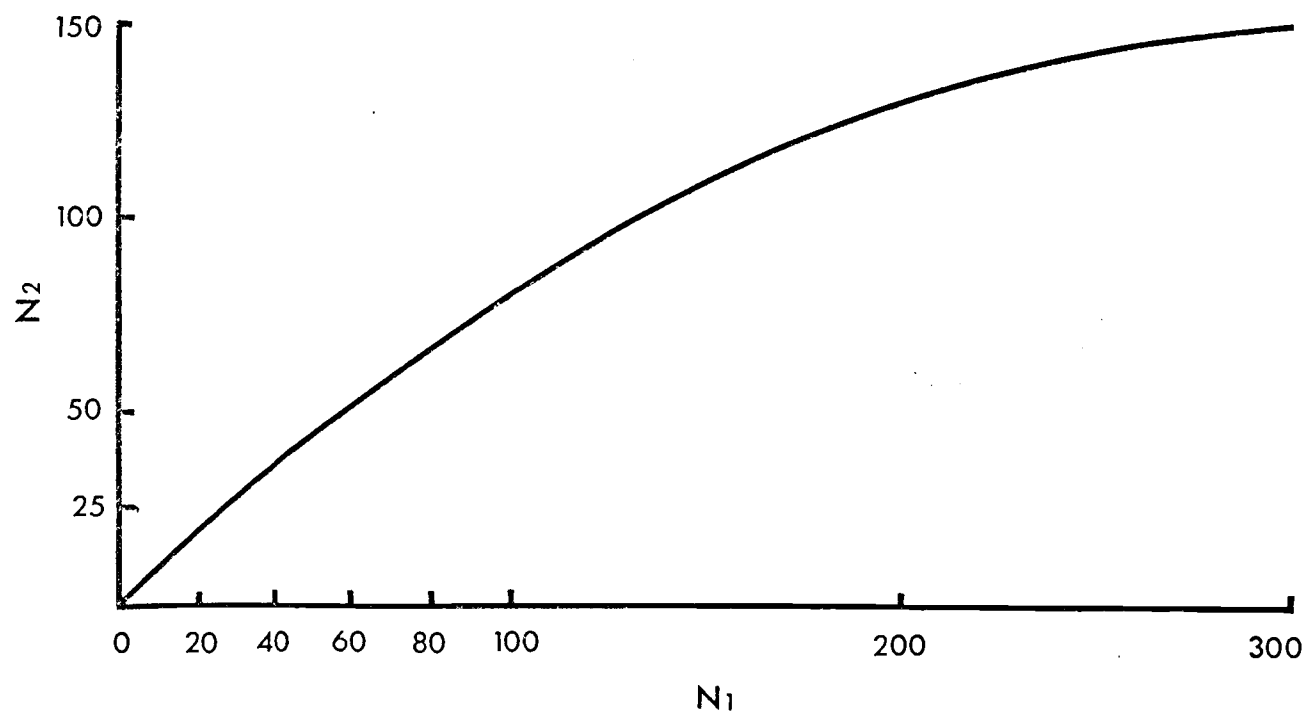
Figure 15. Competition curve showing relationship between
first and second instar larvae
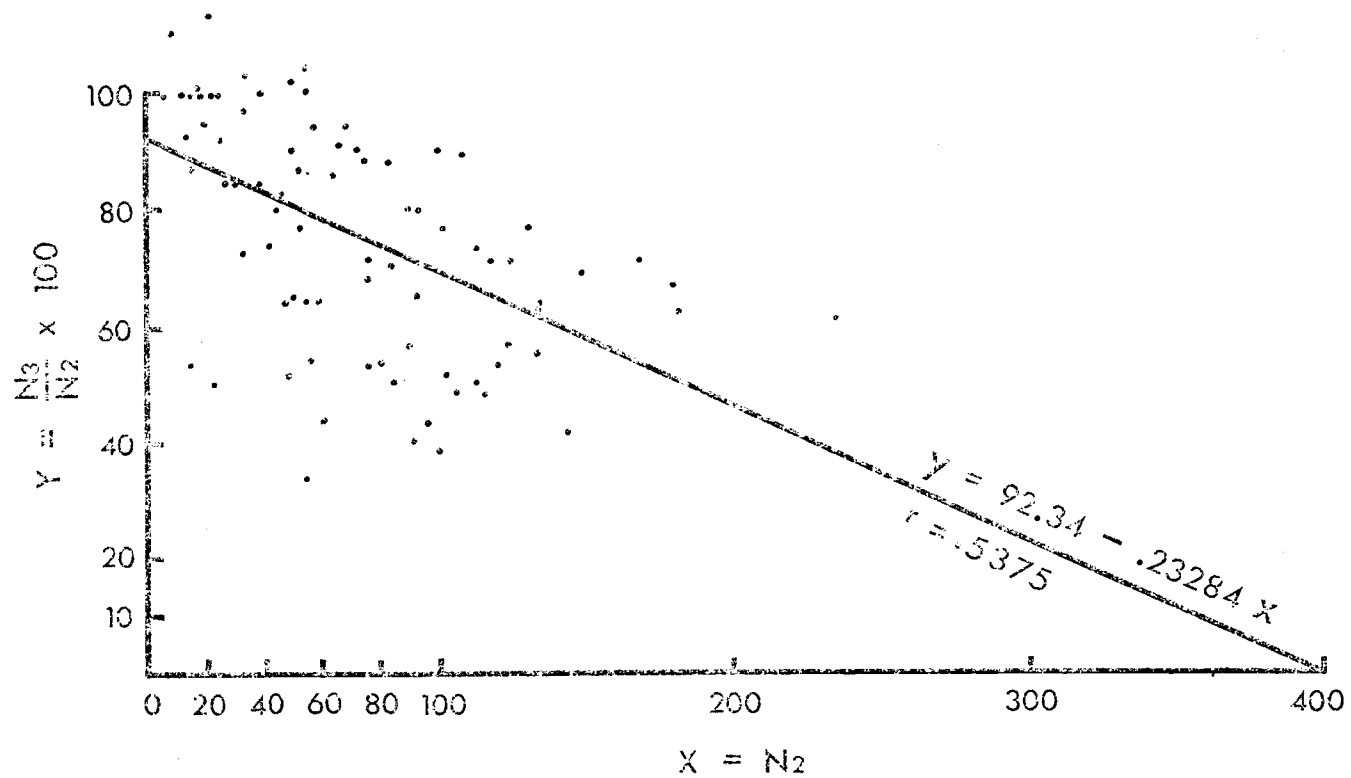
Figure 16. Relationship between survival of second instar larvae
(affected only by competition) and density of second
instar larvae
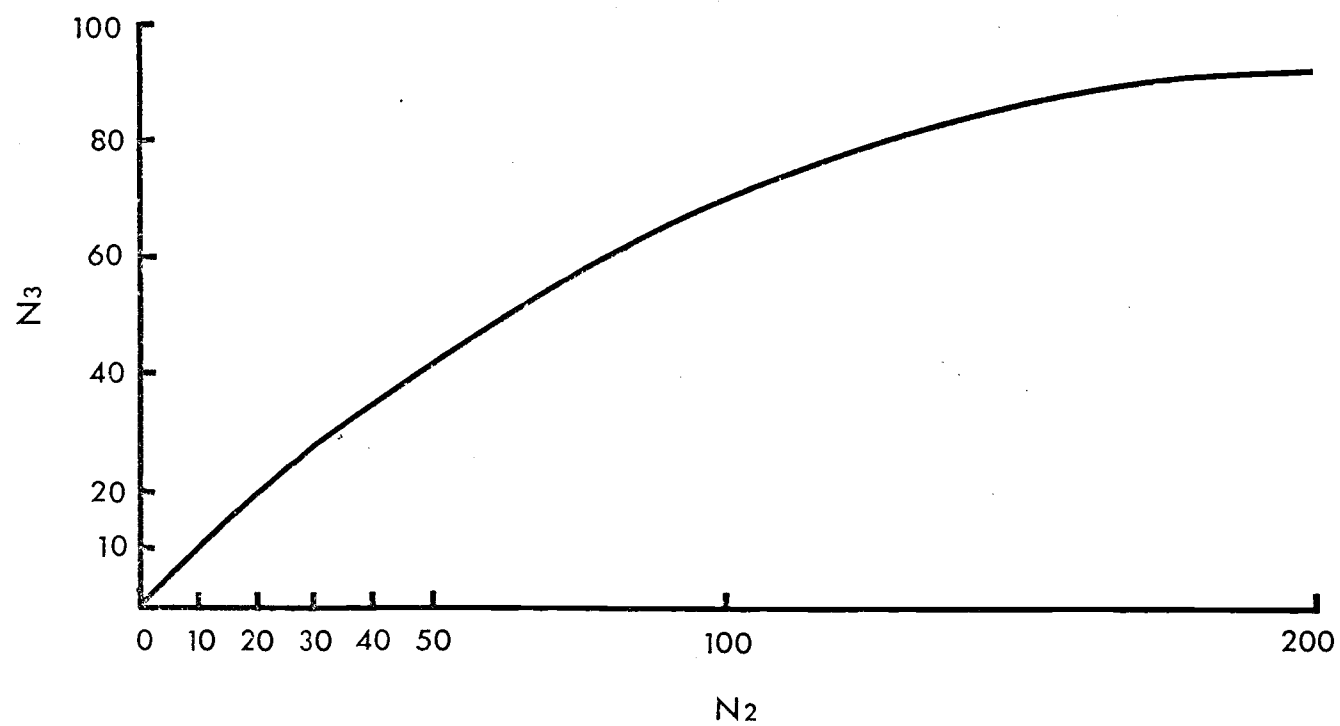
Figure 17. Competition curve showing relationship between second and third instar larvae
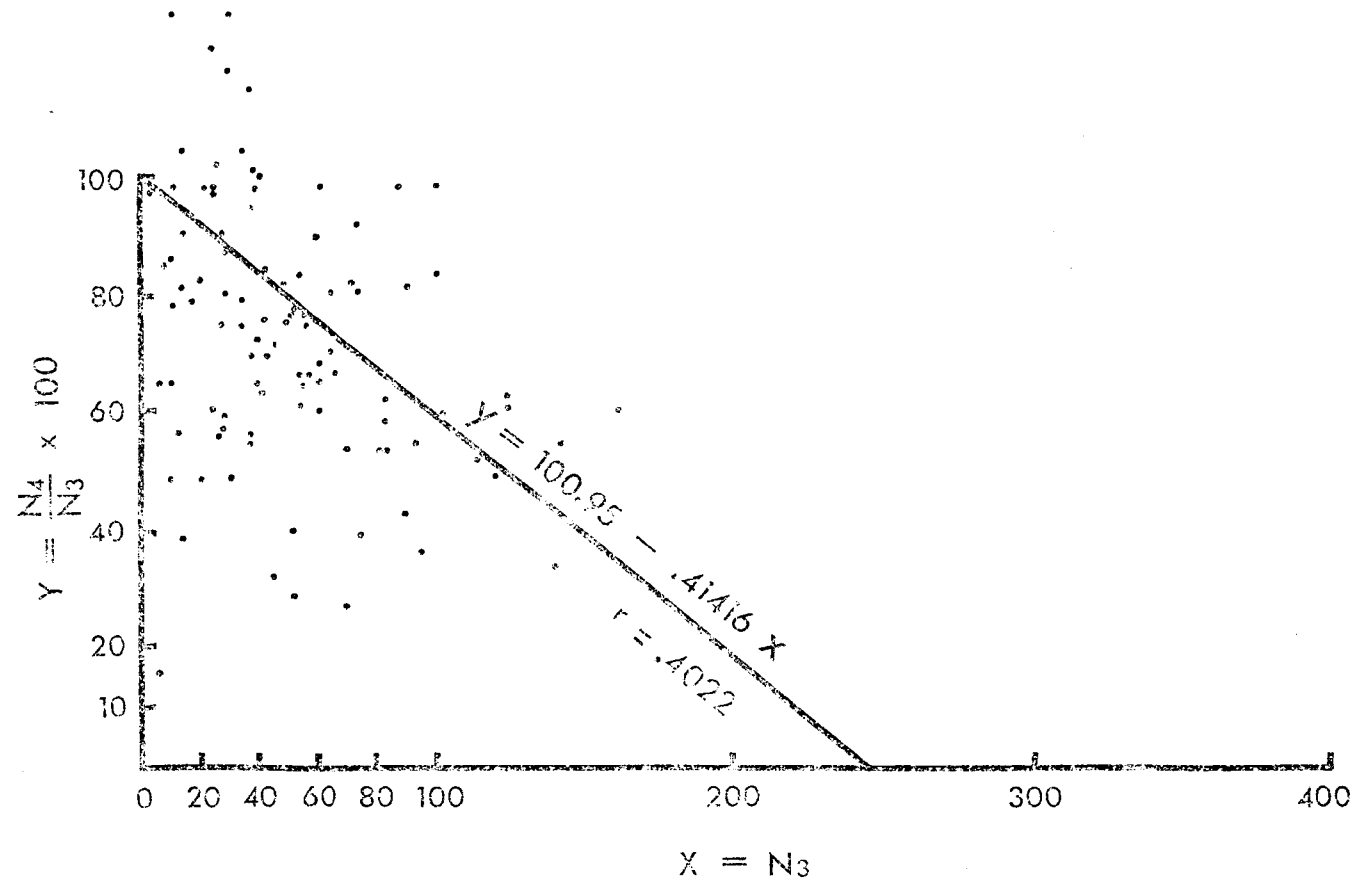
Figure 18. Relationship between survival of third instar larvae
(affected only by competition) and density of third
instar larvae
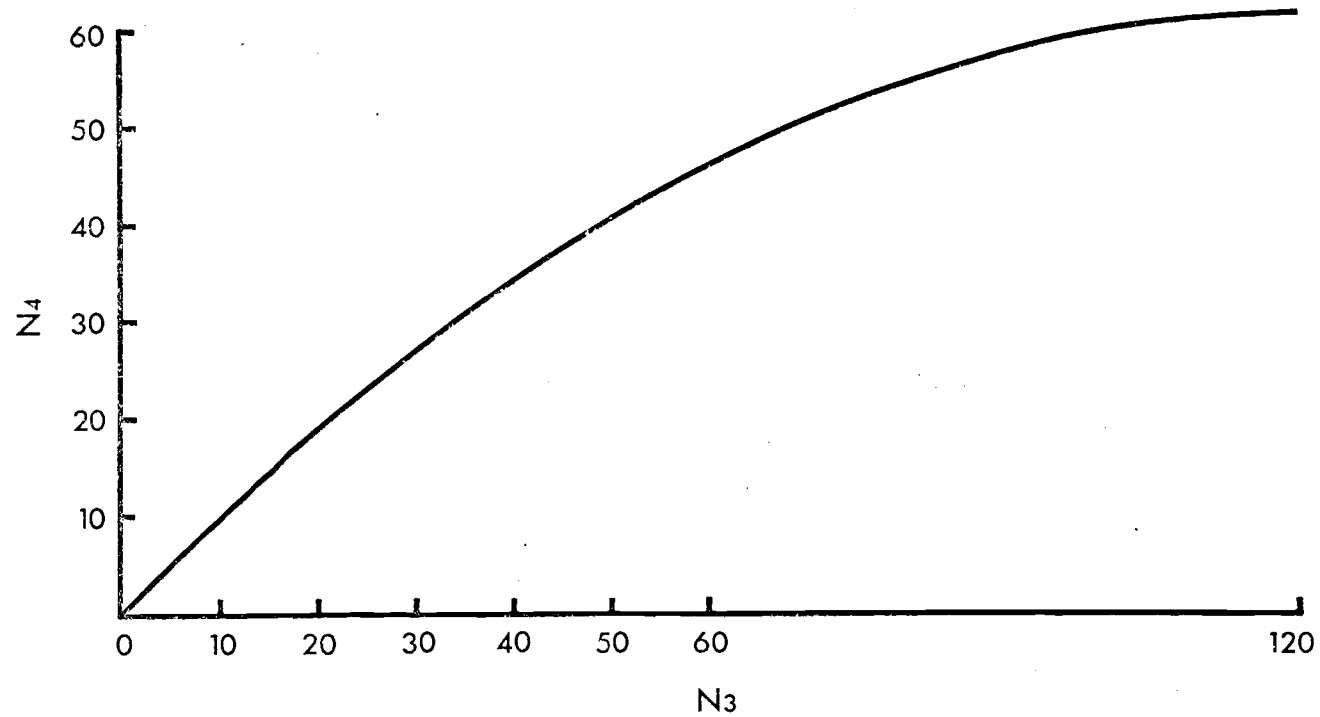
Figure 19. Competition curve showing relationship between
third and fourth instar larvae
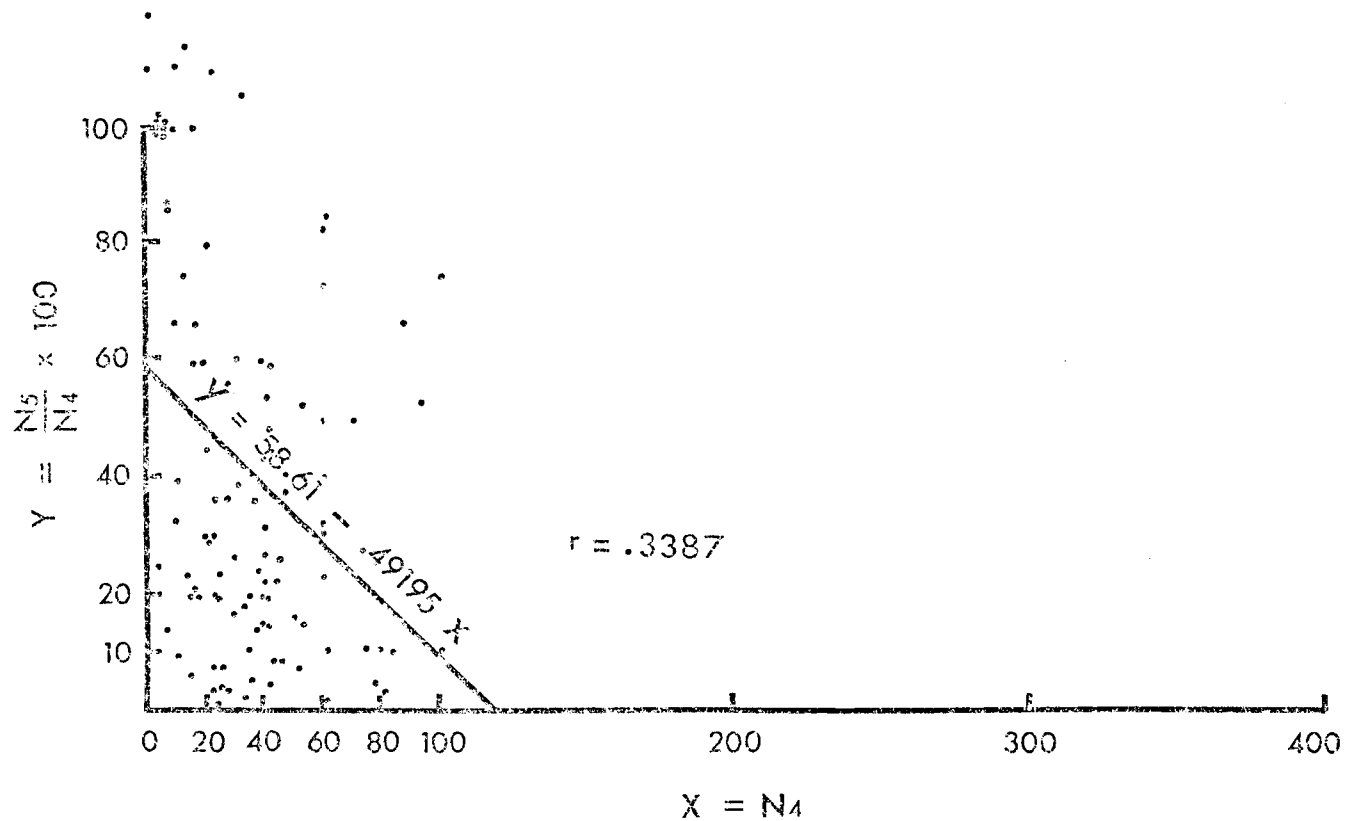
Figure 20. Relationship between survival of fourth instar larvae (affected only by competition) and density of fourth instar larvae
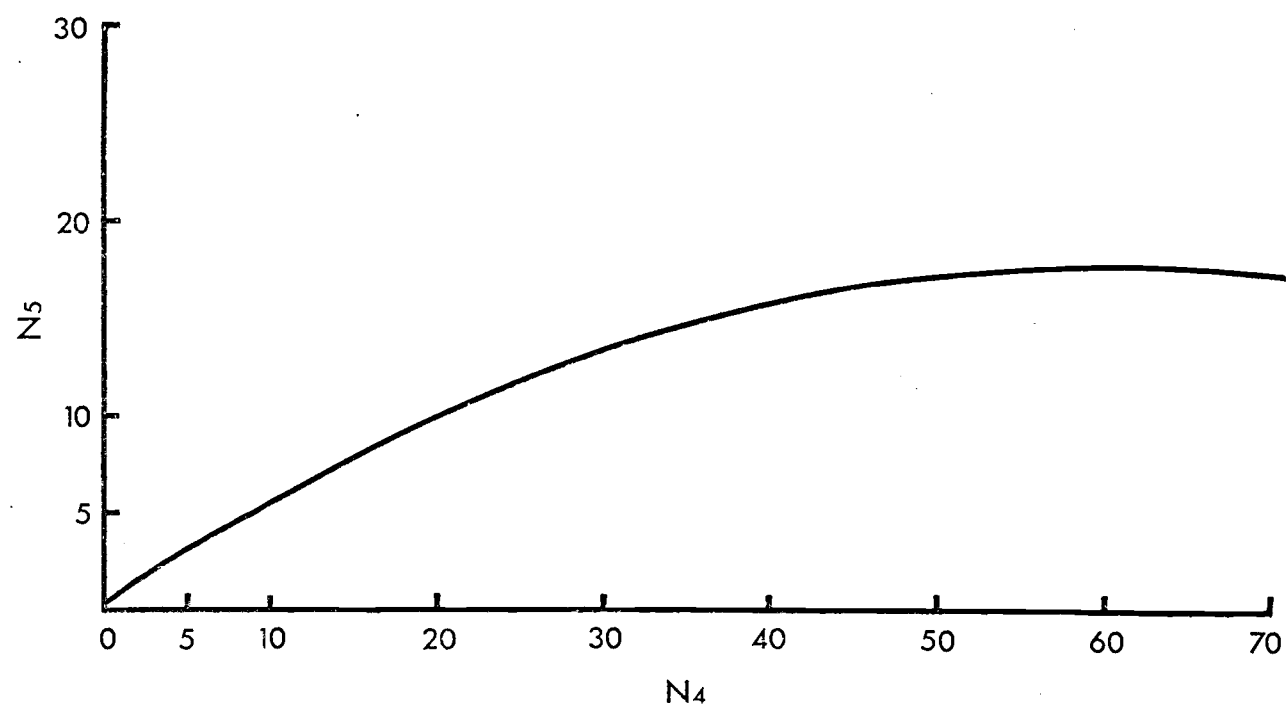
Figure 21. Competition curve showing relationship between fourth instar larvae and callow adults
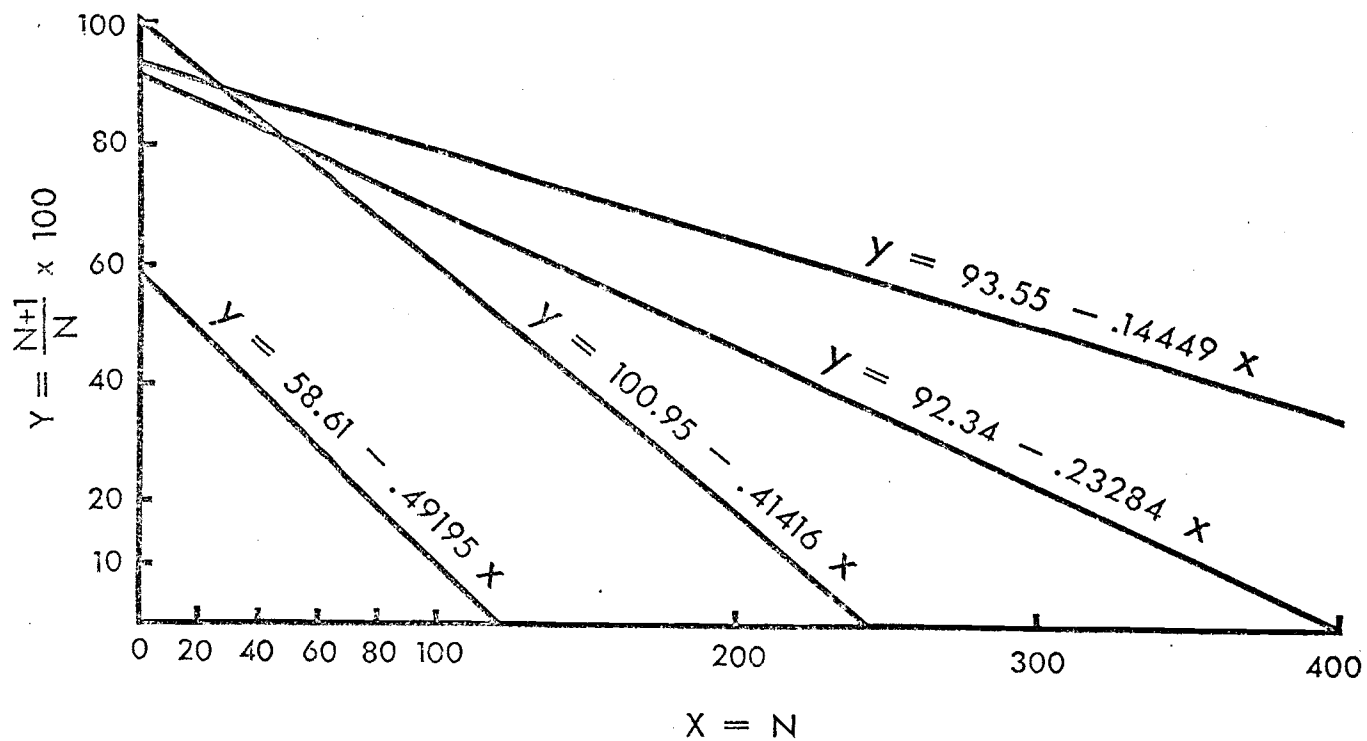
Figure 22.   Figures 14, 16, 18 and 20 combined
to show relationship between N and
survival of N for each instar
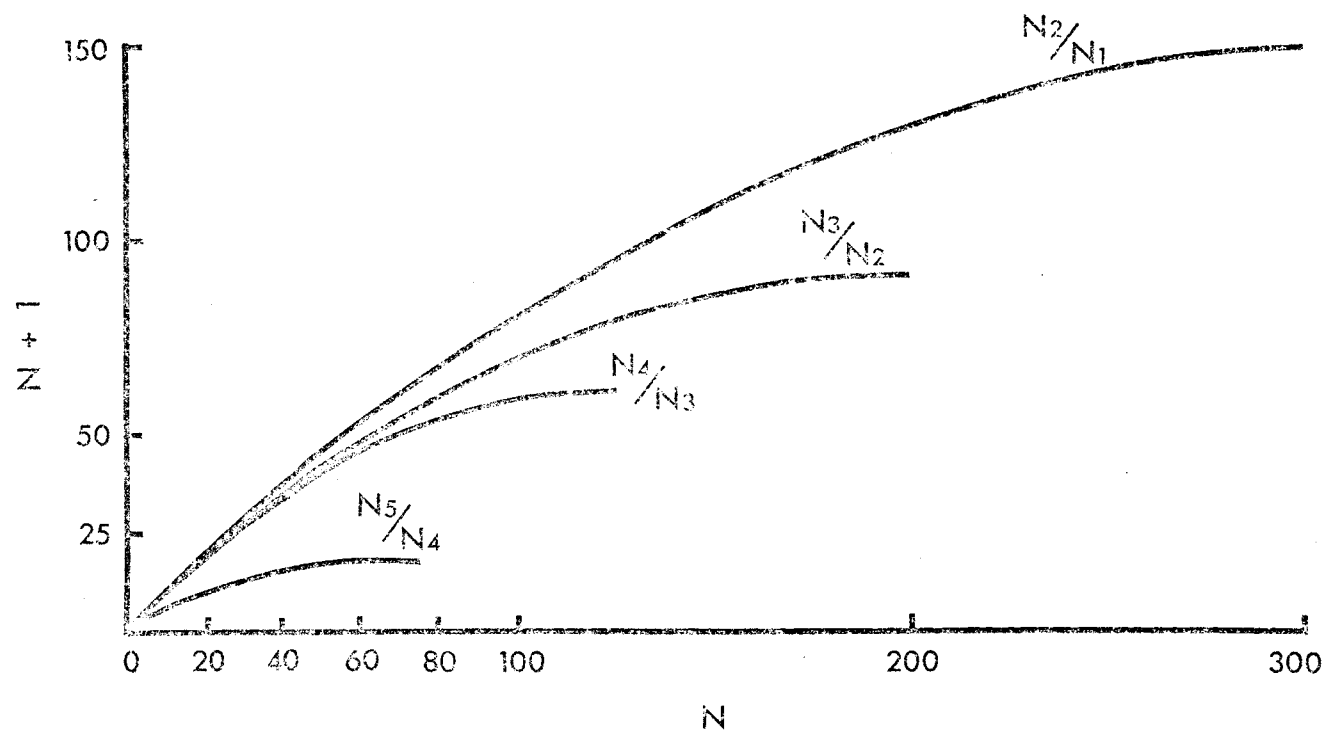
Figure 23. Figures 15, 17, 19 and 21 combined on same scale
to show relationship between N and N + 1 for
each instar

where N_{2-c} = number of larvae surviving to second instar after

competition

S_{1-c} = survival rate of first instar larvae in the presence of

competition

N_1 = number of living first instar larvae

Since S_{1-c} = a + b N_1, then N_{2-c} = N_1 (a+b N_1).

Data from study tree 66-1 illustrates this procedure:

Where N_1 = number of first instars per square foot = 140.83

N_2 = number of second instars per square foot = 77.62

The number of second instars living after competition has taken effect

is:

N_{2-c} = N_1 (a+b N_1) where N_{2-c} is unknown,

N_1 = 140.83, a = .9355 and b = .0014449,

N_{2-c} = 140.83 (.9355-[.0014449] [140.83]) = 103.09

therefore, N_{2-c} - N_1 = 140.83 - 103.09 = 37.74 first instar larvae

dead as a result of competition. The same result can be obtained

directly from Figure 15 since it is merely a pictorial representation

of the mathematics illustrated above. These calculations are performed

for each larval instar for each tree sampled in the life table studies.

The amount of mortality occurring in each instar due to competition is

listed in the life tables in Appendices III and IV.

Of immediate importance is the fact that the effects of

competition are related to density and the relationship is predictable.

The results described here are similar to those reported by McMullen

and Atkins (1961) and Schmitz and Rudinsky (1968) for the Douglas-fir
beetle.

These procedures, as described, allow us to separate mortality
due to competition from mortality due to other factors in the larval
instars. However, it must be realized that many factors are operating
simultaneously and it is not completely realistic, in the example used
to illustrate the procedure, to say that 37.74 first instar larvae died
as a result of competition. The figure of 37.74 first instar larvae
represents a potential number that would die in the absence of other
factors. This competition mortality is subtracted from the total
mortality during that stage and the difference is credited to other
factors, primarily predation. It would probably be as equally
realistic to attack the problem from another direction such as deter-
mining the potential amount of mortality due to predation and crediting
the remainder to other factors such as competition. If potential
mortalities are determined for each mortality factor during a given
stage or age interval, then we would undoubtedly, in most cases,
account for more than the actual total mortality that did occur in that
stage. This is not realistic and in addition, introduces bookkeeping
problems with the life tables which would be difficult to overcome.
Therefore, for the purpose of analyzing the life tables, the potential
mortalities for competition were used although other factors such as
predation, may be shortchanged by such a procedure. When we consider
only two factors such as competition and predation, as they operate

simultaneously, it is interesting to consider how one might affect the other and the significance of the interaction on brood survival.

VII.   LIFE TABLES

One of the major objectives of this study was to construct a

series of life tables for four consecutive generations of the Douglas-

fir beetle.   Allee et al. (1949) describe the life table as

> "a device that records in systematic fashion those
> facts basic to the age distribution of mortality.
> In short, a life table 'keeps the books on death'."

Life tables are not an end in themselves, but should serve as

a tool in the analysis and interpretation of the dynamics of natural

populations.   However, in order that life tables be best utilized to

their fullest extent, it is necessary that the population estimates for

the various stages of the insect be relatively accurate.   Thus the need

for reliable sampling techniques is amply justified (Chapter IV).

Another major requisite in the building of life tables is the knowledge

that allows the development of methods that enable the investigator to

recognize and measure the amount of mortality due to the various factors

that influence populations (Chapter III).

According to Allee et al. (1949), Morris and Miller (1954), and

Harcourt (1969), the first general use made of life tables was to

study human populations for life insurance purposes.   Many examples

for populations of man occur in the literature, representing many

countries, other political units and under many socio-economic condi-

tions.   The first non-human uses of life tables were for insects,

specifically the fruit fly, Drosophila melanogaster and the flour

beetle, Tribolium confusum.   However, the life tables prepared for

populations of these species of insects were representative of labora-
tory conditions.

Deevey (1947) was the first worker to apply the life table
method to the study of natural populations, although as Morris and
Miller (1954) point out,

> "Leopold (1939) was one of the first to appreciate
> the possibilities of the life table in the field
> of practical ecology."

Morris and Miller (1954), in turn, were the first to use the method for
natural populations of an insect, specifically, the spruce budworm
Choristoneura fumiferana (Clem.). Since this time, studies incorpora-
ting life tables have been undertaken for some 20 forest and agriculture
pests, with the majority of the studies being done by Canadian workers.
Included in this number are the spruce budworm (Morris and Miller 1954,
Morris 1963), lodgepole needle miner (Stark 1958, 1959), larch sawfly
(Ives 1964), Black Hills beetle (Knight 1959), pine looper (Klomp 1966),
winter moth (Embree 1965, Varley and Gradwell 1958), gypsy moth
(Campbell 1967), Scolytus scolytus (Beaver 1966), birch leaf miner
(Cheng and LeRoux 1966b), aspen blotch miner (Martin 1956), a number of
orchard insects (LeRoux and Reimer 1959, LeRoux et al. 1963, Paradis and
LeRoux 1965) and three agricultural pests (Harcourt 1963, 1964 and 1966).

Harcourt (1969) reviews the development and use of life tables
in the study of natural insect populations. In this only comprehensive
and up-to-date review of life tables he states that

> "Ecological life tables are one of the tools
> most useful in the study of insect population
> dynamics."

Methods

Life tables can be developed from one of several sources of
data (Deevey 1947):

1. cases where the age at death is directly observed for
    a large and reasonably random sample of the population

2. cases where the survival of a large cohort (born more
    or less simultaneously) is followed at fairly close
    intervals thoughout its existence

3. cases where the age structure is obtained from a
    sample, assumed to be a random sample of the
    population.

The second method is the one that is generally used or more frequently,
a modification of the second method in that survival is estimated, not
by observing the same individuals throughout but rather by comparing
population numbers in periodic samples from different but comparable
segments of the same population. This method also assumes that only
one stage of the life cycle is present at each sampling time.

The following column headings used in developing life tables
for the Douglas-fir beetle were originally proposed by Morris and
Miller (1954), and Morris (1963) and were further described by Har-
court (1969).

x - age interval at which the sample was taken

lx - the number living at the beginning of the stage

noted in the x column (= Nx which is used elsewhere

in analyses)

dx - the number dying within the age interval stated in

the x column

dxF - the mortality factor responsible for dx

100 qx - percentage mortality

Sx - survival rate within x

Thirty-eight life tables each representing one blowdown tree were obtained over the four-year period of the study. Table 15 is an example of a life table representing the survival of a beetle population in one blowdown log. All population numbers in the 1x column represent numbers alive at the beginning of the age interval in terms of numbers per square foot of bark surface.

The numbers alive at the beginning of each age interval were estimated directly and are independent of each other, although each population estimate is subject to sampling error. The dx value is obtained by subtracting the 1x value for an age interval from the previous 1x value. Values of dx for mortalty factors within each larval age interval were obtained by first estimating mortality due to competition (Chapter VI). This competition mortality value was then subtracted from the dx value for the age interval to provide an estimate of mortality due to predation and other factors within each larval stage. Thus mortality due to predation was not estimated directly. The remaining 37 life tables, each of which represents the course of survival of a Douglas-fir beetle population in a blowdown Douglas-fir tree, are contained in Appendix III. Only 18 of the 38 life tables are

Table 15. Life table for the Douglas-fir beetle for study tree 66-1 on the Marys Peak watershed, Oregon.

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	201.89	Infertility, mites, pitched out, other				
			TOTAL	61.06	30.2	.70
Larvae 1st instar	140.83	Competition		37.74	26.8	
		Predators, other		25.47	18.1	
			TOTAL	63.21	44.9	.55
2nd instar	77.62	Competition		19.97	25.7	
		Predators, other		5.32	6.9	
			TOTAL	25.29	32.6	.67
3rd instar	52.33	Competition		10.85	20.7	
		Predators, other		16.23	31.0	
			TOTAL	27.08	51.7	.48
4th instar	25.25	Competition		13.59	58.3	
		Predators, other		4.44	17.6	
			TOTAL	18.03	71.4	.29

Table 15. (Concluded)

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Callow adults Fall	7.22	Overwintering mortality, other TOTAL	<u>4.55</u>	63.1	.37
Spring	2.67	Predators, moisture other TOTAL	<u>2.37</u>	88.9	.11
Emerged Adults	.30		0		
Females x 2	.30	Sex TOTAL	0 0		
Generation TOTALS			201.59	99.85	S_G = .0015

* Number per one square foot of bark surface

complete in terms of having obtained population numbers up to and
including emerging adults. Many of these life tables are incomplete
because the blowdown trees which were being sampled were salvaged at
some time prior to adult emergence or were otherwise not available for
sampling due to inclement weather rendering roads impassable.

Four life tables representing the 1963, 1964, 1965 and 1966
generations of the Douglas-fir beetle on the Marys Peak watershed were
formed by combining mean values from all blowdown logs sampled in any
given generation. These generation life tables are contained in
Appendix IV and are identical to the life tables for each individual
tree except that they consist of mean values for all trees sampled in
each generation.

The method of studying each age interval is as follows:

Eggs

The eggs are counted directly in the field following attack
by adult beetles normally in May (Chapter IV discusses the methods
employed). Thus lx is a direct estimate of the egg population follow-
ing gallery construction and oviposition. The dx value is the propor-
tion of eggs that fail to hatch, are destroyed by mites or other
predators, are pitched out or for other reasons fail to successfully
become established as first instar larvae.

Larvae

First, second, third and fourth instars - lx values for each
larval instar are obtained by two methods. Both methods involve direct
counting of the larval galleries that are present on the bark samples.

Sampling periods in June, July and August provided estimates of live

Douglas-fir beetle brood numbers of larval galleries and numbers of

predators and/or parasites. Larval gallery counts were also obtained

from samples taken later in the generation primarily to estimate

abundance of other stages, i.e. live callow adults in the fall and

in the spring and live callow adults that had successfully overwintered.

The dx values for competition in each instar were obtained as the

result of a series of experiments which are discussed in Chapter VI.

The dx values for predators and other mortality in each instar were

obtained simply by subtracting the dx value for competition from the

total mortality occurring in that age interval.

Callow adults - fall

The lx value was obtained directly by counting the number of

live callow adults that had survived up to October or November.

Sampling this stage was a considerable problem because the callows

burrow into the phloem and each bark sample had to be excavated in

order to obtain accurate counts. Larval galleries, which leave a

permanent record inscribed on the inner bark surface, were also

counted at this time. It was impossible to sample pupal populations

since Douglas-fir beetle pupae pass through this stage in a relatively

short period of time. Thus no lx values for pupae were obtained and

the tables go directly from fourth instar larvae to live callows in the

fall.

Callow adults - spring

This lx value was obtained directly by sampling the blowdown

logs in March, approximately one to two months prior to emergence.

The number of callow adults which successfully overwintered were

counted as were larval galleries on samples that had not deteriorated

to the point where the gallery patterns could not be accurately

distinguished.

Emerged adults

Using methods described in Chapter IV, the numbers of emerging

adults were determined for each of the blowdown trees. Sex ratio is

obtained by determining the sex of the emerged beetles. When this

sex ratio is in favour of males, it is treated as a mortality factor;

when in favour of females, it has the effect of increasing the popula-

tion.

Females

This lx value is the percentage of females applied to lx for

emerging adults and the result is doubled to maintain balance in the

life table. The sex ratio was found to be 1:1 (i.e. 50% females and

50% males). Thus for all the life tables, the lx value for females x2

is the same as the lx value for emerging adults.

The life tables for the Douglas-fir beetle were terminated at

this point and the generation survival (S_G) was determined. This

provides an index of population trend without the effects of fecundity

and adult mortality. Where possible (examples are Morris [1963] and

Harcourt [1969]) additional divisions, such as "normal" females which

are the hypothetical number of females capable of laying a full

complement of eggs and "actual" females that produce the actual egg

population that starts the next generation are included. Generation

survival based on these data would include the effects of fecundity,

adult dispersal and adult mortality. However, for the Douglas-fir

beetle it was impossible to measure beetle densities between the time

of emergence and attack, or the mortality factors that affect the

adults such as failure to mate, female mortality before oviposition

or female mortality after a portion of the eggs had been laid. Nor

was it possible to separate this mortality from the effects of

dispersal or where emigration and immigration may both have occurred

in the same season. Consequently, generation survival has been

calculated without the adult mortality $\pm$ dispersal effects, and

(unfortunately) does not provide a complete picture of population

change through the life cycle.

VIII. ANALYSIS OF LIFE TABLES

The analyses of the Douglas-fir beetle life tables were carried

out using methods described by Varley and Gradwell (1960 and 1970),

Southwood (1966) and Harcourt (1969). In the earlier paper, Varley

and Gradwell (1960) provided a simple alternative method to that pro-

posed by Morris (1959) for identifying the stages at which a key

factor is operating. Morris (1959) stated that factors affecting the

spruce budworm in any one place are of two types – those that cause a

relatively constant mortality from year to year and contribute little

to population variation, and those that cause a variable, though

perhaps much smaller, mortality and appear to be largely responsible

for the observed changes in population. A factor of the latter type

is considered to be a "key factor" which, according to Morris, means

that changes in population density from generation to generation are

closely related to the degree of mortality caused by this factor, which

therefore has predictive value. Morris presented an analysis designed

to determine whether or not mortality at one stage is, at least in part,

caused by a key factor.

Varley and Gradwell (1960) described a simpler, alternative

method of identifying the stage at which a key factor is operating.

This method is a modification of Haldane's logarithmic method for

comparing the different killing powers of a series of successive

mortality factors acting on a population. Haldane's equation for total

mortality $K = k_1 + k_2 + k_3 \ldots + k_i$ where the k-value for each

mortality is the difference between logarithms of numbers per unit

area before and after its action. Haldane used Naperian logarithms

but Varley and Gradwell preferred to use common logarithms.

Varley and Gradwell's method is to calculate the k-values for

each estimated mortality over a number of years and plot them against

time. The contribution of each mortality to the variation of K can be

seen by inspection, or can be studied statistically. Mortality caused

wholly or in part by a key factor is recognized since its k-values will

change with time in the same way as the changes in total mortality.

Southwood (1966) states that the methods developed by Varley

and Gradwell are easier to use than Morris' key-factor analysis.

Varley and Gradwell's method differs from Morris' in that the whole

generation is considered and thus it is immediately apparent in which

age interval the density-dependent and key factors lie, rather than

having to select factors from biological knowledge and correlate each

in turn with the generation mortality.

Luck (1971) compared the two aforementioned methods of

analyzing insect life tables, i.e. Morris' key-factor analysis and

Varley and Gradwell's method. He found that Morris' key-factor

analysis can detect variation in mortality between generations but it

cannot distinguish the density relationship of that mortality. In

contrast, he found that Varley and Gradwell's method apparently can

detect and identify the various types of density-related mortality when

their modified method, the 'proof of density dependence test' is used

in conjunction with the linear regression of k-value against the density on which it acts. Consequently, Morris' key-factor analysis is not recommended by Luck (1971) for use in life table analyses.

Methods

Southwood (1966) describes Varley and Gradwell's method in considerable detail. It is outlined as follows with modifications appropriate to this study:

1. The lx values in the life tables are converted to common logarithms (Table 16).

2. The total generation "mortality" is given by subtracting the log of the population of emerging adults from the log of the number of eggs - this value is referred to as K (Table 16).

3. The series of age-specific mortalities are calculated by subtracting each log population from the previous one (Table 16); these are referred to as k's, so that:

$$K = k_0 + k_1 + k_2 + \ldots\ldots k_i$$

These series of k's - one series for each generation - provide a complete picture of population changes. In the subsequent steps of this analysis the role of each k factor is examined separately, but it must be remembered sampling errors are "hidden" in each k and may be responsible for spurious results.

Table 16. Life table for tree 66-1 prepared for Varley and Gradwell's analysis.

	Nos. per 100 ft.^{2}	Log nos. per 100 ft.^{2}	k's
Eggs – N_0	20189	4.30512	.15643
k_0 (egg mortality)			
Larvae			
1st instars – N_1	14083	4.14869	
k_{1-c} mortality due to competition			.13545
N_{1-c}	10309	4.01324	
k_{1-p} mortality due to predation			.12327
N_{1-p} k_1 total 1st instar mortality			.25872
2nd instars – N_2	7762	3.88997	
k_{2-c}			.12917
N_{2-c}	5765	3.76080	
k_{2-p}			.04205
N_{2-p}	5233	3.71875	
k_2			.17122
3rd instars – N_3	5233	3.71875	
k_{3-c}			.10091
N_{3-c}	4148	3.61784	
k_{3-p}			.21558
N_{3-p}	2525	3.40226	
k_3			.31649

Table 16. (Concluded)

			Nos. per 100 ft.^{2}	Log nos. per 100 ft.^{2}	k's
4th instars - N_4			2525	3.40226	
	k_{4-c}				.33556
	N_{4-c}		1166	3.06670	
	k_{4-p}				.20816
	N_{4-p}		722	2.85854	
	k_4				.54372
Fall callows - N_5			722	2.85854	
	k_5	overwintering mortality			.43203
Spring callows - N_6			267	2.42651	
	k_6				.94939
Emerging adults - N_7			30	1.47712	

$$K = 2.82800$$

4. The next step involves the recognition of the key factor for the index of population trend from adult to adult. This is done by visual correlation, K and k_0 to k_i are plotted against generation and it may easily be seen which k is most closely correlated with K. Alternatively, the correlation coefficients may be calculated.

5. The various k's are then tested for direct density dependence. Firstly, each k is plotted against the numbers entering the stage (age interval) on which it acts; if the regression is significant then density dependence may be suspected. However, the two variables are not independent (they are actually $\log N_x$ and $\log N_x - \log N_{x+1}$) and so the regression could be spurious, due to sampling errors. The second step, therefore, is to plot the log numbers entering the stage ($\log N_x$) against the log numbers of survivors ($\log N_{x+1}$). The regressions of $\log N_{x+1}$ on $\log N_x$ and of $\log N_x$ on $\log N_{x+1}$ should be calculated, and if both regression coefficients depart significantly from 1.0, then the density dependence may be taken as real.

6. If density dependence is shown to be real, attention may now be refocussed on the plot of k's against the numbers entering the stage. The slope of the line, the regression coefficient, should be determined as this will give a measure of how the factor will act; the closer the regression coefficient is to 1.0, the greater the stabilizing

effect of that regulatory factor. If the coefficient is exactly 1.0 the factor will compensate completely for any changes in density; if the coefficient is less than 1.0 the factor will be unable to compensate completely for the changes in density caused by other disturbing factors; whilst a coefficient of more than 1.0 implies overcompensation.

7. Further insight into the mode of action of population factors may be obtained by plotting the k value against log initial density and then joining the points up in a time sequence plot. The different types of factor will trace different patterns: direct density-dependent factors will trace a more or less straight line or narrow band of points, delayed density factors circles or spirals; density-independent factors irregular or zigzag plots, whose amplitude reflects the extent to which they fluctuate.

Results

The data upon which Varley and Gradwell's analysis was performed are in Appendices III and IV, i.e. the individual tree and the generation life table data. These data can be summarized and presented in the form of the general equation, as follows:

$$K = k_0 + k_1 + k_2 + \ldots\ldots k_i$$

where K = total generation mortality and is obtained by subtracting the log of the population of emerging adults (log N_7) from the log of the number of eggs (log N_0); and

k_0 = egg mortality = log N_0 - log N_1

k_1 = first instar mortality = log N_1 - log N_2

k_2 = second instar mortality = log N_2 - log N_3

k_3 = third instar mortality = log N_3 - log N_4

k_4 = fourth instar, pupal and early fall callow mortality =

log N_4 - log N_5

k_5 = overwintering mortality = log N_5 - log N_6

k_6 = spring callow mortality = log N_6 - log N_7,

The mortality during larval instar age intervals was further subdivided as follows:

$k_1 = k_{1-comp.} + k_{1-pred.}$ where

k_1 = first instar mortality,

$k_{1-comp.}$ = mortality during first instar due to competition

$k_{1-pred.}$ = mortality during first instar due to predation.

Similarly,

$k_2 = k_{2-comp.} + k_{2-pred.}$

$k_3 = k_{3-comp.} + k_{3-pred.}$

$k_4 = k_{4-comp.} + k_{4-pred.}$

Thus, two equations can be written, one establishing a relationship between total generation mortality and the various mortalities occurring in each age interval,

$$K = k_0 + k_1 + k_2 + k_3 + k_4 + k_5 + k_6$$

and another equation between total generation mortality and the various

mortalities due to various factors in each of the larval age intervals,

$$K = k_0 + k_{1-c} + k_{1-p} + k_{2-c} + k_{2-p} + k_{3-c} + k_{3-p} + k_{4-c} + k_{4-p}$$
$$+ k_5 + k_6.$$

In order to recognize the key factor, each of the k values (k_0 to k_6)

are correlated with K. This correlation can be done visually as in

Figure 24 or the correlation coefficients can be calculated as in

Table 17.

The highest correlation in the age interval series occurs in

the first instar although all the larval stages are high. Competition

correlations are highest in the first and second instars, in fact,

higher than the corresponding age interval correlation. The highest

correlation for predators (and other) mortality occurs in the fourth

instar.

The next step is to test the various k's for direct density

dependence. This is done by plotting each k against the numbers

entering the stage on which it acts and if the regression is signifi-

cant then density dependence may be suspected.

As shown in Table 18, the only significant r^2 values are

those for the first and third instars for the competition series.

The second instar r^2 in the competition series, although not signifi-

cant, is high as is the r^2 for first instar of the age interval series.

All of the predation and other r^2 are low values.
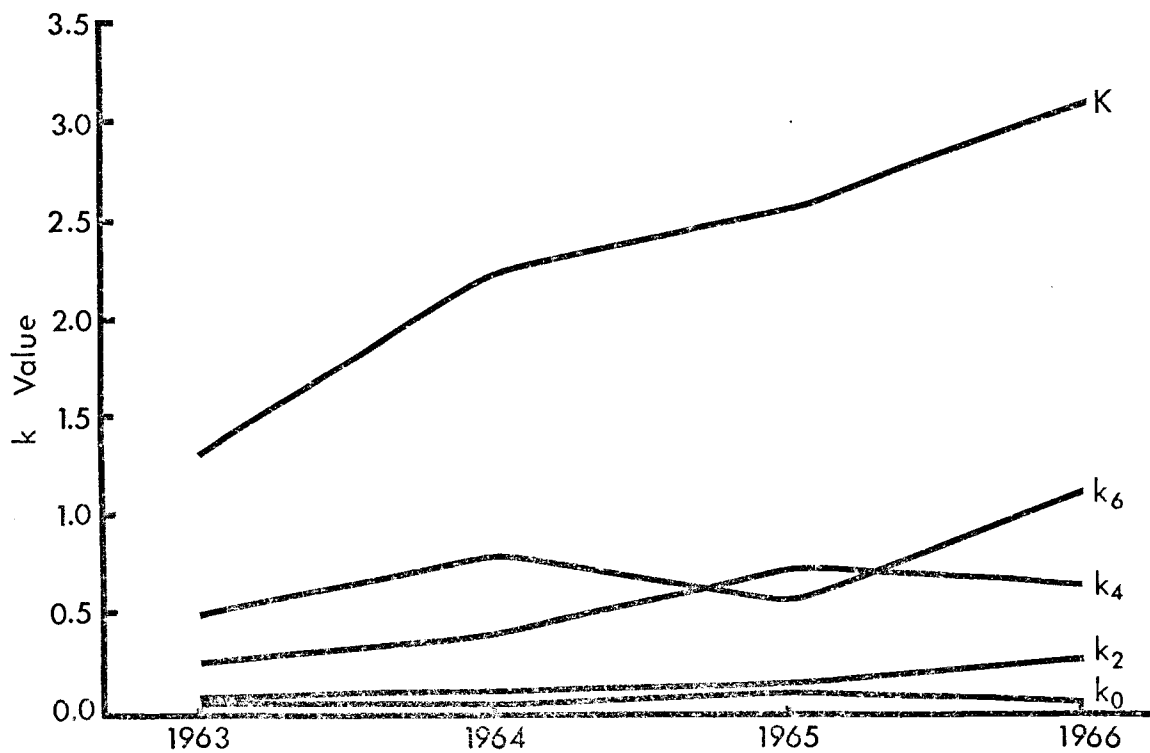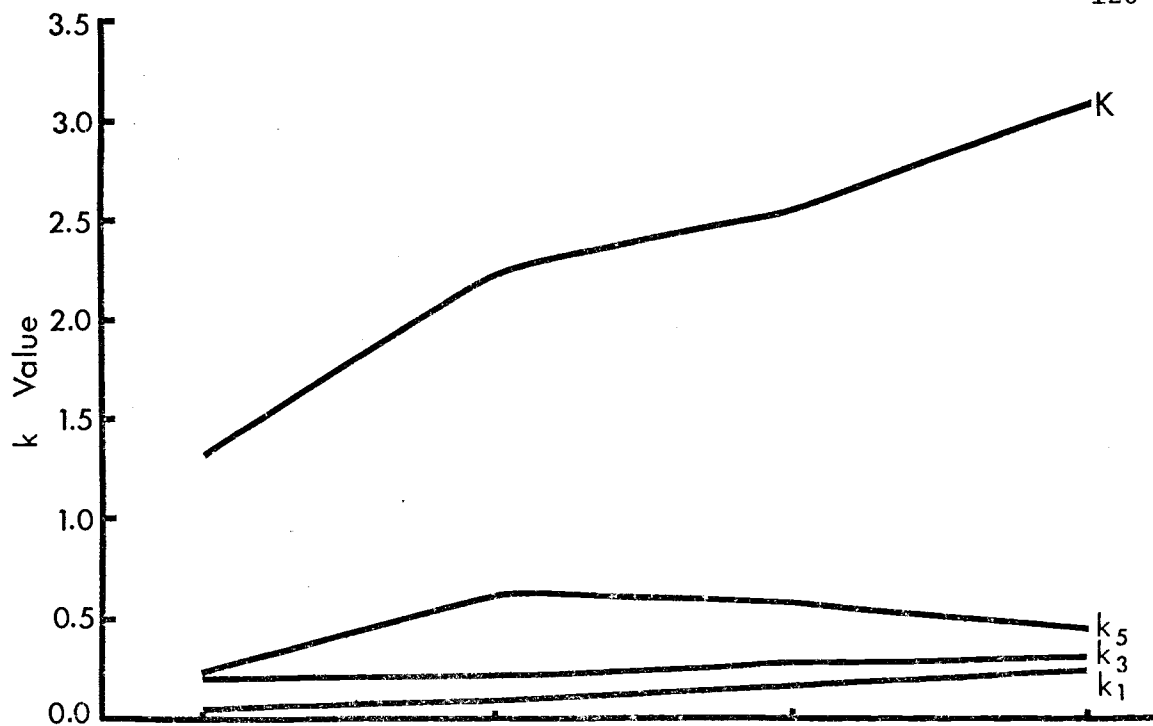
Figure 24. Visual correlation of various k's with K

Table 17. Correlation coefficients (r) of the various k_x values correlated with K for generation life table data.

Age interval	Competition	Predators and others
$r_{Kk_0} = .5585$		
$r_{Kk_1} = .9488*$	$r_{Kk_{1-c}} = .9796*$	$r_{Kk_{1-p}} = .7935$
$r_{Kk_2} = .9150$	$r_{Kk_{2-c}} = .9978**$	$r_{Kk_{2-p}} = .6081$
$r_{Kk_3} = .8840$	$r_{Kk_{5-c}} = .7840$	$r_{Kk_{3-p}} = .2660$
$r_{Kk_4} = .8570$	$r_{Kk_{4-c}} = .8664$	$r_{Kk_{4-p}} = .8389$
$r_{Kk_5} = .6344$		
$r_{Kk_6} = .7661$		

* significant at p = .05
** significant at p = .01

Table 18. r^2 values of the regressions between the various k_x values with the respective N_x values for generation life table data.

Age interval	Competition	Predation and others
$r^2_{k_0 N_0}$ = .4231		
$r^2_{k_1 N_1}$ = .7718	$r^2_{k_{1-c} N_1}$ = .9010*	$r^2_{k_{1-p} N_{1-c}}$ = .3435
$r^2_{k_2 N_2}$ = .4400	$r^2_{k_{2-c} N_2}$ = .8103	$r^2_{k_{2-p} N_{2-c}}$ = .0098
$r^2_{k_3 N_3}$ = .2763	$r^2_{k_{3-c} N_3}$ = .9808**	$r^2_{k_{3-p} N_{3-c}}$ = .1921
$r^2_{k_4 N_4}$ = .2102	$r^2_{k_{4-c} N_4}$ = .4546	$r^2_{k_{4-p} N_{4-c}}$ = 0
$r^2_{k_5 N_5}$ = .0146		
$r^2_{k_6 N_6}$ = .1561		

* significant at $p = .05$
** significant at $p = .01$

The next step is to determine if the density dependence as indicated by any preceding significant regressions is real. This is done by plotting the log numbers entering the stage ($\log N_x$) against the log numbers of survivors ($\log N_{x+1}$). The regressions of $\log N_x$ on $\log N_{x+1}$ and $\log N_{x+1}$ on $\log N_x$ are calculated and if they depart significantly from 1.0 then the density dependence may be taken as real. The only regression coefficients that departed significantly from 1.0 were those involving the third instar for competition, i.e. N_3 on N_{3-c} and N_{3-c} on N_3. The regression coefficient of the relationship of K_{3-c} and N_3 was .234, but if calculated for all competition mortality during the four larval stages, the regression coefficient is .91.

It was decided that this entire preceding analysis, applied to generation population estimates, should be performed on individual tree population estimates. Eighteen of the 40 trees sampled over the four-year time period had complete population data (i.e. N_0, N_1, N_2, N_3, N_4, N_5, N_6 and N_7 estimates). The correlation coefficients for recognition of the key factors are in Table 19.

The highest correlation exists during the second instar of the age interval series but all larval instars are high. The highest correlation in the competition series occurs in the second instar but is not as large as the coefficient for the second instar in the predators and other series.

In testing for direct density dependence the following series

Table 19. Correlation coefficients (r) of the various k_x values correlated with K for individual tree life table data.

Age interval	Competition	Predation and others
$r_{Kk_0} = .2106$		
$r_{Kk_1} = .5852*$	$r_{Kk_{1-c}} = .2856$	$r_{Kk_{1-p}} = .2664$
$r_{Kk_2} = .7384**$	$r_{Kk_{2-c}} = .4981*$	$r_{Kk_{2-p}} = .5387*$
$r_{Kk_3} = .4540$	$r_{Kk_{3-c}} = .0077$	$r_{Kk_{3-p}} = .4882*$
$r_{Kk_4} = .4461$	$r_{Kk_{4-c}} = .2689$	$r_{Kk_{4-p}} = .4058$
$r_{Kk_5} = .0951$		
$r_{Kk_6} = .2320$		

* significant at p = .05

** significant at p = .01

of r^2 values were obtained (Table 20). The only significant regressions were for the egg stage and spring callow adult stage of the age interval series and all the instars of the competition series.

When the regressions of log numbers entering the stage against the log numbers of survivors and _vice versa_ are calculated, $\log N_0$ on $\log N_1$ and $\log N_1$ on $\log N_0$, $\log N_1$ on $\log N_{1-c}$ and $\log N_{1-c}$ on $\log N_1$, $\log N_2$ on $\log N_{2-c}$ and $\log N_{2-c}$ on $\log N_2$, and $\log N_4$ on $\log N_{4-c}$ and $\log N_{4-c}$ on $\log N_4$ are significant indicating that the density dependence is real. The regression coefficient for the relationship for all competition mortality during the larval stages and larval density was .88.

Therefore, summarizing these analyses, the generation life table data indicate that the critical age interval is during the larval stage and that mortality due to competition in the larval stages is the key factor (Table 17). However, mortality due to predation becomes an important factor in the fourth instar. Tests for direct density dependence showed that competition mortality in the first and third instars was significant, thus density dependence is suspected (Table 18). Tests to determine the reality of the density dependence indicated that competition mortality for third instar was truly density dependent. Since the regression coefficient for the relationship between competition mortality for all larval instars and density was .91, the competition mortality factor is almost able to compensate completely for any changes in density.

The individual tree life table data also indicated that the

Table 20. r^2 values of the regressions between the various k_x values with the respective N_x values for individual tree life table data.

Age interval	Competition	Predation and others
$r^2_{k_0 N_0} = .6162**$		
$r^2_{k_1 N_1} = .0624$	$r^2_{k_{1-c} N_1} = .7513**$	$r^2_{k_{1-p} N_1} = .0739$
$r^2_{k_2 N_2} = .0447$	$r^2_{k_{2-c} N_2} = .7205**$	$r^2_{k_{2-p} N_2} = .0930$
$r^2_{k_3 N_3} = .0103$	$r^2_{k_{3-c} N_3} = .8331**$	$r^2_{k_{3-p} N_3} = .1826$
$r^2_{k_4 N_4} = .1186$	$r^2_{k_{4-c} N_4} = .2329*$	$r^2_{k_{4-p} N_4} = .1922$
$r^2_{k_5 N_5} = .0001$		
$r^2_{k_6 N_6} = .5962**$		

* significant at p = .05
** significant at p = .01

critical age interval was during the larval stage and that possible key factors were competition mortality during the second instar and mortality due to predators and other factors in second and third instars (Table 19). Tests for direct density dependence showed that competition mortality in all stages was significant thus density dependence is suspected (Table 20). Tests to determine the reality of the density dependence indicated that competition mortality for first, second and fourth instars was truly density dependent. The regression coefficient for the relationship between larval competition mortality and larval density was .88, very similar to the regression coefficient for generation data.

Another analysis – one similar to Varley and Gradwell's – provided further insight into the mortality processes at work. A simple model that represents the life cycle from the egg stage to emerging adults in terms of survival ratios of each age interval can be derived from the life table data (Harcourt 1969). This model is:

$$S_G = S_0 \ S_1 \ S_2 \ S_3 \ S_4 \ S_5 \ S_6$$

where S_G = generation survival

$$S_0 = \frac{N_1}{N_0} = \text{survival rate of eggs}$$

$$S_1 = \frac{N_2}{N_1} = \text{survival rate of first instar larvae}$$

$$S_2 = \frac{N_3}{N_2} = \text{survival rate of second instar larvae}$$

etc.

and where N_0 = number of eggs per square foot

N_1 = number of first instar larvae per square foot

N_2 = number of second instar larvae per square foot

N_3 = number of third instar larvae per square foot

etc.

Let l_x be the probability of survival to a given stage (this is not the same as the lx column heading in the life tables), then l_0 which is the probability of survival of eggs oviposited must be equal to 1.0, l_1 is the probability of survival of first instar larvae = S_0, l_2 = $S_0 S_1$, l_3 = $S_0 S_1 S_2$ or l_3 = $l_2 S_2$, etc.

The regressions of each of these S values from S_0 to S_6 is calculated separately against S_G (i.e. S_G = Y, the dependent variable and S_0 to S_6 = X, the independent variable) for each year. The larval stages had the highest r^2 values (with the highest values in the first and second instar) and are considered collectively to be the critical age interval. This means that the variance in Y (S_G) is best accounted for by the age interval with the largest r^2.

The next step was to attempt to determine the role of the various mortality factors that are operating during the early larval stages. This was done by calculating a regression of S due to a mortality factor such as competition or predation against S_G. These regressions showed generally that mortality due to competition accounted for most of the variance in S_G, thus competition in the larval stages, particularly during the first, second and third instars

is considered to be the "key factor".

Density-dependence effects of competition mortality were

determined by plotting the S_c rates $\left(S_c = \dfrac{N_{x+1c}}{N_x} \right)$ against the

numbers entering the age interval, i.e. N_x. An example showing S_{1c}

plotted against N_1 is illustrated in Figure 25. The relationship is

curvilinear. It appears that the density-dependent effects of

competition are rather slight up to 110 to 130 first instar larvae

per square foot but from 150 + larvae, competition becomes a very

intense density-dependent factor. The same is true for competition in

the second instar age interval.

One further analysis described in Southwood (1966) was carried

out. The population estimates were converted to logs; P_E = number of

eggs oviposited per square foot, P_R = number of resulting population

per square foot (emerging adults), then, $\log P_E - \log P_R = K$

where K equals total mortality from E to R. P_R is plotted against

P_E and P_R against K and the correlation coefficients are calculated.

r for P_R and P_E = -.904

r for P_R against K = .984

Thus, mortality from eggs to emerging adults is primarily

responsible for the density of the emerging population. With such a

high correlation, it seemed possible to predict emerging population

densities knowing only the original egg density. Consequently, l_7
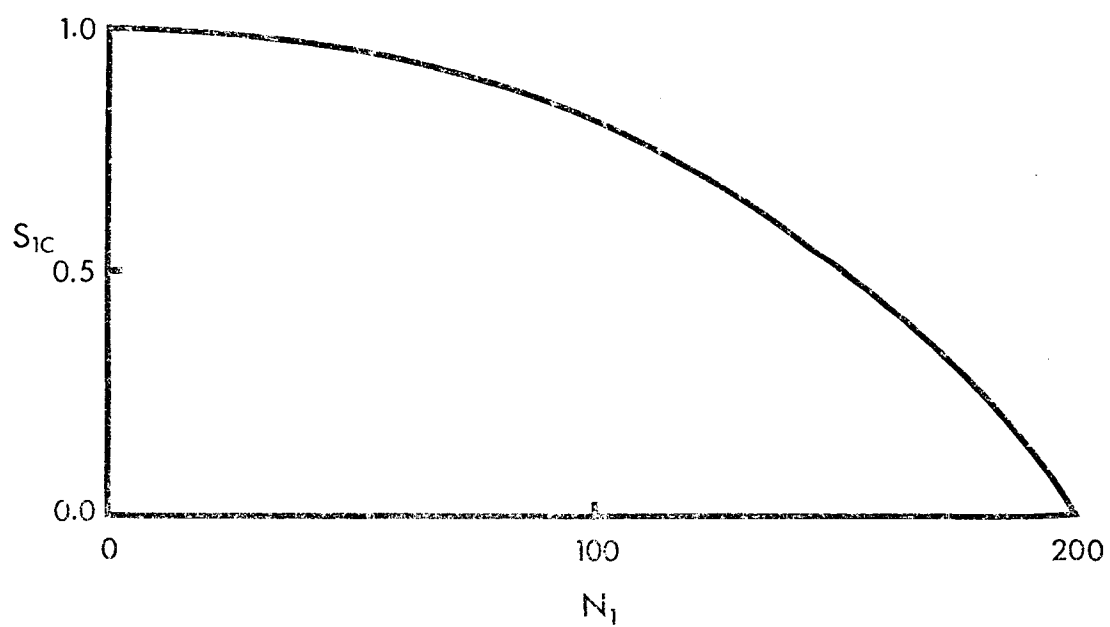
Figure 25. Relationship between competition survival rate and larval density for first instar

values, i.e. probability of survival of emerging adults were

calculated and plotted against egg densities or N_0 values. A linear

regression which was significant, was obtained. Accuracy of the

prediction can be improved if we classify the windthrown trees as

to exposure class, i.e. closed (75 to 100% shaded), open (25 to 75%

shaded) and "clear cut" (completely exposed or 0 to 25% shaded).

Significant linear relationships exist between l_7 and N_0 for both

shaded and open trees, although the slopes of the regressions differ

considerably. No linear relationship exists for completely exposed

trees, usually because no adults are produced.

The equations are:

closed trees $Y = .026837 - .000093\ X$

open trees $Y = .007579 - .000023\ X$

The relationship of l_7 to N_0 can be used to express a direct

estimate of N_7 where $N_7 = N_0\ (a + b\ N_0)$ for closed or open trees.

Graphs were prepared for each sample tree comparing the trend

of predator density (numbers of _Medetera_ _aldrichii_ and

Enoclerus _sphegeus_ per square foot) with the common stage of the host,

Douglas-fir beetle. These graphs showed that there are no predators

(of the above species) present during the host egg stage, that there

are only a few present during the first and second host larval instars,

then the predator densities rapidly increase to a maximum by fourth

instar, pupae and fall callow adults of the host.

Thus, it appears that predators are not present during the

critical early instars of the host in sufficient numbers to be an important mortality factor. However, predation probably becomes a very important factor, possibly the most important one during later stages, particularly fourth instar, pupae and early callows.

Another analysis examined the relationship between host density (expresed in a variety of ways such as parent gallery inches, eggs [N_0] and first instar beetle larvae [N_1] per square foot) and predator density. Predator densities were the maximum number of predators (Medetera + Enoclerus) recorded from the serial samples taken throughout the summer and fall each year. Linear regressions between N_1 and predator density were significant indicating a density-dependent response by the predators, i.e. windthrown trees with high host densities had high predator numbers compared to trees with low host densities and low predator densities. Generally speaking, the density-dependent reaction is considerably more pronounced for Medetera than Enoclerus. This may indicate that Medetera has developed a more efficient method of responding to changes in host density or in finding prey.

IX. DISCUSSION

The major goal of the research described in this dissertation
was to explain why the Douglas-fir beetle is found in one place and
not in another, why they are more numerous in some places than in
others and why there are fluctuations in its numbers. In other words,
this study was designed to explain the population dynamics (i.e. the
distribution and abundance) of the Douglas-fir beetle in windthrown
trees over a four-year period on the Marys Peak watershed in western
Oregon.

Life tables were chosen as the basic method of study in order
to account for specific portions of the total mortality in beetle
populations. In addition, we wished to learn if the intensity of
specific mortality factors varied with population intensity and if so,
how. However, the usefulness of life tables can be limited by poorly
designed population sampling techniques and by failing to recognize
and measure the effects of the various factors that influence popula-
tion density. It is believed that both of these problems were handled
satisfactorily in the course of this study and are described in
Chapters III, IV, V and VI.

There are many theories or ideas of natural control or the self
regulation of animal populations. Most of these theories or ideas can
be grouped into four major conceptual models which are currently being
advocated. The first model states that, (1) density-related processes,
termed "density-dependent", play a key role in the determination of

population numbers by operating as regulating mechanisms. Implicit in

this idea is the concept of self regulation, i.e. mortality factors

become more severe as population density increases. Such mortality

factors are generally biotic such as inter- and intraspecific competi-

tion, parasites and predators, diseases, etc. (2) The second model

states that density-dependent processes play little or no role in

determination of animal abundance, but rather weather or climate is

considered to be the important factor. (3) The third model is a

combination of the first two in that density-related processes regulate

populations within a broader framework of density-independent events.

For example, weather or climate may set the stage upon which density-

dependent factors play their role. (4) The fourth model emphasizes

the influence of the genetic factor in the determination of population

numbers. Advocates of this approach feel that populations are

numerically "self-regulating" through genetically induced changes in

the average vitality of individuals associated with changes in popula-

tion density.

Virtually all of the data obtained in the course of this study

indicates that the larval instars are critical-age intervals in the

life cycle of the Douglas-fir beetle. Most of the mortality during

the larval stage is accounted for by competition. This factor, competi-

tion, is density dependent in its response, increasing in intensity

as the host density increases, particularly in the early instars of the

host. Competition becomes less of a factor in the later larval

instars, pupal and early callow adult stages when predation becomes the major mortality factor. Predation, during this time period, also acts in a density-dependent manner. Of the two major predators (numerically speaking) present throughout this study, Medetera aldrichii was probably responsible for more mortality than Enoclerus sphegeus since Medetera outnumbered Enoclerus about three to one and demonstrated a much stronger density-dependent reaction to host populations.

It seems clearly evident that the population dynamics of the Douglas-fir beetle in windthrown logs are best described by the third conceptual model, i.e. density-related processes regulate populations within a broader framework of density-independent events. Weather is responsible for the amount of blowdown each year and although this is a process completely unrelated to beetle density, it has a most profound influence on the total beetle population. On the other hand, once the beetles have found and attacked fresh hosts, density-related mortality processes then regulate populations within the majority of individual logs. The only exceptions are those windthrown trees that are completely exposed to sunlight and the resulting catastrophic effects of heat cause complete mortality in the exposed portions of the log.

The relationship between the initial population in a log and the resulting emerging population is so strong, because of the density-dependent mortality factors, that numbers of emerging beetles can be

predicted with great accuracy. This relationship could readily be adapted to extensive insect survey methods or to help set priorities for salvage programs. The only data needed would be egg densities per tree, tree exposure, tree size (d.b.h. and length) and an estimate of the total amount of blowdown. Knowing the size of the emerging population and the total amount of windthrown host trees available to the beetle, it should be possible to predict whether or not standing timber will be attacked.

In addition to the contribution towards a greater understanding of the dynamics of Douglas-fir beetle populations in windthrown trees, this latter point concerning predictability of emerging populations is one of the more practical aspects to be gained from this work. Of course, an improved understanding of population dynamics should also lead to predictions of distribution and abundance.

It should be remembered that the life tables used in the analyses are based on incomplete generation survival of Douglas-fir beetle populations in windthrown trees. It was beyond the capabilities of this study to measure adult beetle densities between the time of emergence and the attack of a new host or the factors that affect adult beetle survival during the flight period. In addition, the abundance of beetle populations emerging from or attacking standing trees would have to be measured. It is possible that further work incorporating complete generation survival of Douglas-fir beetle in both windthrown and standing trees would reveal that the adult flight period may well

be the most critical age interval in the life cycle and factors

such as immigration, emigration, and/or amount and availability of

host material may be more important factors in the population dynamics

of the Douglas-fir beetle than competition and predation.

Under these conditions, it is difficult to assess the overall

effects of salvage operations initiated by the U. S. Forest Service on

the Marys Peak watershed and in adjoining areas on the Douglas-fir

beetle population from year to year. It is probable that as the annual

salvage proceeded the total population of beetles in the Marys Peak

watershed area was reduced considerably. Whether this was real

mortality or whether the beetles moved to other areas or whether the

incidence of attack on standing, living trees increased is not known.

The best approach would be to maintain a balance between available

low value host material and attacking beetles such that the available

host material would absorb the majority of attacking beetles at high

attack densities and allow the natural mortality factors to reduce

populations to an acceptable level. This approach should minimize the

chances of living trees being attacked. In other words, a salvage

operation should not attempt complete sanitation but should leave

enough residual low value host material, such as slash and cull logs

for beetles to attack.

Finally, I would like to offer a few comments concerning how

this work could be improved if it were ever done again or if similar

work is attempted for another insect. Probably, the greatest contribu-

tion would be in developing methods to measure complete generation

survival. This was an inadequacy in this particular study and is certainly not an uncommon fault in life table work. The adult stage and/or flight period is, for most insects, the least studied and consequently, least understood stage of the life cycle. Yet it has to be one of the most important phases in the continuation of the life processes for most insect species.

Secondly, the amount of work attempted, particularly field work, was too great for the available resources. It was not possible, because of the volume of field work assumed by the author and others associated with the study, to maintain a proper sequence of gathering, processing, and analyzing data and then applying the results to the development of the study. For example, the sampling techniques used were arrived at basically through practical considerations such as available manpower, money and time. Complete analyses of the sampling data and recommendations for techniques were not available until the completion of the study. However, these analyses showed that the sampling techniques employed for the four years were in fact adequate for the desired purposes.

X. CONCLUSIONS

An investigation of the dynamics of Douglas-fir beetle, Dendroctonus pseudotsugae Hopkins (Coleoptera: Scolytidae), populations in windthrown, old growth Douglas-fir trees was conducted on the Marys Peak watershed near Corvallis, Oregon, from 1963 to 1966. Life tables representing population survival for four generations in 40 individual blowdown trees were constructed. The life tables were analyzed to determine the critical stages of increase or decrease in the life cycle of the Douglas-fir beetle in blowdown trees, to identify major mortality factors and to determine if and how the intensity of these factors varied with the population density.

The following conclusions are based on this investigation:

1. The sampling techniques employed for measuring population densities were adequate (statistically and practically) for the purposes of this study.

2. Attacking female beetles were influenced primarily by the exposure (degree of shade) of the host material. Shaded windthrown or shaded sides of windthrow are preferred and attacked at a greater rate than windthrow that is completely exposed to sunlight.

3. After female beetles are attracted to host material, they proceed to attack in a random fashion, except in those cases where exposure is a factor.

4. Special studies, which were designed to elucidate the

role of intraspecific competition, demonstrated that this factor was capable of causing significant mortality and of acting in a density-dependent fashion.

5. It is relatively simple to construct life tables for major age intervals of the life cycle of the Douglas-fir beetle from the time of attack by females till the progeny emerge. It was not possible to measure and include in the life tables population densities of beetles from emergence to attack.

6. Analysis of the life tables was based on incomplete generation survival. Nevertheless, several analyses demonstrated that the critical-age interval was the larval stage. Intraspecific competition during the first, second and third larval instars was the key factor. This factor acts in a density-dependent fashion and is capable of completely compensating for changes in density of the host.

7. Mortality due to predation by Medetera aldrichii Wheeler (Diptera: Dolichopodidae) and Enoclerus sphegeus Fab. (Coleoptera: Cleridae) became an important factor in the fourth instar, pupal and early callow stages. There is evidence that the predation occurs in a density-dependent manner and that Medetera aldrichii are more responsive (and consequently more effective) to host density than Enoclerus sphegeus.

8. It is concluded that Douglas-fir beetle populations are
   regulated by density-related processes within blowdown
   host material from time of attack to time of emergence.
   The availability of blowdown host material is the result
   of density-independent events, i.e. weather.

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APPENDICES

APPENDIX I

SAMPLE TREE STATISTICS

Table 21. Sample tree statistics - 1963

	Tree Number				
	1	3	4	5	6
d.b.h.	32"	26"	21"	37"	40"
length	188'	156'	130'	166'	115'
direction		N 22° E	N 22° E	N 39° E	N 39° E
category	windthrow	windthrow	windthrow	windthrow	windthrow
condition - rooting	partial	partial	partial	partial	partial
- top	broken	broken	intact	intact	broken
stand exposure	open	open	closed	closed	open
aspect	east	flat	flat	flat	flat
elevation	900'	1800'	1800'	1800'	1900'
shaded side	right	left	left	left	left
bark area (sq. ft.)	886	776	494	956	904

Table 21. Continued

	Tree Number				
	7	8	10	11	12
d.b.h.	41"	43"	42"	25"	24"
length	165'	110'	170'	100'	110'
direction	due E	due E		due N	due W
category	windthrow	windthrow	windthrow	windthrow	cut
condition - rooting	partial	partial	partial	partial	no rooting
- top	broken	broken	intact	intact	broken
stand exposure	closed	open	closed	open	closed
aspect	NW	flat	East	West	flat
elevation	2150'	2000'	2000'	800'	1200'
shaded side	left	left	left	left	right
bark area (sq. ft.)	1210	972	1291	485	504

Table 22. Sample tree statistics - 1964

	Tree Number				
	1	3	5	6	7
d.b.h.	36"	36"	36"	36"	46"
length	171'	140'	156'	132'	125'
direction	S 32° E	N 64° E	N 72° E	N 86° E	S 60° E
category	windthrow	windthrow	windthrow	windthrow	windthrow
condition - rooting	partial	partial	partial	partial	partial
- top	broken	broken	broken	broken	broken
stand exposure	closed	open (clear cut)	open	open	closed
aspect	SE	S	S	flat	SE
elevation	1550'	2100'	2050'	1900'	1550'
shaded side	left	left	left	left	left
bark area (sq. ft.)	1097	896	1103	968	1162

Table 22. Continued

	Tree Number			
	8	9	10	11
d.b.h.	41"	36"	44"	25"
length	156'	129'	135'	135'
direction	S 53° E	due S	S 38° E	E
category	windthrow	windthrow	windthrow	windthrow
condition - rooting	partial	partial	partial	partial
- top	broken	broken	broken	intact
stand exposure	closed	clear cut	open	open
aspect	SE	S	SE	flat
elevation	1550'	1900'	1600'	2700'
shaded side	left	left	left	left
bark area (sq. ft.)	1185	915	1061	636

Table 23.   Sample tree statistics - 1965

	Tree Number				
	3	6	7	8	9
d.b.h.	38"	48"	23"	35"	52"
length	208'	200'	90'	175'	179'
direction	N 25° E	N	N 54° E	S 66° W	N 50° E
category	windthrow	windthrow	cut	windthrow	windthrow
condition - rooting	partial	partial	no rooting	partial	partial
- top	broken	broken	broken	broken	broken
stand exposure	clear cut	open	open	closed	closed
aspect	SE	E	flat	NE	N
elevation	1850'	1700'	1300'	1100'	2450'
shaded side	left	left	left	right	left
bark area (sq. ft.)	1389	1624	330	1054	1594

Table 23.   Continued

	Tree Number					
	10	11	12	13	14	15
d.b.h.	45"	68"	34"	62"	26"	30"
length	207'	197'	168'	210'	127'	126'
direction	N 30° E	S 28° W	W 10° N	N 40° W	N 35° W	N 25° E
category	windthrow	windthrow	windthrow	windthrow	windthrow	windthrow
condition - rooting - top	partial broken	partial broken	no rooting borken	partial broken	partial broken	partial broken
stand exposure	closed	closed	closed	closed	open	closed
aspect	W	E	E	NW	NW	W
elevation	1900'	800'	1050'	1050'	1600'	2600'
shaded side	left	right	right	right	right	left
bark area (sq. ft.)	1437	1987	945	2145	599	776

Table 24. Sample tree statistics - 1966

	Tree Number				
	1	2	3	4	5
d.b.h.	50"	31"	30"	40"	38"
length	194'	140'	174'	123'	193'
direction	N 20° E	N 45° E	N 10° W	N 50° W	N 70° E
category	windthrow	windthrow	windthrow	windthrow	windthrow
condition - rooting	partial	partial	partial	partial	partial
- top	broken	broken	intact	broken	broken
stand exposure	open	clear cut	open	open	clear cut
aspect	W	SE	E	flat	N
elevation	1950'	2050'	2050'	1650'	2200'
shaded side	left	left	left	right	left
bark area (sq. ft.)	1650	825	787	1031	1332

Table 24.   Continued

	Tree Number				
	6	7	8	9	10
d.b.h.	53"	45"	42"	30"	33"
length	212'	172'	180'	179'	141'
direction	N	N 28° E	E	E 20° S	N 20° E
category	windthrow	windthrow	windthrow	windthrow	windthrow
condition – rooting	partial	partial	partial	partial	partial
– top	broken	broken	broken	intact	broken
stand exposure	closed	open	open	closed	open
aspect	N	flat	E	W	NE
elevation	2600'	2800'	2600'	2750'	2650'
shaded side	left	left	left	left	left
bark area (sq. ft.)	1842	1261	1285	815	776

APPENDIX II

DOUGLAS-FIR BLOWDOWN DATA

FOR THE CORVALLIS WATERSHED,

SIUSLAW NATIONAL FOREST,

1962-1966.

DATA OBTAINED FROM U.S. FOREST SERVICE

TIMBER SALES RECORDS

ALSEA MANAGEMENT UNIT.

Table 25. Douglas-fir blowdown data for the Corvallis Watershed, Siuslaw National Forest, 1962-1966. Data obtained from records of U.S. Forest Service timber sales - Alsea Management Unit.

Year	Volume (M bd. ft.)	Bark area (sq. ft.)	
		Attack[1]	Emergence[2]
1962	1,612.5	680,967	489,048
1963	22,335.7	(8,882,686)	(2,698,228)
		4,441,343[3]	1,349,114[3]
1964	1,880.4	1,713,570	1,713,570
1965	1,365.3	1,128,951	737,548
1966	28.1	11,213	8,096

[1] This is the amount of blowdown bark area available on the watershed to attacking beetles each year.

[2] This is the amount of blowdown bark area remaining following salvage operations on the watershed each year from which beetles emerged.

[3] In 1963, only 1/2 of the available blowdown material was attacked by Douglas-fir beetles and it was assessed that adult beetles emerged from only 1/2 of the remaining blowdown following salvage operations.

The first step was to construct a local volume table establishing a relationship between d.b.h. and volume in bd. ft. This was for the Corvallis Watershed, Douglas-fir species and Scribner Decimal C log rule based on .70 form class was used. Raw data came from the 40 blowdown trees that were sampled over the 4-year period and for which we had detailed measurements.

The next step was to construct a local bark area table establishing a relationship between d.b.h. and bark area in sq. ft. The

source of raw data was the 40 blowdown sample trees.

The final step involved a three-way relationship among d.b.h., bark area and volume, thus producing the desired final result.

$$(d.b.h. \longleftrightarrow vol.) \quad + \quad (d.b.h. \longleftrightarrow bark\ area)$$

$$= d.b.h. \longleftrightarrow vol.$$
$$\nwarrow$$
$$bark \quad area$$

Based on timber sale records, located in the Alsea Guard Station, it was possible to determine the volume of blowdown Douglas-fir timber that was present on the Corvallis Watershed each year, except for 1966. For each location, within the watershed, where there was blowdown, a salvage sale was set up. Frequently, this sale would include standing, healthy timber in order to keep the offer attractive to the buyers. If this was the case, then % of blowdown in relation to total sale volume was quoted. Also the sale cruise data included average age and d.b.h. of the timber. With this information and using the d.b.h. - volume - bark area table that was constructed for the watershed, it was possible to convert the volume data to bark area available for attack for each generation of the beetle. Furthermore, the sale records followed the progress of timber removal for each sale and it was possible to determine how much blowdown was left each year when emergence of adults occurred.

Thus timber sale records provided an estimate of blowdown timber for 1962, 1963, 1964 and 1965. In 1966, the amount of blowdown timber was estimated from both timber sale records and a road cruise of the watershed which averaged 47% of the total watershed area.

It is necessary to adjust the 1963 estimate of bark area, from bark area available for attack to bark area actually attacked. Data gathered by Heikenen (personal communication) in the fall of 1963 in western Oregon indicated that 50% of the blowdown from the winter of 1962-63 was not attacked by beetles.

Therefore, the 8,882,686 sq. ft. available for attack must be re-adjusted to 4,441,343 sq. ft. which was actually attacked. In addition, salvage would leave 1,349,114 sq. ft. of bark area from which beetles emerged.

APPENDIX   III

LIFE TABLES

FOR

INDIVIDUAL TREES;

1963, 1964, 1965, 1966.

Life Table - Tree 63-1

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	63.58	Infertility, mites, pitched out, other	TOTAL	7.05	11.1	.89
Larvae 1st instar	56.53	Competition Predators, other	TOTAL	1.20 0 1.20	2.1	.98
2nd instar	55.33	Competition Predators, other	TOTAL	11.37 7.22 18.59	33.6	.64
3rd instar	36.74	Competition Predators, other	TOTAL	5.24 16.92 22.16	60.3	.40
4th instar	14.58	Competition Predators, other	TOTAL	6.89 0 6.89	47.2	.53

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	7.62	Overwintering mortality, other TOTAL	——		
Spring	——**	Predators, moisture other TOTAL	——		
Emerged Adults	——**				
Females x 2	——**	$\frac{Sex}{TOTAL}$	——		
Generation TOTALS			55.89	87.90	$S_G =$

* Number per one square foot of bark surface

** Population estimate was not obtained

Life Table - Tree 63-3

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	40.81	Infertility, mites, pitched out, other				
			TOTAL	− 4.35		1.00
Larvae 1st instar	45.16	Competition Predators, other		1.36 0		
			TOTAL	1.36	3.0	.97
2nd instar	43.80	Competition Predators, other		7.82 2.72		
			TOTAL	10.54	24.1	.76
3rd instar	33.26	Competition Predators, other		4.27 8.35		
			TOTAL	12.62	37.9	.62
4th instar	20.64	Competition Predators, other		10.64 2.95		
			TOTAL	13.59	65.8	.34

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	7.05	Overwintering mortality, other TOTAL	———		
Spring	—— **	Predators, moisture other TOTAL	———		
Emerged Adults	—— **				
Females x 2	—— **	Sex TOTAL	———		
Generation TOTALS			33.76	82.72	S_G =

* Number per one square foot of bark surface

** Population estimate was not obtained

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	10.82	Infertility, mites, pitched out, other	TOTAL	5.76	53.2	.47
Larvae 1st instar	5.06	Competition	.13			
		Predators, other	0			
			TOTAL	.13	2.6	.97
2nd instar	4.93	Competition	.43			
		Predators, other	0			
			TOTAL	.43	8.7	.91
3rd instar	4.50	Competition	.04			
		Predators, other	· 1.57			
			TOTAL	1.61	35.8	.64
4th instar	2.89	Competition	1.24			
		Predators, other	1.26			
			TOTAL	2.50	86.5	.14

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	.39	Overwintering mortality, other TOTAL	___ .39	100.0	.00
Spring	0	Predators, moisture other TOTAL	___		
Emerged Adults	0				
Females x 2	0	$\frac{Sex}{TOTAL}$	___		
Generation TOTALS			10.82	100.00	$S_G = 0$

* Number per one square foot of bark surface

Life Table - Tree 63-5

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	31.11	Infertility, mites, pitched out, other	TOTAL	$\overline{-12.39}$		1.00
Larvae 1st instar	43.50	Competition Predators, other	TOTAL	3.67 0 $\overline{3.67}$	8.4	.92
2nd instar	39.83	Competition Predators, other	TOTAL	6.74 2.79 $\overline{9.53}$	23.9	.76
3rd instar	30.30	Competition Predators, other	TOTAL	3.52 8.14 $\overline{11.66}$	38.5	.62
4th instar	18.64	Competition Predators, other	TOTAL	9.42 .89 $\overline{10.31}$	55.3	.45

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	8.33	Overwintering mortality, other TOTAL	‾4.90‾	58.8	.41
Spring	3.43	Predators, moisture other TOTAL	——		
Emerged Adults	-- **				
Females x 2	-- **	$\frac{Sex}{TOTAL}$	——		
Generation TOTALS			27.68	88.97	S_G =

* Number per one square foot of bark surface

** Population estimate was not obtained

Life Table - Tree 63-6

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	21.51	Infertility, mites, pitched out, other	TOTAL	$\overline{.88}$	4.1	.96
Larvae 1st instar	20.63	Competition Predators, other	TOTAL	1.95 3.21 $\overline{5.16}$	25.0	.75
2nd instar	15.47	Competition Predators, other	TOTAL	1.74 .26 $\overline{2.00}$	12.9	.87
3rd instar	13.47	Competition Predators, other	TOTAL	.62 2.56 $\overline{3.18}$	23.6	.76
4th instar	10.29	Competition Predators, other	TOTAL	4.78 .19 $\overline{4.97}$	48.3	.52

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	5.32	Overwintering mortality, other TOTAL	<u>4.15</u>	78.0	.22
Spring	1.17	Predators, moisture other TOTAL	——		
Emerged Adults	-- **				
Females x 2	-- **	$\dfrac{Sex}{TOTAL}$	——		
Generation TOTALS			20.34	94.56	S$_G$ =

* Number per one square foot of bark surface

** Population estimate was not obtained

Life Table - Tree 63-7

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	37.66	Infertility, mites, pitched out, other	TOTAL	6.72	17.8	.82
Larvae 1st instar	30.94	Competition Predators, other	TOTAL	2.22 0 2.22	7.2	.93
2nd instar	28.72	Competition Predators, other	TOTAL	1.43 0 1.43	5.0	.95
3rd instar	27.29	Competition Predators, other	TOTAL	2.83 6.35 9.18	33.6	.66
4th instar	18.11	Competition Predators, other	TOTAL	9.11 1.23 10.34	57.1	.43

Continued..

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Callow adults Fall	7.77	Overwintering mortality, other TOTAL	2.60	33.5	.66
Spring	5.17	Predators, moisture other TOTAL	____		
Emerged Adults	-- **				
Females x 2	-- **	Sex TOTAL	____		
Generation TOTALS			32.49	86.27	S_G =

* Number per one square foot of bark surface

** Population estimate was not obtained

Life Table - Tree 63-8

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	41.81	Infertility, mites, pitched out, other	TOTAL	$\overline{15.66}$	37.4	.63
Larvae 1st instar	26.15	Competition Predators, other	TOTAL	2.62 0 $\overline{2.62}$	10.0	.90
2nd instar	23.53	Competition Predators, other	TOTAL	.95 0 $\overline{.95}$	4.0	.96
3rd instar	22.58	Competition Predators, other	TOTAL	1.90 6.44 $\overline{8.34}$	36.9	.63
4th instar	14.24	Competition Predators, other	TOTAL	4.66 0 $\overline{4.66}$	32.7	.67

Continued..

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	9.58	Overwintering mortality, other TOTAL	———		
Spring	—— **	Predators, moisture other TOTAL	———		
Emerged Adults	—— **				
Females x 2	—— **	$\dfrac{\text{Sex}}{\text{TOTAL}}$	———		
Generation TOTALS			32.23	77.09	$S_G =$

* Number per one square foot of bark surface
** Population estimate was not obtained

Life Table - Tree 63-10

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	28.22	Infertility, mites, pitched out, other				
			TOTAL	5.71	20.2	.80
Larvae 1st instar	22.51	Competition Predators, other		- 2.36 0		
			TOTAL	- 2.36		1.00
2nd instar	24.87	Competition Predators, other		- .72 0		
			TOTAL	- .72		1.00
3rd instar	25.59	Competition Predators, other		2.47 4.21		
			TOTAL	6.68	26.1	.74
4th instar	18.91	Competition Predators, other		9.10 0		
			TOTAL	9.10	48.1	.52

Continued..

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Callow adults Fall	9.81	Overwintering mortality, other TOTAL	———		
Spring	–– **	Predators, moisture other TOTAL	———		
Emerged Adults	–– **				
Females x 2	–– **	$\dfrac{\text{Sex}}{\text{TOTAL}}$	———		
Generation TOTALS			18.41	65.24	$S_G =$

* Number per one square foot of bark surface

** Population estimate was not obtained

Life Table - Tree 63-11

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	20.75	Infertility, mites, pitched out, other			
		TOTAL	$\overline{4.51}$	21.7	.78
Larvae 1st instar	16.24	Competition Predators, other	1.43 2.54		
		TOTAL	$\overline{3.97}$	24.4	.76
2nd instar	12.27	Competition Predators, other	— .62 0		
		TOTAL	$-\overline{.62}$		1.00
3rd instar	12.89	Competition Predators, other	— 2.00 · 0		
		TOTAL	$-\overline{2.00}$		1.00
4th instar	14.89	Competition Predators, other	6.30 0		
		TOTAL	$\overline{6.30}$	42.3	.58

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	8.59	Overwintering mortality, other TOTAL	———		
Spring	-- **	Predators, moisture other TOTAL	———		
Emerged Adults	-- **				
Females x 2	-- **	$\frac{Sex}{TOTAL}$	———		
Generation TOTALS			12.16	58.60	$S_G =$

* Number per one square foot of bark surface

** Population estimate was not obtained

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	148.52	Infertility, mites, pitched out, other	TOTAL	$\overline{23.84}$	16.0	.84
Larvae 1st instar	124.68	Competition Predators, other	TOTAL	12.90 0 $\overline{12.90}$	10.3	.90
2nd instar	111.78	Competition Predators, other	TOTAL	32.90 0 $\overline{32.90}$	29.4	.71
3rd instar	78.88	Competition Predators, other	TOTAL	25.02 13.21 $\overline{38.23}$	48.5	.52
4th instar	40.65	Competition Predators, other	TOTAL	22.48 0 $\overline{22.48}$	55.3	.45

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	18.17	Overwintering mortality, other TOTAL	15.28	84.1	.16
Spring	2.89	Predators, moisture other TOTAL	1.33	46.0	.54
Emerged Adults	1.56		0		
Females x 2	1.56	Sex TOTAL	0 0		
Generation TOTALS			146.96	98.95	S_G = .0105

* Number per one square foot of bark surface

Life Table - Tree 64-3

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	31.67	Infertility, mites, pitched out, other	TOTAL	$\overline{-15.79}$		1.00
Larvae 1st instar	47.46	Competition Predators, other	TOTAL	1.95 0 $\overline{1.95}$	4.0	.96
2nd instar	45.51	Competition Predators, other	TOTAL	8.31 .40 $\overline{8.71}$	19.1	.81
3rd instar	36.80	Competition Predators, other	TOTAL	5.26 10.56 $\overline{15.82}$	43.0	.57
4th instar	20.98	Competition Predators, other	TOTAL	10.13 4.96 $\overline{15.09}$	71.9	.18

Continued..

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	5.89	Overwintering mortality, other TOTAL	‾.56‾	9.5	.90
Spring	5.33	Predators, moisture other TOTAL	‾5.11‾	95.9	.04
Emerged Adults	.22		0		
Females x 2	.22	Sex TOTAL	0 ‾0‾		
Generation TOTALS			31.45	99.30	S_G = .0070

* Number per one square foot of bark surface

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	133.93	Infertility, mites, pitched out, other	TOTAL	$\overline{32.24}$	24.1	.76
Larvae 1st instar	101.69	Competition Predators, other	TOTAL	21.50 $\underline{1.76}$ $\overline{23.26}$	22.9	.77
2nd instar	78.43	Competition Predators, other	TOTAL	18.56 $\underline{0}$ $\overline{18.56}$	23.7	.76
3rd instar	59.87	Competition Predators, other	TOTAL	14.28 $\underline{14.31}$ $\overline{28.59}$	47.8	.52
4th instar	31.28	Competition Predators, other	TOTAL	17.76 $\underline{1.13}$ $\overline{18.89}$	60.4	.40

Continued..

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	12.39	Overwintering mortality, other TOTAL	4.83	39.0	.61
Spring	7.56	Predators, moisture other TOTAL	6.56	86.8	.13
Emerged Adults	1.00		0		
Females x 2	1.00	Sex TOTAL	0 0		
Generation TOTALS			132.93	99.25	S_G = .0075

* Number per one square foot of bark surface

Life Table - Tree 64-6

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	18.92	Infertility, mites, pitched out, other	TOTAL	6.25	33.0	.67
Larvae 1st instar	12.67	Competition Predators, other	TOTAL	1.05 6.62 7.67	60.5	.40
2nd instar	5.00	Competition Predators, other	TOTAL	.44 .76 1.20	24.0	.76
3rd instar	3.80	Competition Predators, other	TOTAL	.02 1.22 1.24	32.6	.67
4th instar	2.56	Competition Predators, other	TOTAL	1.09 1.41 2.50	97.6	.02

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	.06	Overwintering mortality, other TOTAL	.06	0	.00
Spring	0	Predators, moisture other TOTAL	0		
Emerged Adults	0		0		
Females x 2	0	Sex TOTAL	0 0		
Generation TOTALS			18.92	100.00	$S_G = 0$

* Number per one square foot of bark surface

Life Table - Tree 64-7

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	195.88	Infertility, mites, pitched out, other				
			TOTAL	$\overline{22.01}$	11.2	.89
Larvae 1st instar	173.87	Competition Predators, other		45.25 0		
			TOTAL	$\overline{45.25}$	26.0	.74
2nd instar	128.62	Competition Predators, other		41.14 0		
			TOTAL	$\overline{41.14}$	32.0	.68
3rd instar	87.48	Competition Predators, other		30.86 2.87		
			TOTAL	$\overline{33.73}$	38.6	.61
4th instar	53.75	Competition Predators, other		28.08 0		
			TOTAL	$\overline{28.08}$	52.2	.48

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	25.67	Overwintering mortality, other TOTAL	21.23	82.7	.17
Spring	4.44	Predators, moisture other TOTAL	2.44	55.0	.45
Emerged Adults	2.00		0		
Females x 2	2.00	Sex TOTAL	0 / 0		
Generation TOTALS			193.88	98.98	S_G = .0102

* Number per one square foot of bark surface

Life Table - Tree 64-8

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	72.16	Infertility, mites, pitched out, other TOTAL	 $\overline{-5.23}$		 1.00
Larvae 1st instar	77.39	Competition Predators, other TOTAL	8.22 0 $\overline{8.22}$	 10.6	 .89
2nd instar	69.17	Competition Predators, other TOTAL	4.38 0 $\overline{4.38}$	 6.3	 .94
3rd instar	64.79	Competition Predators, other TOTAL	10.95 0 10.95	 16.9	 .83
4th instar	53.84	Competition Predators, other TOTAL	22.78 0 22.78	 42.3	 .58

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	31.06	Overwintering mortality, other TOTAL	‾‾‾‾ 23.62	76.0	.24
Spring	7.44	Predators, moisture other TOTAL	‾‾‾‾ 5.55	74.6	.25
Emerged Adults	1.89		0		
Females x 2	1.89	Sex TOTAL	0 ‾‾ 0		
Generation TOTALS			70.27	97.38	S_G = .0262

* Number per one square foot of bark surface

Life Table - Tree 64-9

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	61.94	Infertility, mites, pitched out, other				
			TOTAL	-6.80		1.00
Larvae 1st instar	68.74	Competition Predators, other		-1.30 0		
			TOTAL	-1.30		1.00
2nd instar	70.04	Competition Predators, other		10.65 0		
			TOTAL	10.65	15.2	.85
3rd instar	59.39	Competition Predators, other		14.05 6.57		
			TOTAL	20.62	34.7	.65
4th instar	38.77	Competition Predators, other		23.44 10.05		
			TOTAL	33.49	86.4	.14

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	5.28	Overwintering mortality, other TOTAL	2.84	53.8	.46
Spring	2.44	Predators, moisture other TOTAL	———		
Emerged Adults	-- **	Tree was salvaged			
Females x 2	-- **	$\frac{\text{Sex}}{\text{TOTAL}}$	———		
Generation TOTALS			59.50	96.06	$S_G =$

* Number per one square foot of bark surface

** Population estimates could not be obtained

Life Table - Tree 64-10

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	128.26	Infertility, mites, pitched out, other	TOTAL	22.34	17.4	.83
Larvae 1st instar	105.92	Competition Predators, other	 TOTAL	11.21 0 11.21	10.6	.89
2nd instar	94.71	Competition Predators, other	 TOTAL	24.96 0 24.96	26.4	.74
3rd instar	69.75	Competition Predators, other	 TOTAL	19.49 16.82 36.31	52.1	.48
4th instar	33.44	Competition Predators, other	 TOTAL	19.34 2.21 21.55	64.4	.36

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	11.89	Overwintering mortality, other TOTAL	‾‾‾‾ 6.67	56.1	.44
Spring	5.22	Predators, moisture other TOTAL	‾‾‾‾		
Emerged Adults	-- **	Tree was salvaged			
Females x 2	-- **	$\frac{Sex}{TOTAL}$	‾‾‾‾		
Generation TOTALS			123.04	95.93	$S_G =$

* Number per one square foot of bark surface

** Population estimate could not be obtained

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	51.23	Infertility, mites, pitched out, other TOTAL	 $\overline{-10.51}$		 1.00
Larvae 1st instar	61.74	Competition Predators, other TOTAL	9.49 16.31 $\overline{25.80}$	 41.8	 .58
2nd instar	35.94	Competition Predators, other TOTAL	5.76 6.85 $\overline{12.61}$	 35.1	 .65
3rd instar	23.33	Competition Predators, other TOTAL	- 2.75 0 $\overline{- 2.75}$		 1.00
4th instar	26.08	Competition Predators, other TOTAL	14.14 2.81 $\overline{16.95}$	 65.0	 .35

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	9.13	Overwintering mortality, other TOTAL	7.24	79.3	.21
Spring	1.89	Predators, moisture other TOTAL	1.56	82.5	.18
Emerged Adults	.33		0		
Females x 2	.33	Sex TOTAL	0 0		
Generation TOTALS			50.90	99.36	$S_G = .0064$

* Number per one square foot of bark surface

Life Table - Tree 65-3

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	30.11	Infertility, mites, pitched out, other				
			TOTAL	5.00	16.6	.83
Larvae 1st instar	25.11	Competition Predators, other		1.35 0		
			TOTAL	1.35	5.4	.95
2nd instar	23.76	Competition Predators, other		3.13 7.60		
			TOTAL	10.73	45.2	.55
3rd instar	13.03	Competition Predators, other		.58 10.84		
			TOTAL	11.42	87.6	.12
4th instar	1.61	Competition Predators, other		.68 .21		
			TOTAL	.89	55.3	.45

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	.72	Overwintering mortality, other TOTAL	<u> </u> .72	100.0	.00
Spring	0	Predators, moisture other TOTAL	<u> </u> 0		
Emerged Adults	0		0		
Females x 2	0	$\dfrac{\text{Sex}}{\text{TOTAL}}$	$\dfrac{0}{0}$		
Generation TOTALS			30.11	100.00	$S_G = 0$

* Number per one square foot of bark surface

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	96.98	Infertility, mites, pitched out, other	TOTAL	$\overline{12.15}$	12.5	.88
Larvae 1st instar	84.83	Competition Predators, other	TOTAL	15.87 19.10 $\overline{34.97}$	41.2	.59
2nd instar	49.86	Competition Predators, other	TOTAL	4.33 0 $\overline{4.33}$	8.7	.91
3rd instar	45.53	Competition Predators, other	TOTAL	8.15 12.95 21.10	46.3	.54
4th instar	24.43	Competition Predators, other	TOTAL	13.05 7.49 20.54	84.1	.16

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	3.89	Overwintering mortality, other TOTAL	$\overline{3.00}$	77.1	.23
Spring	.89	Predators, moisture other TOTAL	$\overline{.39}$	43.8	.56
Emerged Adults	.50		0		
Females x 2	.50	$\dfrac{\text{Sex}}{\text{TOTAL}}$	$\dfrac{0}{0}$		
Generation TOTALS			96.48	99.48	S_G = .0052

* Number per one square foot of bark surface

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	244.79	Infertility, mites, pitched out, other	TOTAL	78.73	32.2	.68
Larvae 1st instar	166.06	Competition Predators, other	TOTAL	50.55 12.62 63.17	38.0	.62
2nd instar	102.89	Competition Predators, other	TOTAL	27.48 0 27.48	26.7	.73
3rd instar	75.41	Competition Predators, other	TOTAL	22.84 25.46 48.30	64.0	.36
4th instar	27.11	Competition Predators, other	TOTAL	14.84 10.49 25.33	93.4	.07

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	1.78	Overwintering mortality, other TOTAL	$\overline{1.67}$	93.8	.06
Spring	.11	Predators, moisture other TOTAL	$\overline{-1.00}$		1.00
Emerged Adults	1.11		0		
Females x 2	1.11	Sex TOTAL	$\frac{0}{0}$		
Generation TOTALS			243.68	99.55	$S_G = .0045$

* Number per one square foot of bark surface

Life Table - Tree 65-9

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	144.05	Infertility, mites, pitched out, other TOTAL	 $\overline{34.75}$	24.1	.76
Larvae 1st instar	109.30	Competition Predators, other TOTAL	24.31 $\underline{16.66}$ 40.97	37.5	.62
2nd instar	68.33	Competition Predators, other TOTAL	7.39 $\underline{0}$ $\overline{7.39}$	10.8	.89
3rd instar	60.94	Competition Predators, other TOTAL	14.80 $\underline{12.85}$ $\overline{27.65}$	45.4	.55
4th instar	33.29	Competition Predators, other TOTAL	19.23 $\underline{7.23}$ $\overline{26.46}$	79.5	.20

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	6.83	Overwintering mortality, other TOTAL	___		
Spring	-- **	Predators, moisture other Tree was salvaged TOTAL	___		
Emerged Adults	-- **				
Females x 2	-- **	$\frac{Sex}{TOTAL}$	___		
Generation TOTALS			137.22	95.26	S$_G$

* Number per one square foot of bark surface

** Population estimate could not be obtained

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	165.58	Infertility, mites, pitched out, other				
			TOTAL	$\overline{18.77}$	11.3	.89
Larvae 1st instar	146.81	Competition Predators, other		30.66 0		
			TOTAL	$\overline{30.66}$	20.9	.79
2nd instar	116.15	Competition Predators, other		35.58 0		
			TOTAL	$\overline{35.58}$	30.6	.69
3rd instar	80.57	Competition Predators, other		26.12 13.60		
			TOTAL	$\overline{39.72}$	49.3	.51
4th instar	40.85	Competition Predators, other		25.12 2.90		
			TOTAL	$\overline{28.02}$	68.6	.31

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Callow adults Fall	12.83	Overwintering mortality, other TOTAL	<u> </u> 4.39	34.2	.66
Spring	8.44	Predators, moisture other TOTAL	<u> </u> 7.33	86.8	.13
Emerged Adults	1.11		0		
Females x 2	1.11	<u>Sex</u> TOTAL	<u>0</u> 0		
Generation TOTALS			164.47	99.33	S_G = .0067

* Number per one square foot of bark surface

Life Table - Tree 65-11

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	292.70	Infertility, mites, pitched out, other	TOTAL	$\overline{115.29}$	39.4	.61
Larvae 1st instar	177.41	Competition Predators, other	TOTAL	56.91 3.00 $\overline{59.91}$	33.8	.66
2nd instar	117.50	Competition Predators, other	TOTAL	41.15 6.59 $\overline{47.74}$	40.6	.59
3rd instar	69.76	Competition Predators, other	TOTAL	19.50 11.85 $\overline{31.35}$	44.9	.55
4th instar	38.41	Competition Predators, other	TOTAL	23.16 9.03 $\overline{32.19}$	83.8	.16

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Callow adults Fall	6.22	Overwintering mortality, other TOTAL	‾6.00‾	96.5	.04
Spring	.22	Predators, moisture other TOTAL	‾‾‾		
Emerged Adults	-- **	Tree was salvaged			
Females x 2	-- **	$\frac{Sex}{TOTAL}$	‾‾‾		
Generation TOTALS			292.48	99.92	S$_G$ =

* Number per one square foot of bark surface

** Population estimate could not be obtained

Life Table - Tree 65-12

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	85.92	Infertility, mites, pitched out, other TOTAL	<u>6.51</u>	7.6	.92
Larvae 1st instar	79.41	Competition Predators, other TOTAL	14.23 <u>12.70</u> 26.93	33.9	.66
2nd instar	52.48	Competition Predators, other TOTAL	10.43 <u>5.13</u> 15.56	29.6	.70
3rd instar	36.92	Competition Predators, other TOTAL	5.30 <u>9.79</u> 15.09	40.9	.59
4th instar	21.83	Competition Predators, other TOTAL	11.38 <u>7.23</u> 18.61	85.2	.15

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	3.22	Overwintering mortality, other TOTAL	‾‾‾‾ 2.33	72.4	.28
Spring	.89	Predators, moisture other TOTAL	‾‾‾‾ − .50		1.00
Emerged Adults	1.39		0		
Females x 2	1.39	Sex TOTAL	0 ‾‾ 0		
Generation TOTALS			84.53	98.38	S_G = .0162

* Number per one square foot of bark surface

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	232.72	Infertility, mites, pitched out, other				
			TOTAL	$\overline{92.63}$	39.8	.60
Larvae 1st instar	140.09	Competition Predators, other		37.39 7.50		
			TOTAL	$\overline{44.89}$	32.0	.68
2nd instar	95.20	Competition Predators, other		28.40 7.65		
			TOTAL	$\overline{36.05}$	37.9	.62
3rd instar	59.15	Competition Predators, other		13.93 9.55		
			TOTAL	$\overline{23.48}$	39.7	.60
4th instar	35.67	Competition Predators, other		21.02 9.76		
			TOTAL	$\overline{30.78}$	86.3	.14

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	4.89	Overwintering mortality, other			
		TOTAL	4.39	89.8	.10
Spring	.50	Predators, moisture other			
		TOTAL	− .72		1.00
Emerged Adults	1.22		0		
Females x 2	1.22	Sex	0		
		TOTAL	0		
Generation TOTALS			231.50	99.48	S_G = .0052

* Number per one square foot of bark surface

Life Table - Tree 65-14

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	253.90	Infertility, mites, pitched out, other TOTAL	_____ 12.64	5.0	.95
Larvae 1st instar	241.26	Competition Predators, other TOTAL	55.46 0 55.46	23.0	.77
2nd instar	185.80	Competition Predators, other TOTAL	49.86 0 49.86	26.8	.73
3rd instar	135.94	Competition Predators, other TOTAL	65.11 0 65.11	47.9	.52
4th instar	70.83	Competition Predators, other TOTAL	53.99 7.84 61.83	87.3	.13

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	9.00	Overwintering mortality, other TOTAL	————		
Spring	— **	Predators, moisture other Tree was salvaged TOTAL	————		
Emerged Adults	— **				
Females x 2	— **	Sex ————— TOTAL	————		
Generation TOTALS			244.90	96.46	S_G =

* Number per one square foot of bark surface
** Population estimate could not be obtained

Life Table - Tree 65-15

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	68.32	Infertility, mites, pitched out, other				
			TOTAL	$\overline{-3.80}$		1.00
Larvae 1st instar	72.12	Competition Predators, other		11.23 0		
			TOTAL	$\overline{11.23}$	15.6	.84
2nd instar	60.89	Competition Predators, other		7.45 0		
			TOTAL	$\overline{7.45}$	12.2	.88
3rd instar	53.44	Competition Predators, other		11.32 11.24		
			TOTAL	$\overline{22.56}$	42.2	.58
4th instar	30.88	Competition Predators, other		17.47 3.13		
			TOTAL	$\overline{20.60}$	66.7	.33

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	10.28	Overwintering mortality, other TOTAL	———		
Spring	-- **	Predators, moisture other Tree was salvaged TOTAL	———		
Emerged Adults	-- **				
Females x 2	-- **	Sex / TOTAL	———		
Generation TOTALS			58.04	84.95	S_G =

* Number per one square foot of bark surface

** Population estimate could not be obtained

Life Table - Tree 66-1

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	201.89	Infertility, mites, pitched out, other TOTAL	 61.06	 30.2	 .70
Larvae 1st instar	140.83	Competition Predators, other TOTAL	37.74 25.47 63.21	 44.9	 .55
2nd instar	77.62	Competition Predators, other TOTAL	19.97 5.32 25.29	 32.6	 .67
3rd instar	52.33	Competition Predators, other TOTAL	10.85 16.23 27.08	 51.8	 .48
4th instar	25.25	Competition Predators, other TOTAL	13.59 4.44 18.03	 71.4	 .29

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	7.22	Overwintering mortality, other TOTAL	$\overline{4.55}$	63.1	.37
Spring	2.67	Predators, moisture other TOTAL	$\overline{2.37}$	88.9	.11
Emerged Adults	.30		0		
Females x 2	.30	$\dfrac{\text{Sex}}{\text{TOTAL}}$	$\dfrac{0}{0}$		
Generation TOTALS			201.59	99.85	$S_G = .0015$

* Number per one square foot of bark surface

Life Table - Tree 66-2

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	126.44	Infertility, mites, pitched out, other				
			TOTAL	29.58	23.4	.77
Larvae 1st instar	96.86	Competition Predators, other		19.81 35.18		
			TOTAL	54.99	56.8	.43
2nd instar	41.87	Competition Predators, other		7.29 17.18		
			TOTAL	24.47	58.44	.42
3rd instar	17.40	Competition Predators, other		1.09 9.56		
			TOTAL	10.65	61.2	.39
4th instar	6.75	Competition Predators, other		3.02 2.45		
			TOTAL	5.47	81.0	.19

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	1.28	Overwintering mortality, other TOTAL	$\overline{1.06}$	82.8	.17
Spring	.22	Predators, moisture other TOTAL	$\overline{- .11}$		1.00
Emerged Adults	.33		0		
Females x 2	.33	$\dfrac{\text{Sex}}{\text{TOTAL}}$	$\dfrac{0}{0}$		
Generation TOTALS			126.11	99.74	$S_G = .0026$

* Number per one square foot of bark surface

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	139.70	Infertility, mites, pitched out, other	TOTAL	$\overline{-16.24}$		1.00
Larvae 1st instar	155.94	Competition Predators, other	TOTAL	45.19 20.57 $\overline{65.76}$	42.2	.58
2nd instar	90.18	Competition Predators, other	TOTAL	25.85 17.26 $\overline{43.11}$	47.8	.52
3rd instar	47.07	Competition Predators, other	TOTAL	8.73 15.09 $\overline{23.82}$	50.6	.49
4th instar	23.25	Competition Predators, other	TOTAL	12.28 9.41 $\overline{21.69}$	93.3	.07

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Callow adults Fall	1.56	Overwintering mortality, other TOTAL	‾‾‾‾ − .33		1.00
Spring	1.89	Predators, moisture other TOTAL	‾‾‾‾ 1.50	79.4	.21
Emerged Adults	.39		0		
Females x 2	.39	Sex TOTAL	0 ‾‾ 0		
Generation TOTALS			139.31	99.72	S_G = .0028

* Number per one square foot of bark surface

Life Table - Tree 66-4

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	305.11	Infertility, mites, pitched out, other	TOTAL	86.08	28.2	.72
Larvae 1st instar	219.03	Competition Predators, other	TOTAL	62.35 0 62.35	28.5	.72
2nd instar	156.68	Competition Predators, other	TOTAL	68.43 0 68.43	43.7	.56
3rd instar	88.25	Competition Predators, other	TOTAL	31.42 9.00 40.42	45.8	.54
4th instar	47.83	Competition Predators, other	TOTAL	31.05 11.56 42.61	89.1	.11

Continued..

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x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	5.22	Overwintering mortality, other TOTAL	<u>1.78</u>	34.1	.66
Spring	3.44	Predators, moisture other TOTAL	<u>3.00</u>	87.2	.13
Emerged Adults	.44		0		
Females x 2	.44	Sex TOTAL	0 0		
Generation TOTALS			304.67	99.86	.0014

* Number per one square foot of bark surface

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	63.15	Infertility, mites, pitched out, other				
			TOTAL	-1.04		1.00
Larvae 1st instar	64.19	Competition Predators, other		10.09 14.54		
			TOTAL	24.63	38.4	.62
2nd instar	39.56	Competition Predators, other		6.67 4.92		
			TOTAL	11.59	29.3	.71
3rd instar	27.97	Competition Predators, other		2.98 11.32		
			TOTAL	14.30	51.1	.49
4th instar	13.67	Competition Predators, other		6.58 3.09		
			TOTAL	9.67	70.7	.29

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Callow adults Fall	4.00	Overwintering mortality, other TOTAL	2.89	72.2	.28
Spring	1.11	Predators, moisture other TOTAL	___		
Emerged Adults	-- **	Tree was salvaged			
Females x 2	--	Sex / TOTAL	___		
Generation TOTALS			62.04	98.24	$S_G =$

* Number per one square foot of bark surface

** Population estimate could not be obtained

Life Table - Tree 66-6

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	295.32	Infertility, mites, pitched out, other	TOTAL	80.88	27.4	.73
Larvae 1st instar	214.44	Competition Predators, other	TOTAL	80.26 20.82 101.08	47.1	.53
2nd instar	113.36	Competition Predators, other	TOTAL	38.61 13.80 52.41	46.2	.54
3rd instar	60.95	Competition Predators, other	TOTAL	14.81 11.45 26.26	43.1	.57
4th instar	34.69	Competition Predators, other	TOTAL	20.28 .85 21.13	60.9	.39

x	1x	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of 1x	Survival rate within x
Callow adults Fall	13.56	Overwintering mortality, other TOTAL	$\overline{11.00}$	81.1	.19
Spring	2.56	Predators, moisture other TOTAL	$\overline{2.26}$	88.3	.12
Emerged Adults	.30		0		
Females x 2	.30	Sex / TOTAL	0 / 0		
Generation TOTALS			295.02	99.90	S_G = .0010

* Number per one square foot of bark surface

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	132.90	Infertility, mites, pitched out, other TOTAL	<u> </u> -2.77		1.00
Larvae 1st instar	135.67	Competition Predators, other TOTAL	35.34 <u>16.88</u> 52.22	38.5	.62
2nd instar	83.45	Competition Predators, other TOTAL	22.61 <u>25.67</u> 48.28	57.8	.42
3rd instar	35.17	Competition Predators, other TOTAL	4.79 <u>15.21</u> 20.00	56.9	.43
4th instar	15.17	Competition Predators, other TOTAL	7.41 <u>6.06</u> 13.47	88.8	.11

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	1.70	Overwintering mortality, other TOTAL	1.37	80.6	.19
Spring	.33	Predators, moisture other TOTAL	.26	78.8	.21
Emerged Adults	.07		0		
Females x 2	.07	Sex / TOTAL	0 / 0		
Generation TOTALS			132.83	99.95	S_G = .0005

* Number per one square foot of bark surface

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	194.78	Infertility, mites, pitched out, other	TOTAL	$\overline{-21.50}$		1.00
Larvae 1st instar	216.28	Competition Predators, other	TOTAL	76.82 0 $\overline{76.82}$	35.5	.64
2nd instar	139.46	Competition Predators, other	TOTAL	55.97 18.15 $\overline{74.12}$	53.1	.47
3rd instar	65.34	Competition Predators, other	TOTAL	17.06 14.39 $\overline{31.45}$	48.1	.52
4th instar	33.89	Competition Predators, other	TOTAL	19.68 10.73 $\overline{30.41}$	89.7	.10

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	3.48	Overwintering mortality, other TOTAL	.37	10.6	.89
Spring	3.11	Predators, moisture other TOTAL	2.68	86.2	.14
Emerged Adults	.43		0		
Females x 2	.43	Sex TOTAL	0 0		
Generation TOTALS			194.35	99.78	S_G = .0022

*
  Number per one square foot of bark surface

Life Table - Tree 66-9

x	1x	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of 1x	Survival rate within x
Eggs	18.64	Infertility, mites, pitched out, other				
			TOTAL	.86	4.6	.95
Larvae 1st instar	17.78	Competition Predators, other		1.60 6.60		
			TOTAL	8.20	46.1	.54
2nd instar	9.58	Competition Predators, other		.95 5.85		
			TOTAL	6.80	71.0	.29
3rd instar	2.78	Competition Predators, other		.01 2.38		
			TOTAL	2.39	86.0	.14
4th instar	.39	Competition Predators, other		.16 .23		
			TOTAL	.39	100.0	.00

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	0	Overwintering mortality, other TOTAL	− .22		
Spring	.22	Predators, moisture other TOTAL	.22	100.0	.00
Emerged Adults	0		0		
Females x 2	0	Sex TOTAL	0 0		
Generation TOTALS			18.64	100.00	$S_G = 0$

* Number per one square foot of bark surface

Life Table - Tree 66-10

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	10.86	Infertility, mites, pitched out, other	TOTAL	.42	3.9	.96
Larvae 1st instar	10.44	Competition Predators, other	TOTAL	.83 6.39 7.22	69.2	.31
2nd instar	3.22	Competition Predators, other	TOTAL	.27 1.73 2.00	62.1	.38
3rd instar	1.22	Competition Predators, other	TOTAL	0 .69 .69	56.6	.43
4th instar	.53	Competition Predators, other	TOTAL	.22 .14 .36	67.9	.32

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	.17	Overwintering mortality, other TOTAL	___ .17	100.0	.00
Spring	0	Predators, moisture other TOTAL	___ 0		
Emerged Adults	0		0		
Females x 2	0	Sex TOTAL	0 0		
Generation TOTALS			10.86	100.00	$S_G = 0$

* Number per one square foot of bark surface

APPENDIX IV

LIFE TABLES

1963 Generation Life Table - All Trees

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	35.323	Infertility, mites, pitched out, other TOTAL	$\overline{4.256}$	12.0	.88
Larvae 1st instar	31.067	Competition .962 Predators, other .852 TOTAL	.962 .852 1.814	5.8	.94
2nd instar	29.253	Competition Predators, other TOTAL	3.035 1.633 4.668	16.0	.84
3rd instar	24.585	Competition Predators, other TOTAL	2.432 6.489 8.921	36.3	.64
4th instar	15.664	Competition Predators, other TOTAL	6.913 0 6.913	44.1	.56

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	8.751	Overwintering mortality, other TOTAL	3.298	37.7	.62
Spring	5.453	Predators, moisture other TOTAL	1.947	35.7	.64
Emerged Adults	3.506		0		
Females x 2	3.506	Sex / TOTAL	0 / 0		
Generation TOTALS			31.817	90.07	S_G = .0993

* Number per one square foot of bark surface

1964 Generation Life Table - All Trees

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	99.285	Infertility, mites, pitched out, other TOTAL	<u>10.520</u>	10.6	.89
Larvae 1st instar	88.765	Competition Predators, other TOTAL	13.267 <u>.840</u> 14.107	15.9	.84
2nd instar	74.658	Competition Predators, other / TOTAL	17.437 <u>.605</u> 18.042	24.2	.76
3rd instar	56.616	Competition Predators, other TOTAL	14.248 7.548 21.796	38.5	.62
4th instar	34.820	Competition Predators, other TOTAL	18.284 2.261 20.545	59.0	.41

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	14.275	Overwintering mortality, other TOTAL	$\overline{10.757}$	75.4	.25
Spring	3.518	Predators, moisture other TOTAL	$\overline{2.414}$	68.6	.31
Emerged Adults	1.104		0		
Females x 2	1.104	$\dfrac{\text{Sex}}{\text{TOTAL}}$	$\dfrac{0}{0}$		
Generation TOTALS			98.181	98.89	.0111

* Number per one square foot of bark surface

1965 Generation Life Table - All Trees

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	153.969	Infertility, mites, pitched out, other	TOTAL	31.367	20.4	.80
Larvae 1st instar	122.602	Competition Predators, other	TOTAL	30.432 7.744 38.176	31.1	.69
2nd instar	84.426	Competition Predators, other	TOTAL	21.506 3.315 24.821	29.4	.71
3rd instar	59.605	Competition Predators, other	TOTAL	16.283 12.173 28.456	47.7	.52
4th instar	31.149	Competition Predators, other	TOTAL	18.617 6.792 25.409	81.6	.18

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	5.740	Overwintering mortality, other TOTAL	4.223	73.6	.26
Spring	1.517	Predators, moisture other TOTAL	.643	42.4	.58
Emerged Adults	.874		0		
Females x 2	.874	Sex TOTAL	0 0		
Generation TOTALS			153.095	99.43	.0057

* Number per one square foot of bark surface

x	lx	dxF	dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx	No.* dying during x	dx as a percentage of lx	Survival rate within x
Eggs	166.469	Infertility, mites, pitched out, other TOTAL	27.393	16.4	.84
Larvae 1st instar	139.076	Competition Predators, other TOTAL	41.796 15.293 57.089	41.0	.59
2nd instar	81.987	Competition Predators, other TOTAL	26.826 11.227 38.053	46.4	.54
3rd instar	43.934	Competition Predators, other TOTAL	10.108 11.388 21.496	48.9	.51
4th instar	22.438	Competition Predators, other TOTAL	12.725 4.732 17.457	77.8	.22

x	lx	dxF		dx	100 qx	Sx
Age interval	No.* alive at beginning of x	Factor responsible for dx		No.* dying during x	dx as a percentage of lx	Survival rate within x
Callow adults Fall	4.981	Overwintering mortality, other	TOTAL	3.222	64.7	.35
Spring	1.759	Predators, moisture other	TOTAL	1.495	85.0	.15
Emerged Adults	.264			0		
Females x 2	.264		Sex TOTAL	0 0		
Generation TOTALS				166.205	99.84	S_G = .0016

* Number per one square foot of bark surface