FIELD EVALUATION OF DENDROSOTER PROTUBERANS AS A BIOLOGICAL CONTROL AGENT FOR SCOLYTUS MULTISTRIATUS, THE PRIMARY VECTOR OF DUTCH ELM DISEASE

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ABSTRACT

FIELD EVALUATION OF DENDROSOTER PROTUBERANS AS A BIOLOGICAL CONTROL AGENT FOR SCOLYTUS MULTISTRIATUS, THE PRIMARY VECTOR OF DUTCH ELM DISEASE

By

James George Truchan

The ability of Dendrosoter to survive Michigan winters has been demonstrated by both supercooling and actual field releases. The northern distribution for Dendrosoter and Scolytus potentially occurs throughout Michigan's lower peninsula. Biologically Dendrosoter starts emergence in early April and two generations per year are indicated. Following the initial field release the parasite was recovered in small numbers but no subsequent recoveries were made. Tree crown areas were also sampled with rotary nets to detect activity, but with negative results.

American elm bark thickness was measured and Dendrosoter was found to be very severely limited in effectiveness by increasing bark thickness and tree DBH. In the smallest branches the parasites' ovipositer can only reach 50% of the cambial area with the percentage decreasing with increasing branch size. Spathius was shown to have approximately the same length ovipositor, suggesting that possible interspecific competition was occurring. This competition for the same host resource could account for Dendrosoters lack of success.

James George Truchan

A method of sampling closed grown American elms was determined and found to be reliable in giving estimates within 20% of the total Scolytus egg-galleries present.

The analysis for possible density-dependent regulation of Scolytus by the native parasites revealed that both Entodon and Spathius were having no effect in causing the observed density dependent beetle regulation. Both parasites together accounted for 2% of the observed 96.1% total beetle mortality. No increase in parasitism with increasing host density was observed. The operation of other non-selective mortality factors completely masked any regulatory properties of the parasites. Due to the action of these non-selective density-dependent mortality factors any possible regulatory effect of the native parasites was not apparent in this study.

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By

James George Truchan

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TABLE OF CONTENTS

LIST OF TABLES

Table | Page

LIST OF FIGURES

INTRODUCTION

In 1950 the first case of Dutch elm disease was reported in Michigan. Since this initial infection in the Detroit area, the pathogen Ceratocystis ulmi (Buism.) and its primary bark beetle vector Scolytus multistriatus Marsham have continued their spread throughout the state.

Most major communities affected have instituted chemical control programs. This method of control when used in conjunction with a diseased tree removal program has generally succeeded in reducing urban vector populations and keeping tree losses at a minimum. However, this type of chemical suppression program is at best a interim measure having several disadvantages in that it has to be repeated every year, has a very high operational cost; and the possibility of undesirable environmental contamination always exists.

With these disadvantages in mind, a biological control program was instituted at Michigan State University in 1965. Through the cooperation of the European Parasite Laboratory, Agricultural Research Service, U.S.D.A., a braconid parasite Dendosoter protuberans (Nees) Wesm. was brought into this country from Nanterre, Seine, France, for release and evaluation as an added source of mortality against the European elm bark beetle. This parasite is the most abundant member of the parasite complex that operates on this bark beetle in Europe. By establishing this parasite in rural situations it was hoped that

the beetle populations would be reduced to a level that would minimize its movement into urban areas. In 1965 and 1966, an effective parasite rearing program was developed and releases were made into woodlots in the East Lansing area. In 1967 a followup analysis of these initial releases indicated that the parasite had established and overwintered successfully in very small numbers. However, no long term quantitative studies could be carried out, as most of the elms in the release areas had died. This present study was then initiated in late 1967 with its primary objective being to measure the native parasite and bark beetle populations and the effect of the introduced parasite on these established populations.

Two 20-acre woodlots were located at St. Charles, Michigan, and 17,961 parasites were released in one plot and 5,293 in the other plot. Following this initial release, the remainder of the effort was directed toward developing methods and techniques applicable to obtaining quantitative information on both beetles and parasites. Density estimates were obtained for within tree populations and aerial populations. This information was required to evaluate the potential of Dendrosoter as an effective biological control agent on Scolytus populations. Analysis was also carried out to ascertain the effectiveness of the natural mortality factors in regulating elm bark beetle populations.

LITERATURE REVIEW

The geographic center of origin for Ceratocystis ulmi is at the present time not known. However, it has been hypothesized that it must be Asiatic in origin, as the only species of elm showing natural resistance are Asiatic in origin. The European literature on the disease has been reviewed by Readio (1935) who presented the following information: the disease was first described, in South Holland as a dieback of Elm, by Spierenburg in 1919. The causal organism, a fungus, was first isolated and described from wood tissue cultures of diseased trees by Schwarz in 1922. She named the new species Graphium ulmi. Buisman later found and described the perfect stage of the fungus, as an ascomycete, Ceratostomella ulmi. Hunt (1956) has revised this group of fungi and causal agent is now named Ceratocystis ulmi (Buisman) Moreau.

The disease was first discovered in the United States in 1930 at three locations in Ohio (May and Gravatt, 1931). The source of the infection was thought to be elm burl logs imported from Europe (Beattie, 1934). Readio (1935) found from an analysis of the disease distribution records that there were at least six separate introductions made. The pathogen has presently spread throughout most of the natural range of the American elm in the United States and Canada. The pathogen was first detected in Michigan in 1950 in the city of Detroit.

Since that time the disease has spread throughout most of the lower peninsula, and is becoming widespread in the upper peninsula.

All species of elm in this country are susceptible to the disease, and little or no natural resistance has been formed. However, some infected trees do recover (Banfield, 1968). Initial infection is characterized by a yellowing and wilting of the leaves followed by defoliation, death of the branches and finally the entire tree. Death of the complete tree may occur the same year or may take 2-3 years after initial infection.

The fungus attacks the water conducting vessels or xylem elements in a tree, plugging them with tyloses and brown gum-like substances, which prevent the upward movement of water from the roots. It has been suggested that a toxin is also produced, transported by sap movements, causing death of the wood ahead of the actual fungal mycelium. Landis (1969) has recently reviewed the literature in this regard and reported results consistent with this theory. Once the wood has been killed, the fungus produces fruiting bodies on the wood and in the bark. These fruiting structures (coremia) develop only in protected areas, such as cracks or insect galleries, found beneath the bark. Each coremium consists of a large number of spores suspended in a sticky matrix. These spores when introduced into the vessels of a healthy tree, increase rapidly by budding, and produce the characteristic disease symptoms (Banfield, 1941).

Two elm bark beetles, Scolytus multistriatus Marsham, the smaller European elm bark beetle, and Hylurgopinus rufipes (Eichoff), the native elm bark beetle, have been identified as the vectors of

C. ulmi in North America (Collins et al., 1936). S. multistriatus is the principal vector in the United States (Collins, D., 1938; Collins, et al., 1936; Rankin, 1941; Wallace, 1940) and is rapidly becoming the dominant species in southern Ontario (Finnegan, 1957). H. rufipes is the principal vector elsewhere in Canada and plays a very important role in transmission in northern areas of the United States (Collins, 1941; Collins et al., 1936; Rankin, 1941).

Scolytus multistriatus is an introduced species, being first reported in this country in 1909 by Chapman (1910), although it was probably introduced several years previous (in Collins, C., 1938). The biology of S. multistriatus in the United States has been adequately presented by Readio (1935) and Wallace (1940). The beetle overwinters in the larval stage with adult emergence taking place in late May to early June. Some of the adults feed in the 2-3 year old twig crotches of healthy elms. An excellent description of the injury caused by this type of feeding is given by Wolfenbarger and Buchanan (1939). The feeding of adults contaminated with fungal spores is the primary route of infection for the fungus to healthy trees, although infection does occur between adjacent trees whose roots are grafted.

S. multistriatus egg-galleries are constructed parallel with the wood grain, in the cambial region, of recently killed or dying trees. The smaller sized branches are preferred; however, the trunks of large trees may also be attacked. The average number of eggs laid per gallery is 68.5 $\pm$ SE 1.6 as reported by Wallace (1940). Beaver (1967c.) reported an average of 67.0 eggs per gallery from his work in England. There are five larval instars and, depending on summer

temperatures and the part of the country involved, larval development may continue and produce adults in late summer. These adults will be either reproduce a second complete and a partial third generation (Brown, 1965; Williams and Brown, 1969; Collins et al., 1936; Wallace, 1940), or they will be killed by low temperatures. The latter may occur in northern areas where larval development is stopped by cool fall temperatures and only a small portion of the early larvae complete development. These summer adults then feed and construct egg galleries; however, very few larvae develop far enough to survive the winter (Finnegan, 1957). Fox (1958) states that in southern Michigan the success of second generation larvae was very high, giving rise to the majority of the next season's spring adults. Observations at St. Charles, Michigan, indicate that second generation survival was low. Thus, in Michigan the Scolytus may have 1-1/2 or 2 generations per year. Figure 1 illustrates the life cycle as it occurs at St. Charles, Michigan; year to year differences in survival would change the thickness of the winter larval band.

The American elm bark beetle, Hylurgopinus rufipes, is native to this country and is probably distributed throughout the natural range of American elm (Whitten, 1960). Detailed biological investigations have been carried out in the northeastern United States by Martin (1938) and Kaston (1939). Finnegan (1957) working in southeastern Ontario found no difference in the biology as reported above. Butcher et al. (1966) presents 1964 and 1965 emergence patterns for the beetle which indicate that there is little or no difference from the biology as reported in Ontario.

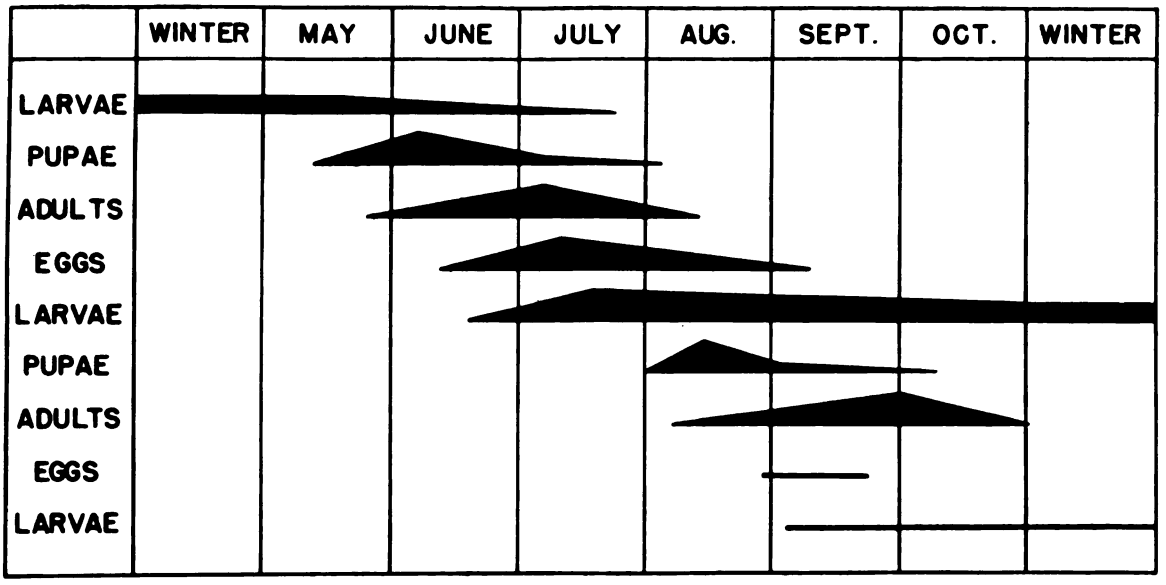


Figure 1.--Life cycle of Scolytus multistriatus at St. Charles, Michigan (after Finnegan, 1957).

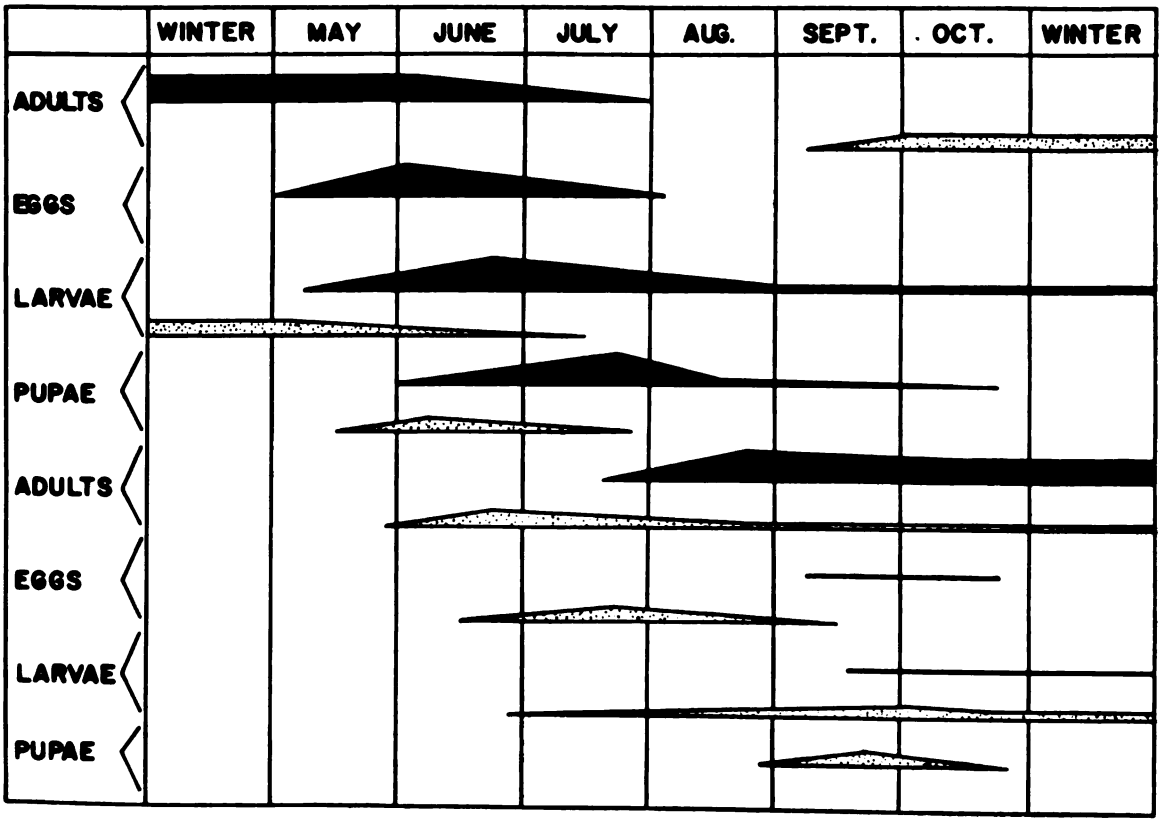


Figure 2.--Life cycle of Hylurgopinus rufipes at St. Charles Michigan (after Finnegan, 1957).

In Michigan there is one and a partial second generation of the beetle per year. The majority of the population overwinters in the adult stage in hibernation tunnels constructed in the bark of healthy elms. Becker (1935) gives an excellent description of these tunnels. With the advent of warm temperatures in the spring, the adults resume feeding in the hibernating tunnels occasionally scoring the xylem. Such contacts are for the most part ineffective in innoculating trees with the fungus. After feeding, the characteristic biramous egg gallery is constructed running across the wood grain under the bark of diseased or dead elm. Kaston (1939) reports the female beetle lays an average of 60 eggs per gallery, while Martin (1938) reported 56.1 ± 0.77. Larval development continues through the spring with the first adults emerging in late July. These new adults feed in the bark of the larger diameter branches of healthy elms until fall when they overwinter as adults in the bark tunnels. A few of the more advanced adults, however, may construct egg galleries in late summer, giving rise to overwintering larvae. A higher percentage of innoculation from adults contaminated with fungal spores occurs with the beetles maturing from these overwintering larvae. They emerge and construct their feeding tunnels later in the spring after the trees have formed the spring vessels (Collins, 1941).

The life cycle of the beetle as it occurs in Ontario is given in Figure 2 and is taken to represent the beetles development at St. Charles, Michigan.

In the absence of Dutch elm disease neither of the above mentioned bark beetles is of any economic importance as they are secondary

invaders and do not attack healthy trees. When both species are found together with the disease, S. multistriatus is considered to be more aggressive in attacking breeding material, thereby limiting the H. rufipes population to small numbers (Collins, 1941). Because of this competition, most current chemical control methods in the United States are directed specifically at S. multistriatus. Finnegan (1957) states, however, that H. rufipes is greatly underestimated as a vector and consideration should be given to it in any control program, even if S. multistriatus is abundant in the area. In regard to control of these two beetles, both species are very inefficient in infecting trees when compared to the number of sources of inoculum, the number of beetles emerging carrying the fungus from these sources, and the actual number of inoculation points made by the beetles in healthy trees (Rankin, 1941). Parker et al. (1948) found that only 6-8% of the feeding wounds made by S. multistriatus actually placed fungal spores in contact with the xylem cells. Collins (1941) indicates that the percentage of infections resulting from H. rufipes feeding is considerably less than that for S. multistriatus.

Biological control of pests, as an idea is probably as old as mankind itself; however, the first attempts at using this method in controlling insect populations did not take place until the early 1800's. The first successful use did not occur until the late 1800's, with the introduction of the ladybird beetle into California for the control of an introduced pest, the cottony cushion scale. The spectacular success of this new method of control caught the attention of entomologists and the public alike. Funds were then made available in

the hope that most of our most serious introduced pests could be controlled economically through the use of this method (Balch, 1959). The underlying assumption of this method is that a pest species introduced into a new environment will frequently multiply unchecked because its natural enemies have been left behind. The obvious solution then is to gather and introduce as many of these natural enemies as possible. This was the state of the art for a number of years; many thousands of individuals of numerous parasitic and predaceous insect species were introduced into the United States and Canada. A few documented successes were forthcoming, but the majority of the releases have been unsuccessful. The biological control attempts in this country through 1950 have been summarized by Clausen (1956). Dowden (1962) updated part of Clausen's list by summarizing the biological control attempts against forest insects through 1960. In Canada, a review of selected biological control attempts has been presented by Turnbull and Chant (1961). A more comprehensive and detailed review has been presented by McLeod et al. (1962).

Biological con-rol has developed and progressed from the early technical applications to the present state of an applied science. This progress has been possible through the development of quantitative methods to handle the complexities involved in pest population management with biotic agents. To this end considerable discussion has been presented concerning the self-regulation of insect populations. Excellent reviews have been presented by Thompson (1956), Solomon (1957), and Nicholson (1958). Considerable debate is also currently in progress on the merits of introducing a complex of natural enemies as

opposed to single species introductions (Balch, 1960; Turnbull and Chant, 1961).

Recently, with the advent of new selective pesticides, the integration of chemical and biological control has become possible. For many pests where only chemical control has been used in the past, the use of these new compounds allows the natural enemies to maintain populations and thus augments the natural control process. van den Bosch and Stern (1962) present a review of the literature and the advantages pertinent to this type of control method.

There is no record of any previous attempt to introduce natural enemies of S. multistriatus into this country. There have been two attempts to control other bark beetles by importing natural enemies. The first, an introduction of a clerid beetle, Thanasimus formicarius (L.) for the control of the southern pine beetle in the forests of West Virginia, was unsuccessful (Dowden, 1962). The second attempt was the introduction into Canada of Rhizophagus sp. and Rhopalicus tutela (Walk.) as biotic agents against the Eastern spruce beetle, Dendroctonus piceaperda Hopk. No evidence of survival was reported (McLeod et al., 1962). There have been several studies reported on the effect of parasitic fungi, bacteria and nematodes on the survival of S. multistriatus. Doane (1959) reported that up to 97% of the beetle larvae were killed by the muscardine fungus, Beauveria bassiana (Bals.) Vuill., in one epizootic he observed. Doane (1960) also reported that three species of bacteria were transmitted from larvae to larvae through bite wounds inflicted by neighboring larvae. Valek (1967) reviewed the literature on the detrimental effects of nematodes

in bark beetles and was unable to demonstrate any of those reported effects in his research on S. multistriatus.

Bushing (1965) published a synoptic list of parasites, reported on the family scolytidae for North America north of Mexico. He lists six species that have been reported as parasites of S. multistriatus. Only three species, Spathius canadensis Ashm., Cheiropachus colon (L.), and Entodon leucogramma (Ratz.), have been found commonly enough in association with S. multistriatus (Valek, 1967; Williams and Brown, 1967; Kennedy, 1970) to indicate their possible importance as mortality factors on the bark beetle populations. S. canadensis, a native species of braconidae, is a very non-specific parasite, having been recorded from 19 species of scolytidae and curculionidae (Bushing, 1965). Kaston (1939) reported the biology of this insect as he found it on H. rufipes. As a parasite of S. multistriatus, Williams and Brown (1969) working in Missouri reported it the most abundant native parasite. Kennedy (1970) reported similar results for both Ohio and Missouri. In Michigan, Valek (1967), however, found few individuals of S. canadensis in his trap-log studies. Cheiropachus colon is a European pteromalid that was presumably introduced into this country with S. multistriatus. An account of the biology and immature stages is given by Russo (1938) and Beaver (1967a.) for Europe and England respectively. This species, although common, has not been found in large numbers in the United States. Both of the above species oviposit through the bark, lay their eggs on or near the beetle larvae, with their larvae developing externally on the host larvae. C. colon has a much shorter ovipositor than S. canadensis and, thus, is limited to areas on the tree with thin bark.

The third parasitic species reported, Entodon leucogramma, an eulophid, is of European origin and was probably also introduced with the beetle. The biology of this parasite makes it potentially the most important of the three species. It is an egg-larval parasite. The adult female goes into the S. multistriatus egg-gallery and oviposits in the beetle eggs. The parasite larvae develop internally and either emerge from the fourth instar beetle larvae or overwinter inside the larvae and emerge early the following spring (Beaver, 1966a.). This parasite's habit of ovipositing in the bark beetle egg-gallery makes it less likely to be limited by bark thickness. Valek (1967) found this species the most numerous in Michigan. Kennedy (1970) reported it also numerous in Ohio.

The most common predator of S. multistriatus is a clerid beetle, Enoclerus nigripes (Say). Both the adult and larval stages are predaceous and reported to be quite numerous at times (Valek, 1967; Williams and Brown, 1969). The biology of this species is given by Kaston (1939) who found it attacking H. rufipes. Predation by woodpeckers has also been reported to be of local significance on S. multistriatus. Wallace (1940) observed the activity of a woodpecker as it methodically stripped the bark from an infested elm and devoured the exposed larvae. He reported the hairy woodpecker, Dendrocopus villosus, and the downy woodpecker, Dendrocopus pubescens, the most common bird predators of S. multistriatus in Connecticut. Other workers have recorded the attack of woodpeckers on S. multistriatus infested material, but no data has been published on their importance as a mortality factor. However, Knight (1958) working with the

engelman spruce beetle found that woodpeckers reduced the beetle population on the average from 45 to 98%. Beaver (1966b.) also found woodpeckers to be a important mortality factor in his population table study of the larger European elm bark beetle, Scolytus scolytus.

The Braconid parasite Dendrosoter protuberans, a native European parasite of S. multistriatus, was first introduced into this country from France in 1964 for biological studies and field releases. Shipments were initially made to the United States Forest Service Laboratory at Delaware, Ohio. In 1965, a shipment was also received by Michigan State University at East Lansing, Michigan.

Russo (1938) described the biology of D. protuberans as it was found on Pheotribus scarabaeoides (Bern.), a European olive bark beetle. Beaver (1967a.) describes aspects of the biology on S. multistriatus and S. scolytus in England. Studies carried out to date in this country have been concerned with mass rearing, overwintering success, establishment, and field determination of generation time. Techniques for mass rearing the parasite have been worked out by Valek (1967) and Kennedy (1970). Some concern was expressed whether this species could survive severe winter conditions. This has proven not to be the case as the parasite has overwintered successfully in Michigan, Ohio and Missouri (Truchan and Butcher, 1970; Kennedy, 1970; Williams and Brown, 1969). Establishment has been only reported from Missouri where Williams and Brown (1969) recovered individuals in 1967 from a 1966 field release. Generation time as reported by Kennedy (1970) from Ohio ranged from 28 to 52 days compared to S. multistriatus which ranged from 51 to 62 days. Two generations of D. protuberans per year are possible at least in

Ohio. D. protuberans oviposits through the bark onto the host larvae, so bark thickness could be a very important limiting factor. Beaver (1967a.) reported a mean ovipositor length of 2.4 mm while Valek (1967) calculated the linear regression of number of parasites emerging on bark thickness. The relationship was significant with the X-axis intercept between 6.0 and 6.5 mm as the average maximum bark thickness below which D. protuberans is functional. All of the above studies have used trap-logs and no quantitative data has been presented relating to the parasites effectiveness on natural bark beetle populations when added to the indigenous parasite and predator complex.

MATERIALS AND METHODS

Emergence Barrel

The sampling of adult bark beetle and parasite populations on a tree basis necessitated the development of a reliable and efficient extraction device. The criteria established were: (a) capacity--the device had to be capable of holding a large volume of wood and individual logs up to 12 inches in diameter. (b) Durability--ability to withstand outdoor use for periods up to two years. (c) Temperature and moisture relationship--temperature within the device could not deviate far from air temperature and the moisture level had to remain low enough to prevent fungal growth on the logs. (d) Efficiency--all insects, both the bark beetle and its parasites had to be collected immediately upon emergence to prevent reinfestation.

Many different types of collection containers have been constructed and used in various studies for the extraction of bark beetles from the trap-logs. Fox (1958) used vented 5-gallon metal pails; however, fungus and mold growth disrupted the beetle emergence. Valek (1967) used a modified 55-gallon fiber drum, but it could not be placed out of doors, and beetle reinfestation also occurred inside the barrels. Several types of containers have also been reported that were primarily designed for the continuous rearing of bark beetles where reinfestation of the logs is desirable (Griswold, 1948; Clark and Osgood, 1964).

The extraction container developed for use in this study consisted primarily of a standard 35-gallon lever-lock steel drum. The lid was removed from the barrel and a 9-inch high x 11-inch wide hole was cut offset to the edge of the lid. The exact position of the hole was determined by placing a 12-inch wide x 10-inch high (inside dimensions) 1-inch angle-iron frame against the lip and scribing the lid 1/2-inch inside the frame so as to leave a 1/2-inch strip of metal extending inside the frame. The bottom corners of the welded frame were cut off at a 45° angle to get the frame as close to the lid lip as possible. Cutting the hole was accomplished by using electric powered metal shears and a high speed carbarundum cut-off wheel in a hand grinder. Twelve 5/16-inch diameter holes were drilled through the frame and lid. Cadmium plated 1/4-inch x 1/2-inch long bolts were then used to fasten the frame to the lid.

Plans for the construction of the collection apparatus are given in Figure 3. All the wood is 3/4-inch exterior plywood with all joints held with glue and lathe nails. After the wooden frames are constructed, the #20 mesh screen cone is soldered together and a wide mouth canning jar ring is inverted and soldered to the cone. (Note: if acid core solder is used, the screen and lid must be washed with soap and water after soldering.) Fastening the cone to the bottom of the wooden frame is accomplished by placing 3/4-inch x 1/8-inch strips on the flaps of the cone and securing the wood and screen to the frame with a staple gun. Fastening the plexiglass front piece onto the wooden frame with screws completes the collection apparatus. This collector is then attached to the barrel lid with four screws, placed through the 1/2-inch wide strip

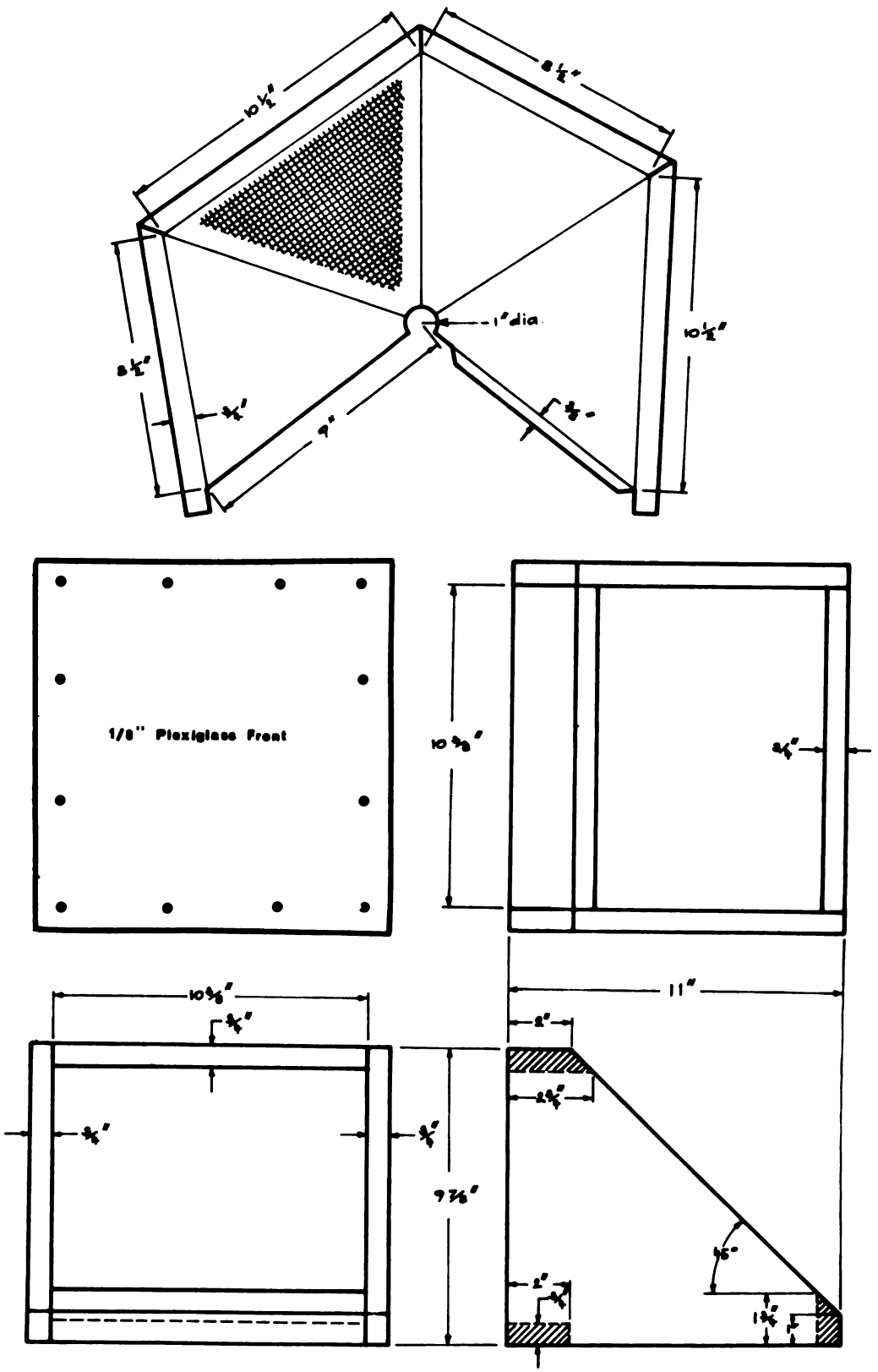


Figure 3.--Layout for constructing emergence barrel collection apparatus.

of metal extending inside the angle-iron frame, into the back of the wooden frame. A strip of caulking compound is first laid inside the frame to seal the lid to the wood. All that remains for the completion of the barrel is to fit the plywood platform into the bottom of the barrel. A piece of exterior plywood 3/8-inch thick x 14 1/2-inches wide x 38-inches long was laid in the barrel, measured, cut off in length, and the edges sealed with caulking compound. When the lid was placed on the barrel, there was a continuous flat surface into the collection apparatus (see Figure 4). The lid was held onto the barrel with three one-inch C-clamps placed around the lip. A one-pint canning jar filled half-way with 95% ethyl alcohol was used to collect and preserve the emerging insects. Fifty barrels were constructed for use in this study at an average material cost of $10 each.

Evaluation of this device in reference to the established criteria was also carried out. The capacity was more than adequate; log bolts up to 13 inches in diameter by 25 inches in length could be contained easily. A problem was encountered with these larger size logs in that the barrel platform would bow in the center. Use of 1/2-inch plywood corrected the situation. The barrel is extremely durable, for after two years continuous field use only the wood showed signs of weathering. Temperature conditions inside the barrel were measured by placing a #20 guage copper-constantin thermocouple inside one barrel painted black and one painted white. One thermocouple was also placed in a standard hygrothermograph shelter located next to the barrels. The temperature differences, under varying light intensities, were recorded on a Honeywell multipoint recording potentiometer. Three days were selected on the

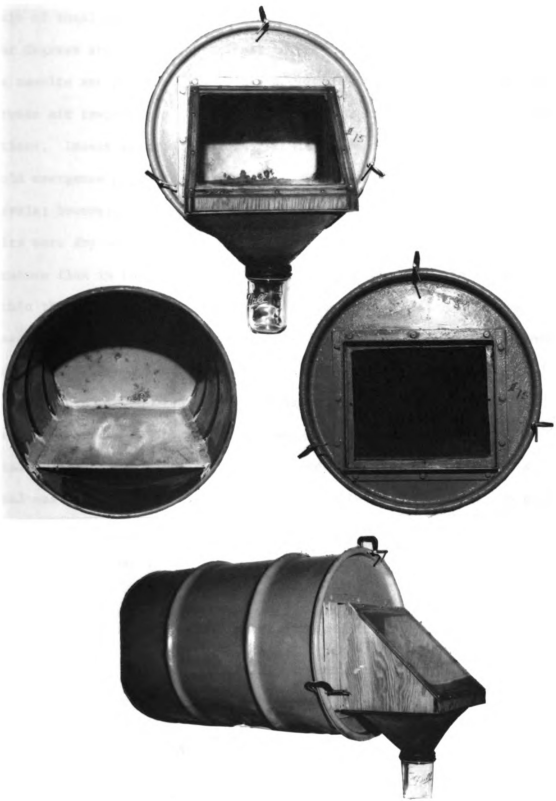


Figure 4.--Emergence barrel.

basis of total amount of solar radiation received, and the number at hour degrees above 50°F was calculated $\frac{(\text{max} + \text{min} - 50)}{2}$ for each point. The results are presented in Figure 5. There is a very close agreement between air temperature and the white barrel under the three light conditions. Insect emergence records should therefore reflect the true field emergence pattern. Moisture was not measured directly in the barrels; however, no fungus or mold growth was observed, and the log bolts were dry when finally removed from the barrels. The daily temperature flux in the field probably facilitated the exchange of air within the barrel causing the logs to dry normally. Efficiency was measured by carefully removing the logs from the barrel after emergence had ceased. The residue remaining was examined and the number of dead insects found was recorded. The number remaining inside for each species was added to the number collected by the device to obtain the total number of insects (ie., density) emerging from the logs. This total was then divided into the number collected by the device, to give the percent efficiency. Data obtained for each species considered is presented in Table 1.

TABLE 1.--Average percent of the total emergence that was collected by the emergence barrel over all densities for each insect species

Species	Mean	Range	No. Observations
S. multistriatus	98.2	66.7 to 100	22
H. rufipes	94.7	75.0 to 100	19
D. protuberans	99.2	94.4 to 100	17
S. canadensis	92.3	66.7 to 100	22
E. leucogramma	100.0	100.0 to 100	22

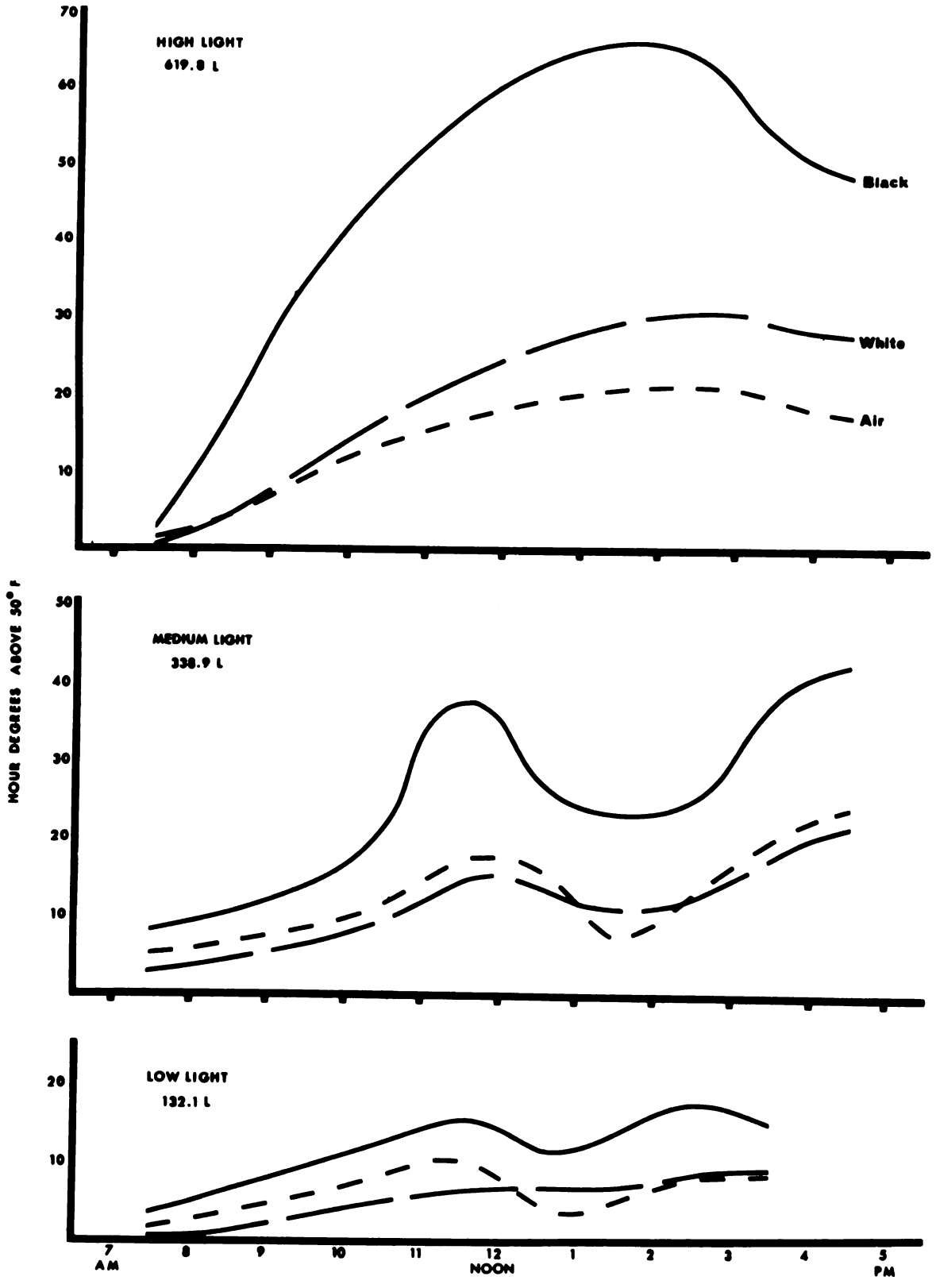


Figure 5.--Temperature relationship between black and white barrels.

It can be seen that the barrel is 90+ percent efficient in collecting both the emerging bark beetles and parasites. E. leucogramma adults were never found remaining inside the barrel regardless of the total number emerging. The collection efficiencies for the remaining species decreased somewhat with decreasing total density, when 10 or less individuals emerged. In this study the insect densities encountered were always much larger, so this decrease was not a problem. Reinfestation of the logs by the bark beetles was not apparent in any of the logs examined.

Emergence Bag

This device was developed to provide a cheap and efficient method for completely collecting all the emerging insects from a large number of individual log bolts. The completed bag is pictured in Figure 6 along with a view illustrating the attachment of the log. All the insects emerging from the log bolt were collected in the one-pint canning jar attached to the bottom of the bag. Ethylene glycol was used in preference to alcohol, as a killing and preserving agent, because the vapor would be non-toxic to the insects developing within the log. Average material cost per bag was about 75 cents.

The funnel portion of the device was constructed from a 34-inch by 48-inch deep #4 mill black polyethylene bag. The bag was cut in half diagonally from corner to corner with the exposed edges sewn together to form a cone. A 4-inch diameter embroidery hood, with #20 mesh Saran screen, was then inserted to provide ventilation into the cone. The log bolt was attached to a 14-inch diameter by 3/4-inch thick plywood disc with a 16 penny spike. The log and disc were then

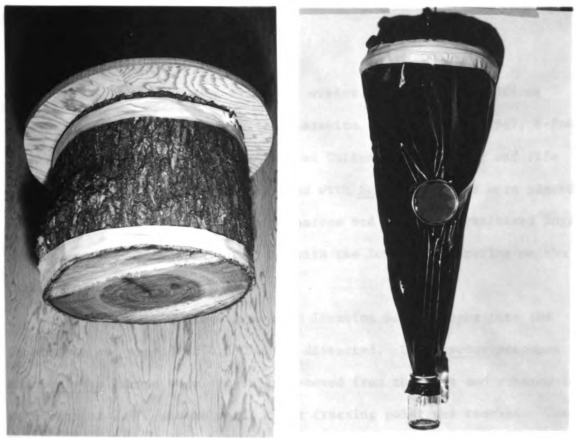


Figure 6.--Emergence bag.

suspended by a short chain onto an overhead rack. Attachment of the plastic cone to the disc, with masking tape, completed the assembly procedure.

Parasite Overwintering
Success in Michigan

Three locations with different winter temperature conditions were selected for overwintering the parasite. In August of 1967, 6-foot square cages were set up in woodlots at Galien, East Lansing and Fife Lake, Michigan. Logs heavily infested with Scolytus larvae were placed in each cage with both the adult parasites and heavily parasitized logs. The cages were removed in late fall with the logs overwintering on the forest floor.

In March, 1968, logs from each location were brought into the laboratory and stored at 4.5°C until dissected. Dendrosoter prepupae and Scolytus larvae were carefully removed from the logs and supercooled at a rate of 2.8°C/minute until their freezing point was reached. The term "supercooling" refers to the process of cooling below 0°C without the formation of ice crystals, and the supercooling point of an insect is the temperature at which freezing occurs. Insects that are able to survive freezing are termed "freezing-tolerant," whereas those killed by freezing are termed "freezing-susceptable." Dendrosoter and Scolytus fall into this latter group, where freezing is fatal. The method used to obtain the freezing points has been described by Truchan and Butcher (1970). Forty-five specimens from each location were supercooled as soon as possible after the logs were brought in from the field.

In April the cages were again placed at each location. Emergence barrels were also set up at each location to determine overwintering

success (Figure 7). The barrels were stocked with different diameter logs taken from each cage.

Tree Bark Temperature Relationship

In conjunction with the overwintering study, an experiment was set up to measure the bark and cambium temperatures at different aspects in a standing elm tree. This information would be useful in determining the actual temperature variations encountered by bark beetles and parasites overwintering on different sides of a tree and at various heights above ground.

An infested American elm 8 inches in DBH (diameter at breast height) and 40 feet tall was located in a woodlot on Michigan State University property. Thermocouples (#20 guage cooper-constantin) were placed on the north and south sides of the tree at three different levels (3, 15 and 28 feet) up the trunk. Two thermocouples were located on each side, one at the bark surface under a thin bark scale, and the second inserted into the cambial region directly below the first. The hole made for inserting the second point was filled with modeling clay to prevent erroneous readings. A standard weather bureau instrument shelter was located adjacent to the tree with a thermocouple point placed inside to measure air temperature.

The temperature at each of the 13 points was recorded on a Honeywell Electronic 16*, multipoint recorder. The recorder was located in an insulated steel shed near the tree. A thermostatically controlled electric space heater was placed in the shed to maintain air temperature at 50°F. A 15-minute interval timer was wired into the chart drive system of the recorder to allow only 15 minutes of operation

Figure 7.--Overwintering setup at three locations in Michigan.

during each hour. With the timer, 48 hours of recording could be contained on a single chart roll.

The recorder was operated 24 hours a day from January 25 to February 8, 1968. During the 14-day period, the temperature was recorded for a total of 344 fifteen minute hours.

Parasite Field Release and Evaluation

For this portion of the research woodlots had to be located with enough elm trees left alive to support several years of study on the beetle and parasite populations. Two woodlots approximately 20 acres in size were located near St. Charles, Michigan. Both areas were of the black ash-American elm-red maple forest type with elm the most abundant species. The first woodlot (Plot W) is located in Saginaw County T., 10N-R., 3E and is in the SW 1/4 of the NW 1/4 of Section 9. This plot contained trees that averaged 10 inches in DBH. The second woodlot (Plot C) is also in Saginaw County T., 10N-R., 3E in the SW 1/4 of the NW 1/4 of Section 16. The elm in this plot were of smaller DBH, averaging about 5 inches.

During early September, 1967, logs that were heavily infested with Scolytus and parasitized by Dendrosoter in the laboratory were placed in the center of each plot. The parasites were allowed to emerge and disperse naturally from the release site. In late fall after emergence was completed the logs were returned to the laboratory and the parasite emergence holes counted. In plot W a total of 17,961 holes were counted and in Plot C 5,293 holes. Valek (1967) reported a laboratory sex ratio of 2 females to 1 male. Using this information in

Plot W 11,974 female and 5,987 male parasites were released and in Plot C, 3,529 females and 1,764 males were liberated.

Trap logs 3-4 inches in diameter and heavily infested with Scolytus larvae were placed in the four cardinal directions from the point of release in each woodlot. Four logs were placed in each direction; two at 25 and two at 50 feet. Several logs were also placed at the point of release. These logs were collected in the spring and placed in emergence barrels. Woodpeckers heavily attacked the logs during the winter months so the logs from the 25 and 50 foot distances were combined into one barrel to slow down dessication.

In early May an infested 7-8 inch DBH tree, close to the release point in each plot was cut down, taken apart and grouped into log lengths within the same diameter increment (ie., 2-3, 3-4. . . 7-8 inches in dia.). All logs within each increment were placed in a separate emergence barrel. Later during the summer, in August, another infested tree 6-7 inch DBH was cut in each plot and handled in the same manner.

The pint-collecting bottles on the emergence barrels were changed weekly in all cases. The insects collected were later identified and counted in the laboratory.

Rotary Flight Trap

The rotary flight trap is a mechanical device that actively samples insect flight activity. It is independent of wind direction and insect behavior. Data collected is quantitative and can be expressed in terms of absolute numbers of insects per cubic volume of air. From these activity patterns useful biological information on dispersal can

be determined. In this study the activity patterns would indicate parasite establishment and population increase without destructive sampling of trees. However, as Helgesen and Haynes (1969) have pointed out, if the terrestrial segment of the population is not known the activity patterns cannot be interpreted on a total population basis. The following formula was also presented for calculating the volume of air sampled per sweep

$$V = 2\pi^2 r^2 R$$

where: R = radius of sweep (pivot to net center)

r = one-half diameter of net face

with the following trap operating at 30 rpm 1,395 cubic feet of air would be sampled each minute.

The first description of a rotary flight trap was published by Williams and Milne (1935). Chamberlin and Lawson (1940) presented a modified version and Nicholls (1960) published an updated version incorporating the principles used in the previous traps. Rudinsky and Daterman (1964) used a single net modification in a study on bark beetle attraction. Juillet (1962) compared four types of flight traps (the window pane, Malaise, rotary and sticky traps) and found that the rotary trap was the most reliable and versatile for most groups of insects.

The rotary trap presented here was developed and built in conjunction with personnel of the Cereal Leaf Beetle control program at Michigan State University. It consists simply of two adjustable conical nets that rotate around a central axis with power provided by a direct drive gear reduction motor. The trap in operation (Figure 8) consists

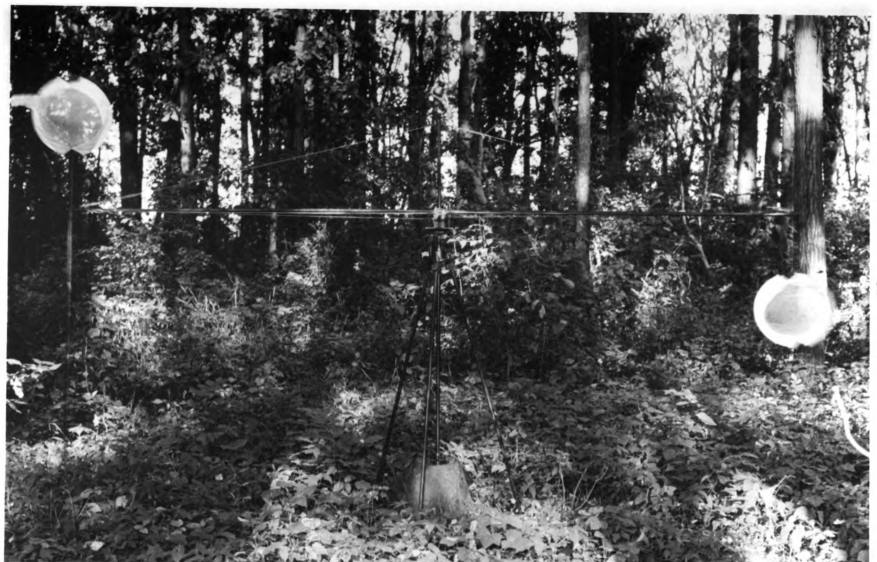


Figure 8.--Rotary trap in operation.

of two main components: a 12-foot long boom and net section and a 5-foot high support and motor section.

In 1968 two traps placed 100 feet apart were used in each of the two 20-acre study woodlots. The net heights were set at 3 feet and 6 feet above ground level. Power was provided by two Sears 1750 watt alternators. For the 1969 field season, only two traps were operated in Plot C. One trap was operated with nets at ground level and 6 feet above, and the other trap was placed on a 12-foot high scaffold with its nets operating 12 and 18 feet above the ground. In both years the traps were run from 8:00 a.m. to 6:00 p.m. on Monday, Wednesday and Friday, every week, weather permitting. The nets were emptied each afternoon and evening in 1968 and only in the evening in 1969. All samples were preserved with 95% ethyl alcohol in one-pint canning jars and transported to the laboratory for sorting and counting.

Weather records during operating periods were obtained from a standard recording hygrothermograph located in the center of each woodlot.

Bark Thickness Influence on Dendrosoter Success

Bark thickness is important since host larvae cannot be reached if they are beneath a thickness of bark greater than the parasites ovipositor length. Valek (1967) reports a significant decrease in the number of Dendrosoter emerging from logs with thick bark. He calculated a linear regression line which intercepted the X-axis between 6 and 6.5 mm (0.24 to 0.26 inches respectively) of bark thickness. No data were presented on what percentage of the bark was actually less than the mean ovipositor length of the parasite.

This experiment was set up to provide information on the percent of the cambium that could be reached by the parasite at different bark thicknesses both within and between trees of different DBH's. From a bark thickness-log diameter relationship developed for another study (see Elm Tree Quantification) the diameter increment of logs with a bark thickness of .26 inches was calculated to be 4-5 inches. Using this diameter log as a guide to where parasitism should approach zero, four trees, one from each of the following DBH increments 5-6, 7-8, 9-10 and 11-12 inches, were cut and sampled. Ten samples about 12 inches long were cut at random from each of the following branch diameter increments 2-3, 3-4, 4-5 and 5-6 inches, from each of the four trees. Before cutting, each sample was wrapped with masking tape to prevent the bark scales from being knocked off.

Measurement of each sample was carried out by using a pair of screw-type adjustable dividers and a wheel-type map measurer. The parasites mean ovipositor length was calculated by measuring 145 laboratory reared individuals. This mean ovipositor length was set on the dividers and each sample was then marked on the cambium when the bark thickness was equal to or less than the divider set. The map measurer was rotated once completely around the circumference of the cambium and the number of inches recorded (B). For the second measurement, the areas marked were not measured (A). Calculation of the percent of the cambium available to the parasite was accomplished by using the following formula:

$$\text{percent cambium available} = 100 - \frac{(A)}{(B)}$$

Tree Quantification and
Sampling Method Development

The development of a reliable sampling method for determining the populations of Scolytus and its parasites, produced by a given tree, necessitates the selection of an unchanging standard sized sampling unit, and the quantification of this sampling units distribution within the various tree strata (branch sizes) (Morris, 1955, 1960). The size and distribution of the insect populations can then be determined by a self-weighting stratified sampling design which maximizes the accuracy of the population estimate (Southwood, 1966). This type of design is used when it is not known initially which of the strata will be more variable (Snedecor and Cochran, 1967). Estimates of sampling error, used for calculating optimum number of samples can be determined by taking two samples from each strata (Southwood, 1966; Snedecor and Cochran, 1967).

The sampling unit selected for use in this study was a square foot of cambial surface area (C.S.A.). This unit is unchanged throughout the entire tree and is readily calculated from the following formula:

$$\text{C.S.A. } ft^2 = \frac{2\pi(R-B)\ (Lx12)}{144}$$

where: R = Radius of the log in inches

B = Bark thickness in inches

L = Length of log in feet

The bark thickness value was calculated from a linear regression formula based on the relationship between bark thickness and log diameter. The bark data was obtained from seven closed-grown American elms that

were also measured as to the following parameters: DBH, total height, crown height, crown width and age. Each tree was cut down and the limbs sectioned and grouped into strata based on 1-inch differences in diameter (0-1, 1-2, 2-3, 3-4 . . . DBH). The total length of all the logs in each strata was recorded. Bark thickness was measured with a Swedish bark thickness guage. Two measurements were taken on opposite sides of all logs at two foot intervals down the entire length contained in the strata.

Using the length and bark thickness data in the above formula, the total amount of cambial surface area was calculated for each strata and the total tree. The complete data for each tree, parameter measurements, strata C.S.A. and total C.S.A. was analyzed using Michigan State University's CDC 3600 computer with the Ag. Exp. Stations Least Squares Routine No. 7. All possible regressions were calculated to determine the best single and/or combination of parameters that would predict total C.S.A. and individual strata C.S.A.

Four trees with various DBH's falling within each of the following diameter increments: 4-5, 5-6, 6-7, . . . 11-12 inches were felled. All the strata except 0-1 and 1-2 were sectioned out, measured and the C.S.A. calculated. These data were then combined and averaged for the four trees within each DBH increment to give the C.S.A. distribution for each strata contained within the average tree. This information on the average tree was used to prepare a table giving the length of log that had to be cut, from each stratum contained within a given DBH tree, to yield a 10 percent sample of the total C.S.A. contained within the tree. The 0-1 and 1-2 inch strata were found to produce very few beetles or parasites under field conditions so they were not considered further.

During the spring of 1968, trees that had leafed out died, and were currently under heavy attack by Scolytus, were sought in plot C. A tree within each DBH increment except the 7-8 and 11-12 inch ones were located and marked. The trees were allowed to stand throughout the summer, fall and winter. In early spring of 1969 the trees were felled, and two 20 percent samples were taken at random from each strata using the table developed previously. The samples were brought back to the laboratory and placed in separate emergence bags for extraction of the beetles and parasites. Logs from each strata not included in the samples were also returned to the laboratory and placed in separate emergence barrels.

RESULTS AND DISCUSSION

Dendrosoter Overwintering Success in Michigan

The mean supercooling points obtained from the three locations where the parasite was overwintered are presented in Table 2. The mean supercooling points indicate that Dendrosoter can overwinter successfully in most areas of southern Michigan (Figure 9). In 1967-68 the lowest temperature of -28.6°C was recorded at Fife Lake. This is not reflected in the data as the logs were covered with several feet of snow, which undoubtedly affected the conditioning that occurred. The Fife Lake data shows the highest supercooling point and the lowest temperature. Supercooling points for Scolytus although exhibiting more variation, are not different from those of the parasite; so the maximum resistance to cold is about the same for both species and the northern ranges should overlap.

In regard to the spread of Dutch elm disease, Fox (1957) presented a map indicating that the disease was spread throughout the southern half of the state. In the following 12 years, the spread has continued northward; and the disease is now present in most northern counties of the lower peninsula. In the Fife Lake area, the most abundant bark beetle was found to be Hylurgopinus. In supercooling studies carried out by Kaston (1939) on Hylurgopinus, he reported the larvae froze at -24.4°C $\pm$ 0.2°. This coincides with the above data for

TABLE 2.--Supercooling data for D. protuberans prepupae and S. multistriatus larvae from 3 locations in Michigan for winter of 1967-68 (after Truchan and Butcher, 1970)

Location	Date into laboratory (Mar. 1968)	Dendrosoter		Scolytus	
		Mean supercooling point °C ± SD	Range	Mean supercooling point °C ± SD	Range
Galien	15	-24.0°±1.43	-26.9° to -22.4°	-24.8°±3.67	-26.9° to -19.0°
E. Lansing	8	-24.1°±0.82	-25.2° to -23.0°	-23.6°±5.17	-28.6° to -17.9°
Fife Lake	1	-23.5°±2.36	-25.2° to -19.0°	-22.7°±5.48	-26.9° to -16.2°

Figure 9.--The mean extreme temperature (°C) in Michigan during January for the period 1950-68 (U.S. Weather Bureau Data).

Scolytus; however, Kaston reported all the larvae survived after being frozen, indicating that Hylurgopinus is possibly a freezing tolerant species. No data was reported on adult supercooling. These data offer a possible explanation for the dominance of this species in the Fife Lake area, and its increased importance reported from nothern Ontario by Finnegan (1957). In 1968 heavily infested logs were again placed in the Fife Lake area to overwinter. The logs were placed on racks above the snowcover. In March they were brought back into the laboratory. No specimens were found alive. The lowest temperature recorded from Fife Lake was -25.0°C in December. At this one temperature based on the data in Table 2, at least 93% total mortality would be expected. How this value was obtained is discussed below.

Salt (1950) has demonstrated that for a specified degree of cold-hardiness (ie., ability to supercool) the probability of freezing is dependent on two factors: temperature and time. With these two factors interacting in nature, it is unrealistic to state that an insect feeezes at -10°C: it either remains at -10°C for a period of time before freezing or it freezes immediately when the temperature reaches -10°C. The first instance involves variable time at a fixed temperature and the second variable temperature at a fixed time (Salt, 1960). The data presented in Table 2 is of the second type where time is held constant and the temperature is varying, yielding the mean value for a probability distribution with a zero time element. With this type of distribution, the probability of obtaining nucleation (ie., freezing) increases as the temperature decreases until a temperature is reached where the probability approaches 1, and all of the remaining individuals will

freeze. Table 3 gives the probability distributions obtained from averaging the individual freezing point data, the means of which are presented in Table 2, for the three areas. It should be remembered that these data represent only the limits of supercooling for a particular case and that more freezing is possible at the higher temperature if the time factor is considered.

TABLE 3.--The percent of the total population killed by freezing as the temperature is lowered to each point

	Mean Freezing Temperature °C	-20	-23.1	-24	-24.2	-25	-25.3	-26	-26.4
Scolytus	24.0	20	45	50	58	67	79	93	100
Dendrosoter	24.0	2	39	76	95	100			

To make reliable predictions of freezing mortality under field conditions, data are needed on the effect of variable time at fixed temperatures on the overwintering populations. In reference to Table 3, if the temperature drops to -24°, we can say that at least 50% of the beetles and 76% of the parasites will be killed; however, if the temperature remains at -24° for several days, we have no estimate of what this time factor will add in the way of greater mortality.

Another consideration relative to the previous presentation is the actual temperatures encountered by the overwintering insects in the bark of a standing tree. Beal (1934) measured the bark and cambial temperatures on six bark beetle infested ponderosa pine trees in Oregon. He reported bark thickness as the most important factor in determining air-cambial temperature relationships. The bark thickness he was

working with ranged from 1/2" to 2" thick. In a period of rapidly falling temperature, an air temperature of -26°F was recorded with a cambial temperature ranging from 8 to 29° higher. He also reported differences on the north and south sides of trees but attributed no importance to these differences. Keen and Furniss (1937), working with the western pine beetle Dendroctonus brevicomis in ponderosa, pine reported an inverse relationship of bark thickness to beetle mortality for bark bark greater than 1/2 inch thick. They also reported greater beetle mortality on the north side of infested trees as compared to the south side.

The temperature data recorded from the tree wired for this study is presented in Table 4. The lowest temperature recorded during the operating period was -17.6°C which is not lethal in an absolute sense; therefore, number of hours the temperature at each point was below 0°C is presented for comparative purposes.

TABLE 4.--Number of hours the temperature recorded at each point was less than 0°C for the period from January 25 to February 8, 1968

Level Code	Height (feet) Above Ground	North		South		Branch Diameter (in.)	Bark Thickness (in.)
		Bark	Cambium	Cambium	Bark		
A	3.0	165	176	160	162	5.5	0.31
B	15.0	186	176	165	171	6.7	0.36
C	28.0	196	188	184	187	8.6	0.45

Air Temperature: Hours below 0°C = 186

Solar Radiation Received = 2,084 Langleys

The relationship shown between the cambium on both sides of the tree is in agreement with the data from the literature in that the duration of cold temperature is prolonged in the north facing cambium of the tree. As has been pointed out previously, the longer the temperature stays at a lethal point, the greater the potential mortality. Thus in the south facing cambium where the temperature is fluctuating due to solar insolation the effect of a lethal temperature is not as severe due to the shorter amount of time spent in the lethal range. The effect of bark thickness is not clear as it is confounded within the height and diameter differences.

In March, strips of bark three inches wide by four feet long were removed from the middle of the trunk on both the north and south sides of the above tree. In the laboratory the strips were examined for living larvae. Only six were found in the north strip while 36 were found in the south strip. Assuming all other factors to be operating with equal intensity greater beetle survival is indicated in the south facing cambium.

Emergence records obtained from each of the areas where Dendrosoter was overwintered for use in the supercooling study are given in Figure 10. Initial emergence at all three locations starts quite early in April. However, Kennedy (1970) reported the same early spring emergence from Ohio. From a survival standpoint the temperature in Michigan often goes below freezing during April, probably causing some mortality among the early emerging individuals. From a beneficial standpoint this early emergence also indicates that the overwintering Scolytus larvae are available for parasitism by Dendrosoter in the

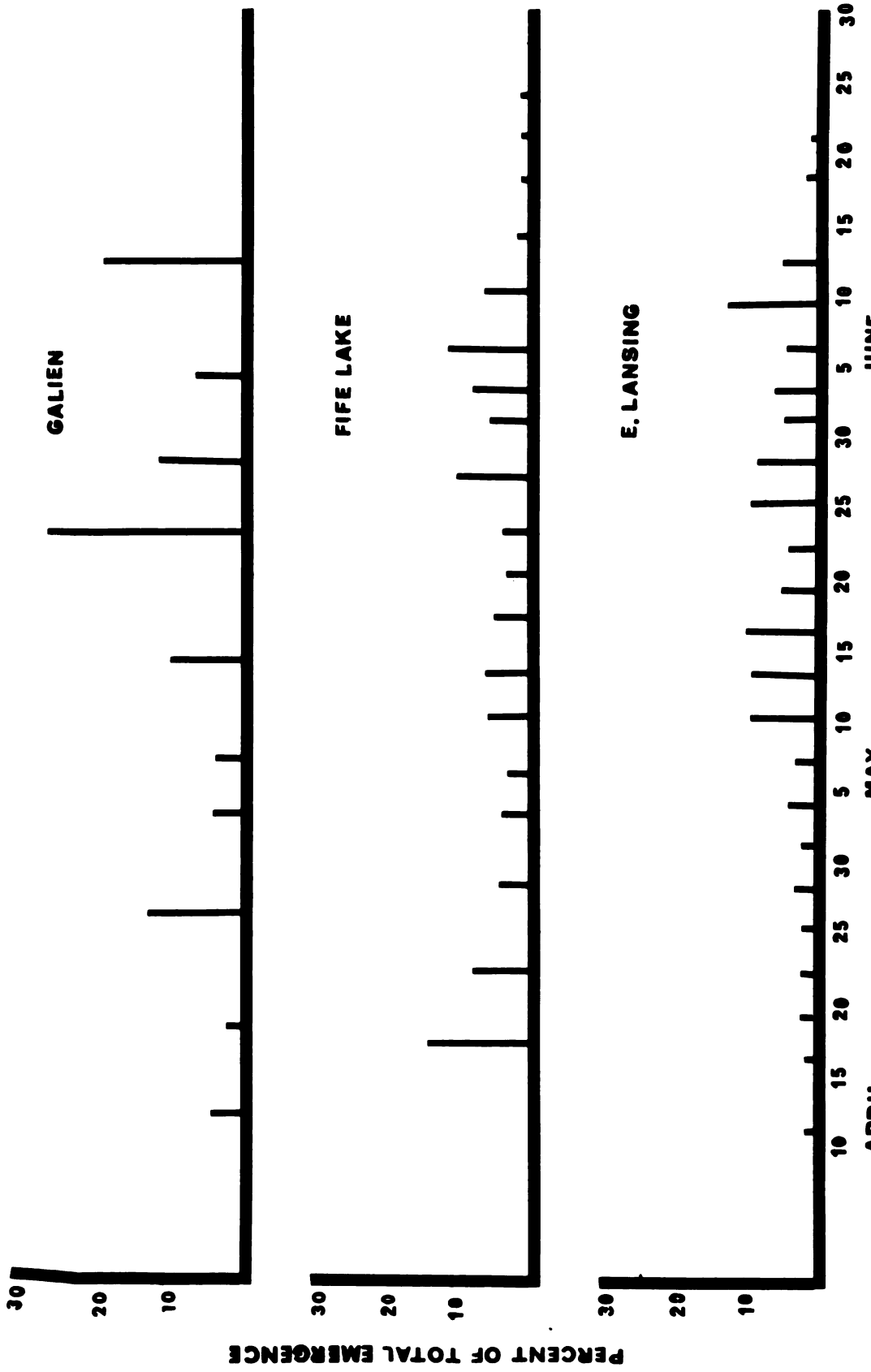


Figure 10.--Percent of total emergence that took place in each location on a given date for D. protuberans in 1968-69.

spring. Parasitism at this point in the development could be most important in reducing the size of the spring beetle populations.

Dendrosoter Field Release and Evaluation

The results of the trap-log study are presented in Table 5. As shown the parasite has dispersed and overwintered successfully in both plots. Plot-W shows a consistently higher return; this is not unexpected due to the larger size of the initial release. No significance is apparent in the direction of spread except possibly in plot W where 46 individuals were collected from the logs east of the release point. The prevailing westerly winds may account for this movement. As mentioned previously the logs in both woodlots were damaged very severely by woodpeckers so the data presented should be interpreted only as successful overwintering and recovery of Dendrosoter in both plots following field releases.

TABLE 5.--Number of Dendrosoter recovered in 1968 from trap-logs overwintered at the release site and in the 4 cardinal directions out from the 1967 release points

	Number Released		Number Parasites Recovered from Four Trap-Logs				
Plot	Male	Female	Release Site	North	South	East	West
W	4,491	13,472	43	0	9	46	3
C	2,647	3,971	23	1	0	0	3

Two trees, one from each plot, that were heavily infested with Scolytus larvae during the 1967 parasite release period were cut as described earlier and placed in emergence barrels. The emergence data

collected are presented on an equal area basis for each branch diameter class (Figure 11). This analysis allows for a quantitative comparison of the within tree distribution and relative abundance of both the beetles and parasites. The data from each tree was averaged together as the differences observed between trees was slight (the emergence data for the individual trees is given in Appendix B). Dendrosoter was successful in establishing itself in both plots. The distribution within the trees shows a gradual decline with increasing branch diameter. This decrease is probably due to bark thickness; however, this factor will be discussed in some detail later. Both Spathius and Entodon exhibit a similar distribution but are numerically more abundant. Entodon does not oviposit through the bark so the numerical decrease is more likely to represent a response to decreasing host density. Spathius oviposits through the bark which is again reflected by the steeper numerical decrease in the larger branches similar to that shown for Dendrosoter.

Both bark beetles are present in the plots; however, their within tree distribution is exactly the opposite. Scolytus shows decreasing abundance as the branch diameter gets larger, while Hylurgopinus increases numerically in the larger sized logs. This relationship appears biologically to be a matter of preference, in breeding site selection, as the egg gallery distribution (Appendix B) follows the same pattern. The presence of both beetle species in the same tree makes the assessment of parasitism difficult, in that both Dendrosoter and Spathius are non-specific parasites capable of developing on either beetle species. (Dendrosoter has been reared from Hylurgopinus infested logs in our laboratory). It is not known whether Entodon can successfully oviposit

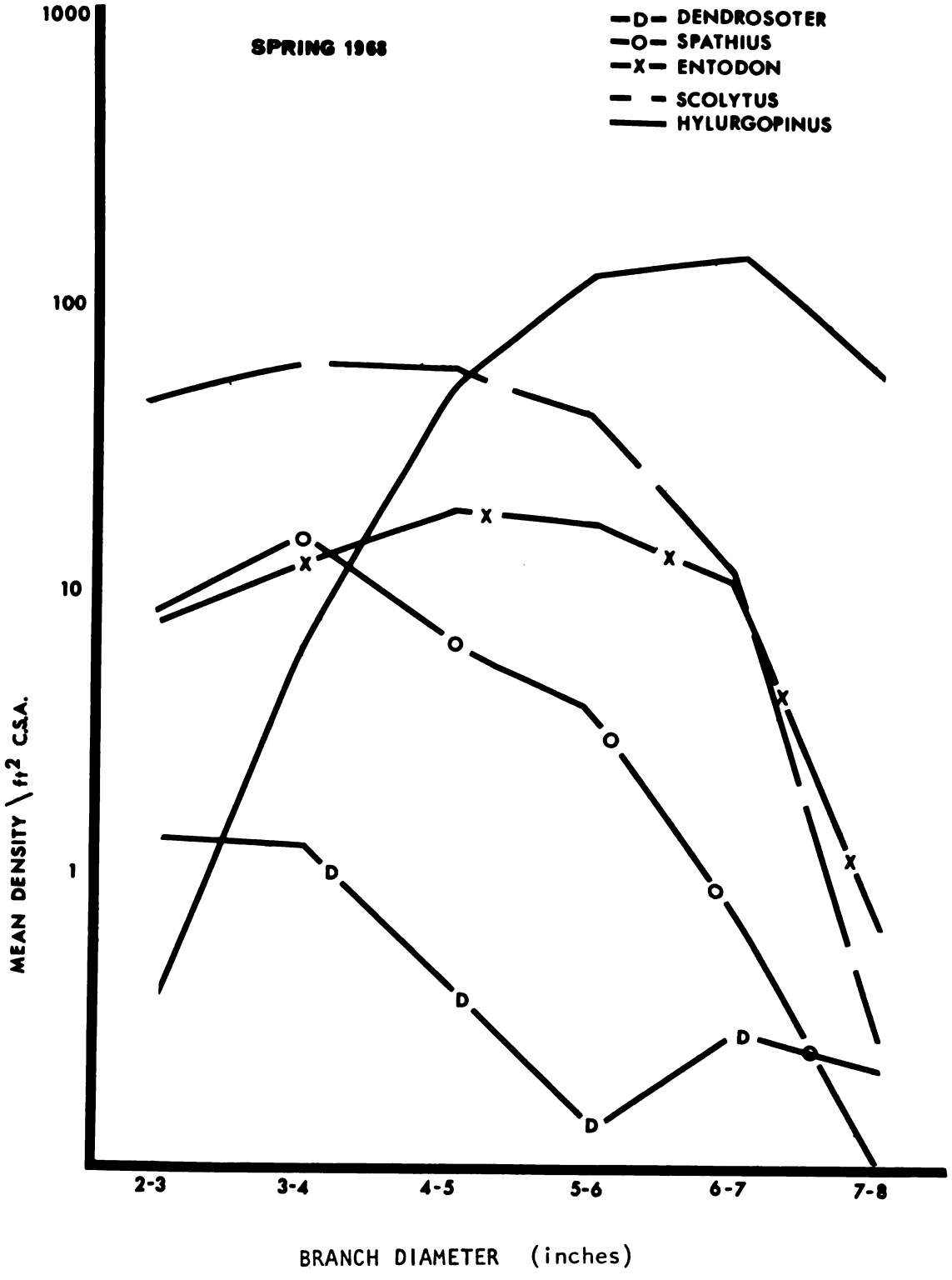


Figure 11.--Average number of insects collected per ft^2 C.S.A. for each branch diameter from two 7-8" DBH trees (Spring 1968).

in the smaller egg galleries of Hylurgopinus. However, Beaver (1966a.) suggests that this species is restricted to the genus Scolytus. Without a detailed biological investigation, the proportion of parasitism occurring on Hylurgopinus cannot be determined precisely. However, the majority of parasite overlap would occur in the larger branches where Hylurgopinus is most abundant. Thus by assuming that all parasites are operating only on Scolytus, the percent parasitism calculated for the larger branches would be an overestimate. Allowing for this error, all the parasites will be assumed to be operating only on Scolytus for the remainder of the text.

To continue following parasite establishment throughout the season, another set of trees 6-7 inches in DBH were located. These trees had died in the spring and were under heavy attack by Scolytus during late spring and early summer. In late August the trees were felled, cut, and placed in emergence barrels. Sample collection continued weekly throughout October until emergence had ceased. The trees were allowed to overwinter in the barrels and collection was continued the following spring. The data from the fall collections are presented in Figure 12 and the spring data in Figure 13. Only one specimen of Dendrosoter was collected in the fall indicating that a second generation in late summer is a possibility. The large number of Hylurgopinus collected indicates the size of the summer adult population. The very small emergence of Scolytus is noted and also that the emergence is quite evenly distributed throughout the tree. Spathius and Entodon exhibit the same distribution pattern observed in the spring with the only noticeable difference evident in the smaller numbers and steeper

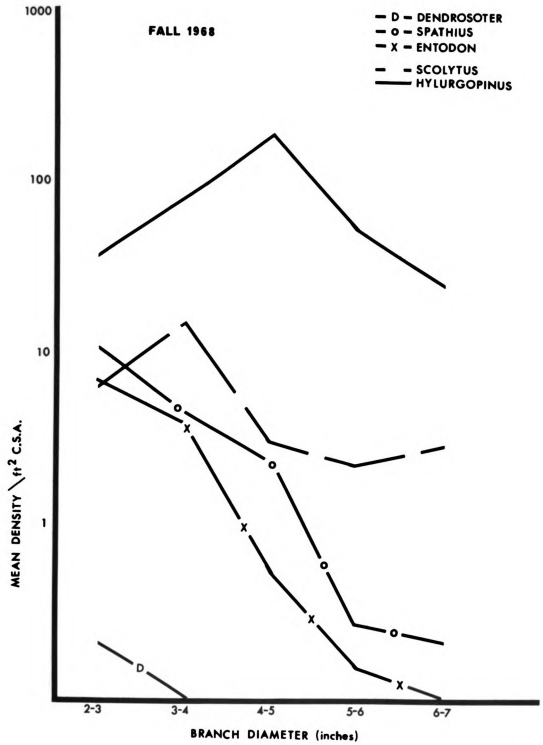


Figure 12.--Average number of insects collected per ft^2 C.S.A. for each branch diameter from two 6-7" DBH trees (Fall 1968).

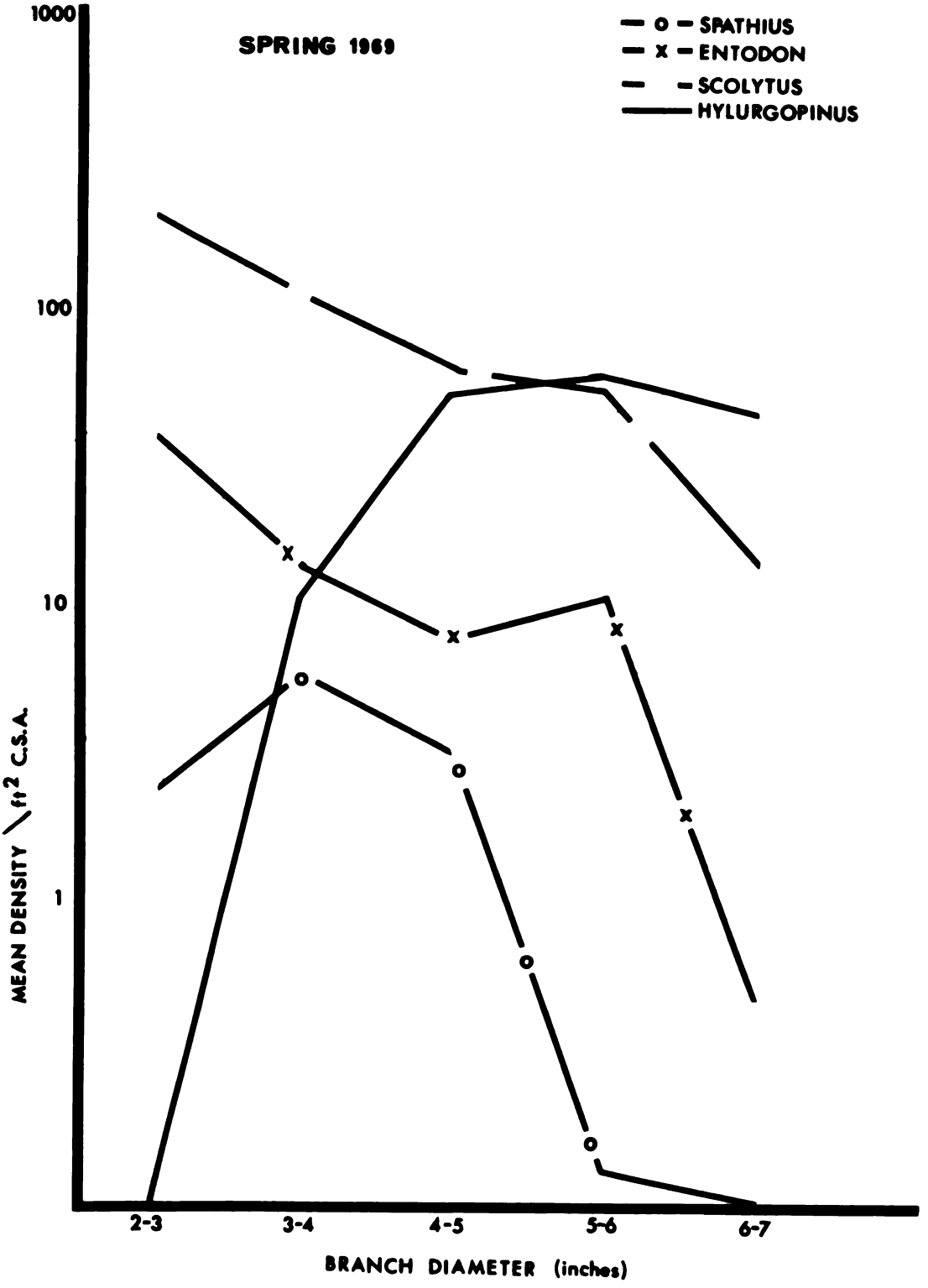


Figure 13.--Average number of insects collected per ft^2 C.S.A. for each branch diameter from two 6-7" DBH trees overwintered in barrels (Spring 1969).

decrease observed for Entodon. The spring collections indicated that Dendrosoter was not present in any area of the trees as no specimens were recovered. The emergence data for the remaining species follows the same general patterns described previously. One exception is evident for Scolytus. The distribution shows an almost linear decrease with increasing branch diameter as compared to the curvilinear decrease noted in the previous spring's data. A detailed treatment of this difference will be presented later in the text. Also of interest is that of the total Scolytus emergence recorded in the fall 1968 and spring 1969 for both trees, only 6 percent occurred in the fall. This supports an earlier statement that there is only one effective Scolytus generation per year in the study areas.

Rotary flight traps were also used in conjunction with the tree sampling in an attempt to measure the successful establishment of Dendrosoter in each plot. Two traps were operated from April to September, 1968, on the schedule mentioned previously. Although Dendrosoter individuals were collected in the trap-logs and tree sampling studies, no specimens were collected with the rotary trap nets. The flight activity patterns for the native parasites and the bark beetles, which were collected, are presented in Figure 14 and 15. The 435,000 cubic feet equals the amount of air in 1/4 of an acre of forest, with trees 40 feet tall. The sample dates given represents the average catch from both plots for the previous week. The volume of air contained in a 20 acre woodlot with trees averaging 40 feet in height, was calculated to be about 35 million cubic feet. The four nets operating in each plot sampled a volume of air equal to four times the above amount,

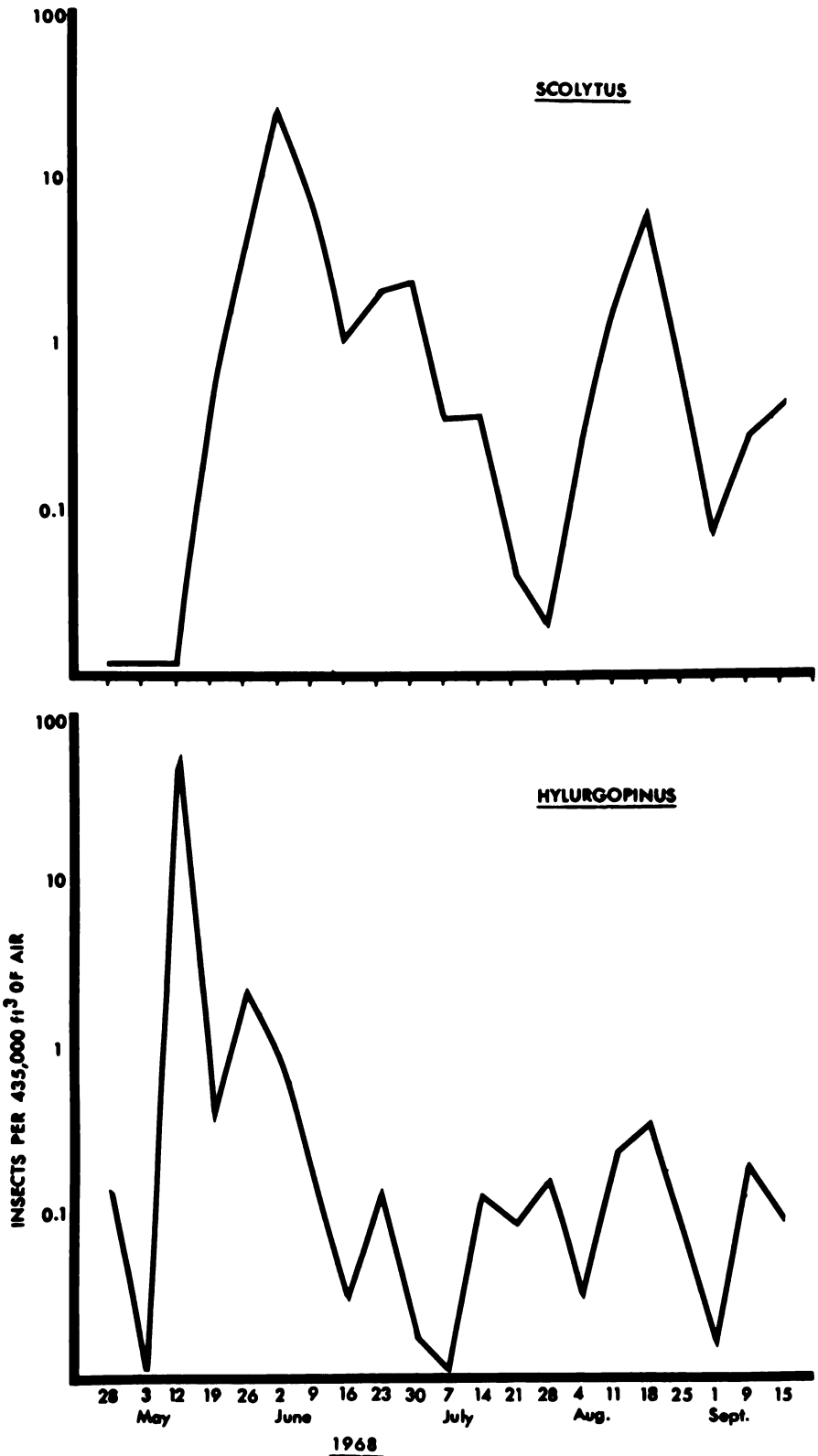


Figure 14.--Mean aerial density of Scolytus and Hylurgopinus in plots W and C for 1968.

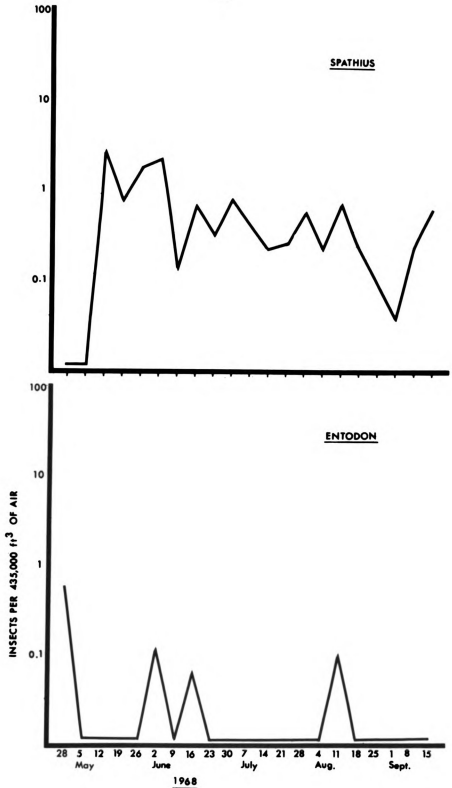


Figure 15.--Mean aerial density of Spathius and Entodon in plots W and C for 1968.

during the 1968 season. This sized sample should have detected any parasite activity; however, the population was at a very low level, compared with the native parasites, and may have escaped detection. Other possible explanations are: that Dendrosoter possibly is able to avoid being captured by the sampling nets, or is remaining at a different height within the forest out of reach of the nets. It is possible, therefore, that the nets are not good sampling devices for the parasite. The effect of the problem is demonstrated by Entodon in Figure 15, where the aerial yield is much less than that shown for Spathius; both species had about the same within tree density. The collection of Spathius in good numbers suggests that Dendrosoter which operates in the same manner should also be available for collection.

The traps were run again in the spring of 1969 to determine if the Dendrosoter population was too small to be detected in 1968 and also if the parasites were staying in the tree crown area. Only Plot-C was selected for sampling because the smaller sized trees would present more host larvae within the parasite's oviposition range, resulting in a larger population. One of the two traps used was placed on a platform to sample air in the crown area. Four levels of air were sampled at 3, 6, 12 and 18 feet above the ground. Both traps were operated from early May until mid-July in 1969. Total cubic feet of air sampled exceeded twice the volume of the woodlot, with again no Dendrosoter being collected at any level. Either the parasite population is still at a very low level or it has not survived. In either case no large numerical response has been apparent with the sampling carried out to date in both plots. The data collected for the beetles and native parasites is

presented in Figures 16 and 17. Very little difference was found between the different levels so they were combined for presentation.

It is again evident that Entodon is not being sampled equally as the numbers collected are much lower than those for Spathius although the spring, 1969, tree data (Figure 13) show Entodon more abundant. Entodon is also well synchronized with Scolytus in that emergence occurred in 1968 and 1969 during the later segment of beetle flight, when egg-galleries would be readily available. Spathius exhibits no distinct peaks during both years; activity is slightly greater during the spring and tapers off gradually toward fall.

The flight patterns for both beetle species reflected their respective overwintering stage. Hylurgopinus overwintering as an adult was active in early May during both years with the 1968 data indicating flight in late April also. Scolytus flight started in mid-May after completion of larval development and pupation. During the first few days of Scolytus activity, a greater proportion of the population in flight consisted of female beetles. This observation supports the evidence presented by Meyer and Norris (1964) indicating that the female is the pioneer beetle in locating suitable elm breeding material.

The influence of temperature on flight initiation by Scolytus, Spathius and Entodon was also examined. Temperature accumulations up to the day of first flight are shown in Table 6. Air temperature data was obtained from the U.S. Weather Bureau Station one mile from the research plots, and Arnold's (1960) method of calculating heat units was used. A threshold of 50°F gave the most consistant results for Scolytus and Spathius while 40°F was a more consistent predicting threshold for Entodon.

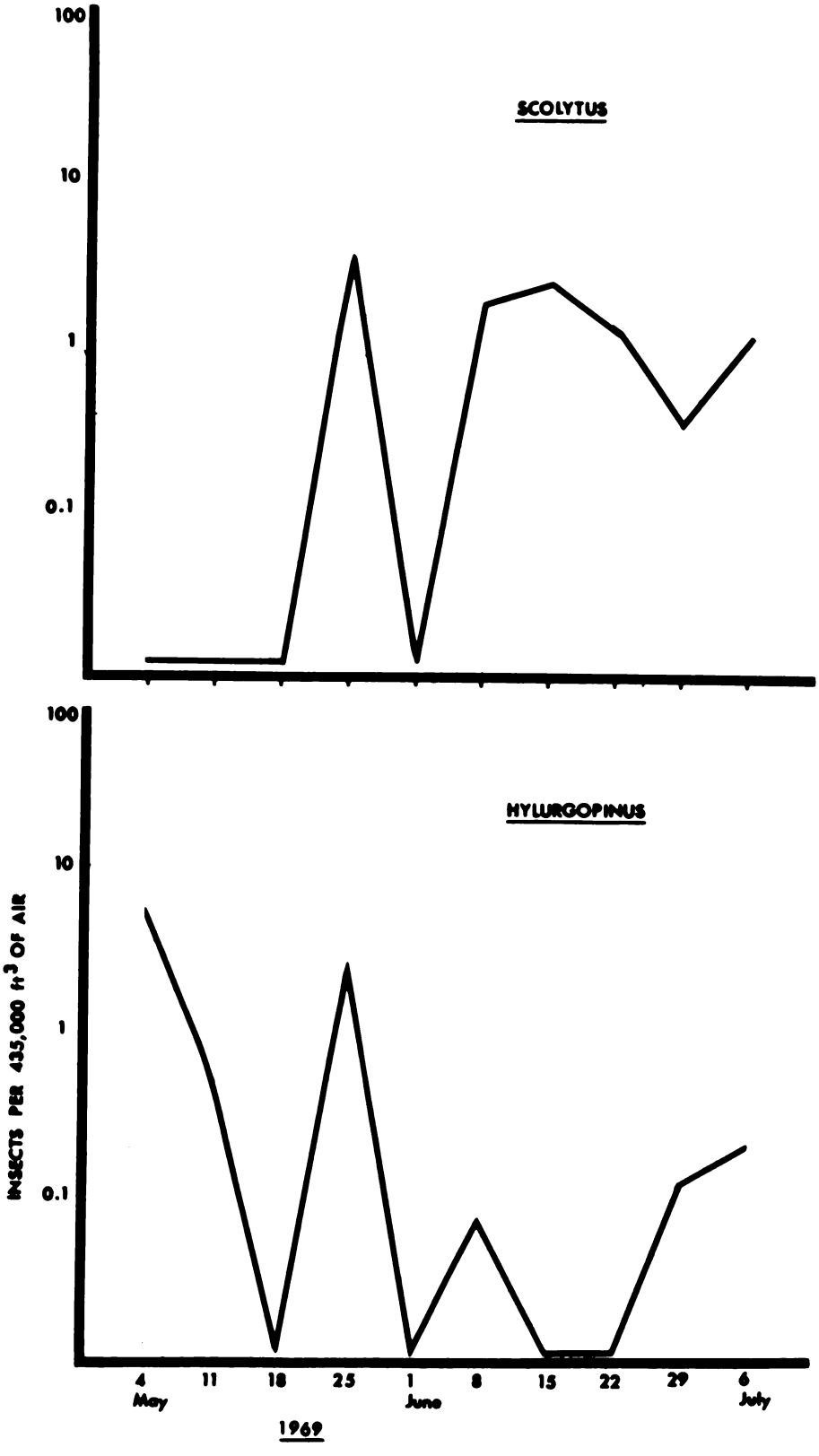


Figure 16.--Aerial density for Scolytus and Hylurgopinus, all levels combined in plot C for the spring, 1969.

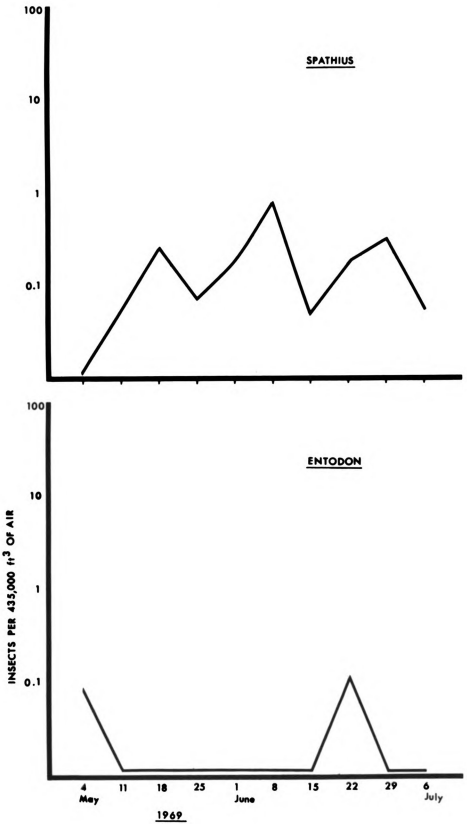


Figure 17.--Aerial density for Spathius and Entodon, all levels combined in plot C for the spring, 1969.

TABLE 6.--Temperature accumulations up to the day of first flight for Scolytus, Spathius and Entodon at St. Charles, Michigan

	Date of First Flight		Heat Units			
			Base 40°F		Base 50°F	
Species	1968	1969	1968	1969	1968	1969
Scolytus	May 24	May 28	863	181	381	377
Spathius	May 15	May 16	713	624	304	290
Entodon	April 30	May 7	493	493	200	223

Kapler (1967) reported temperature data on Scolytus emergence in Iowa. He found that a threshold of 40°F gave the most consistent results: with an average of 655 heat units accumulated before emergence began. By averaging the heat units for Scolytus at base 40°F in Table 6, 841 units are required for flight initiation. This difference in heat unit requirements for emergence and flight has also been reported by Meyer and Norris (1964). They found in Wisconsin that beetle dispersal flight occurred at temperatures above 70°F with 80°F the optimum, while emergence started when temperatures reach 60 to 65°F.

Bark Thickness Influence on Dendrosoter Success

The percent of the cambium that can be reached by a parasite's ovipositor is a measure of the parasite's potential success in reaching host larvae under a given section of bark. Since host larvae cannot be reached if they are under a section of bark greater than the ovipositor length, parasitism is then limited to areas in the crown with smooth, uniformly thin bark and to thin-bark crevices in the trunk region.

Analysis for the distribution of the thin-bark areas was carried out using multiple linear regression techniques. The results of the relationship of the percent of the bark less than Dendrosoter's mean ovipositor length (3.2 mm $\pm$ S.D. 0.8) to branch diameter (X_1) and tree DBH (X_2) is given in Figure 18. The overall regression is significantly different from zero at the 1 percent level, with the R value of 0.938 accounting for 87.9 percent of the variation in percent of cambium available by the regression on branch diameter and tree DBH. Examination of the partial correlation coefficients showed that branch diameter, with DBH held at its mean value, $r_{y \cdot 1} = 0.902$ had the greatest effect and was significant at the 1% level. DBH with a $r_{y \cdot 2} = 0.259$ was not significant. However, DBH is included in the presentation to illustrate the tendency for larger sized trees to have a smaller percentage of the cambium available to the parasite.

Based on Valek's (1967) data, the parasite potential should have approached zero in branches 4-5 inches in diameter, without considering bark fissures. It is evident from the data that a small percentage of the cambium can be reached in branches larger than 5-6" in diameter. The relationship presented is linear for the branch sizes measured; however, the overall relationship would probably have been curvilinear if larger branches had been included. A curvilinear relationship for parasite potential was presented for Coeloides brunneri on Douglas-fir by Ryan and Rudinsky (1962). The above authors also reported percent parasitism to follow the same pattern, although falling slightly below the available area curve in the larger branches. This difference was explained as being due to the parasites having to search a larger area

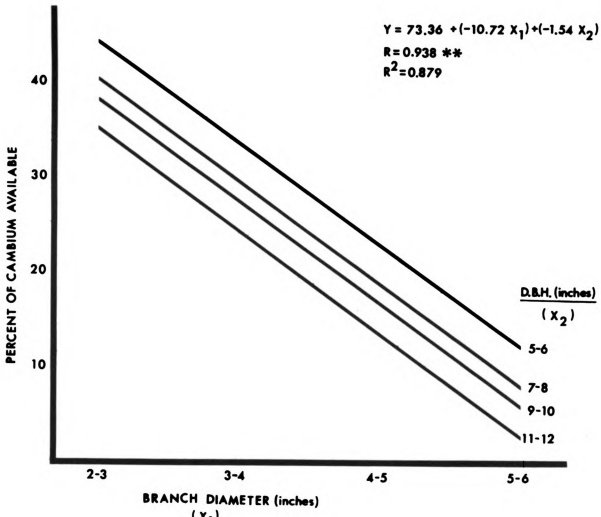


Figure 18.--The relationship between percent cambial area available for parasitism by D. protuberans, branch diameter and DBH.

to find a host under thin bark. No adequate data is available on percent parasitism by Dendrosoter under field conditions.

The apparent failure of Dendrosoter to establish successfully can possibly be explained with the parasite potential data used in relationship to the mean ovipositor length of Spathius. Measurement of 78 field collected Spathius gave a mean ovipositor length of 2.8 mm ± SD 0.6. In the measurement of Dendrosoters' ovipositor length, only laboratory reared individuals were available. These are generally larger in size yielding a somewhat optimistic mean ovipositor length. Beaver (1967) reported 2.4 mm as the mean length recorded in England. If we assume that both species have approximately the same length ovipositor and are biologically similar, then they both could be competing for the same available host resource. With Spathius already well established in the area Dendrosoter would find fewer host larvae available. This relationship could change from year to year until a level of equilibrium is reached with either one parasite or the other being eliminated. But, other factors such as winter temperatures, host searching ability and biological differences could also be causing the apparent unsuccessful establishment, with competition only of minor significance.

The important consideration, assuming the Dendrosoter has not established, is whether parasitism by Spathius, which has a similar ovipositor length, can be an effective source of bark beetle mortality. The upper limits for this parasites' effectiveness are equally well represented by Figure 18.

Elm Tree Quantification

The relationship developed between bark thickness and branch diameter is given in Figure 19. The relationship is significant at the 1% level with an r = 0.891 accounting for r^2 = 79.5% of the variation in bark thickness by the regression on branch diameter. The greater variation evident in the mean values obtained from the larger branches is due to decreasing sample size, in that a progressively smaller number of the trees sampled had branches in the larger diameter increments. The data were transformed using base $_{10}$ logarithms and recalculated. A lower r-value was obtained indicating the transformation was not effective. An analysis was also made by recalculating the means based on equal sample size. This relationship, developed using 7 paired bark samples per increment, was significant with an r = 0.783 which accounted for 61.4% of the variation around the line. Based on predictability alone however, the original regression still explained the most variation, so the equation presented was used for all subsequent calculations of bark thicknesses, used in determining cambial surface area. The formula used to obtain C.S.A. from log length, branch diameter and bark thickness was presented earlier.

Using the above formula the C.S.A. for each branch increment within each of the seven trees was calculated and totaled. These data along with measurements of: age, DBH, total height, crown height and crown width, were analyzed using multiple regression techniques to determine which parameter or parameters would best predict the amount of C.S.A. within each branch increment and for the total tree.

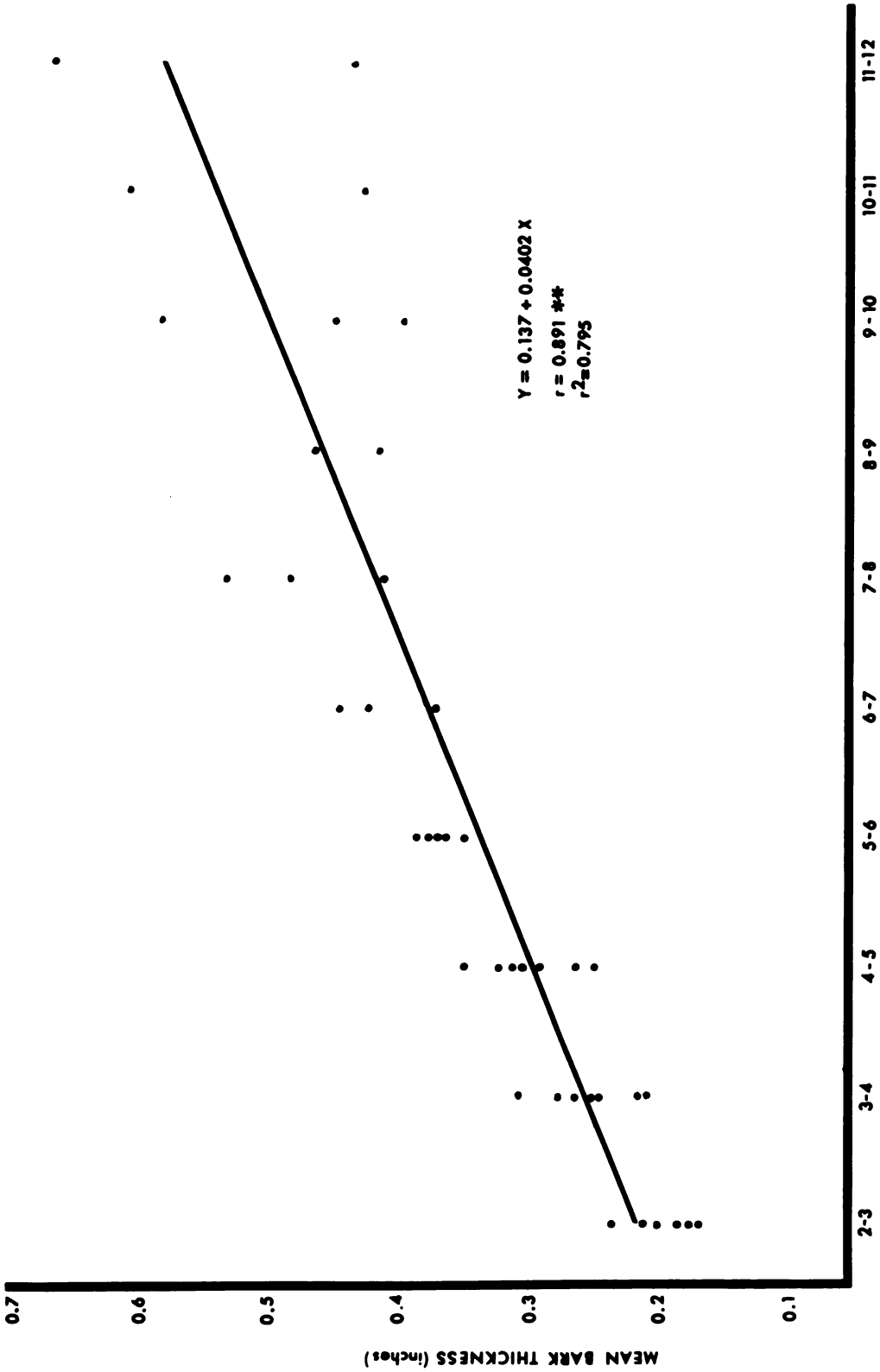


Figure 19.--Relationship between branch diameter and mean bark thickness for closed grown American elm.

The first overall regression calculated included all of the parameters listed as independent variables (X's) with total C.S.A. as the dependent (Y) variable. The results obtained were very unusual. The overall R^2 = 0.9999 was very high with the partial correlation coefficients for each X variable also equal to 0.99, indicating that each variable alone with the others held at their mean values, was explaining most of the variation in total C.S.A. This is a very difficult situation to analyze and frequently occurs with highly intercorrelated parameters (Draper and Smith, 1966). Examination of the simple correlation matrix for all of the parameters shows this to be true (Table 7). All of the variables are positively intercorrelated with the majority significant at the 5% level ($r > .754$ sig. 5% level with 5df).

TABLE 7.--Matrix of simple correlation coefficients obtained between each of the variables listed and total C.S.A.

	Age	DBH	Total Height	Crown Height	Crown Width	Total C.S.A.
Age	1.000					
DBH	0.912	1.000				
Total Height	0.823	0.667	1.000			
Crown Height	0.906	0.986	0.744	1.000		
Crown Width	0.879	0.955	0.583	0.907	1.000	
Total C.S.A.	0.804	0.959	0.473	0.935	0.906	1.000

Considering the high correlation obtained between DBH and total C.S.A. alone, the multiple regression analysis was discarded and a simple

linear relationship calculated. The data from the previous analysis were combined with data obtained from 24 other trees to develop the relationship presented in Figure 20. The regression is highly significant with 91.5% of the variation in total C.S.A. explained by the regression on DBH.

With the above equation for predicting total C.S.A. available, all that remains is to be able to subdivide the total back into the proper proportions for each respective branch increment within a given size tree. Although considerable effort was spent using both mathematical and statistical tools, no reliable method was found predictable in redistributing the total C.S.A. back into the proper branch sizes. The main problem was that with the larger DBH trees, many of the branch increments would not appear due to forking of the bole. This caused a complete change in the distribution pattern, compounding the observed DBH and branch diameter changes within and between trees. To circumvent this problem a table was constructed from the average number of square feet of C.S.A. found in each branch increment from four trees in each DBH increment. These data are presented in Table 8.

Using the information presented in Table 8, a sampling table was also constructed giving the length of log necessary to be cut from each branch increment to equal a 10% sample of the C.S.A. in an entire tree. The amount of C.S.A. comprising the sample was also calculated (Table 9).

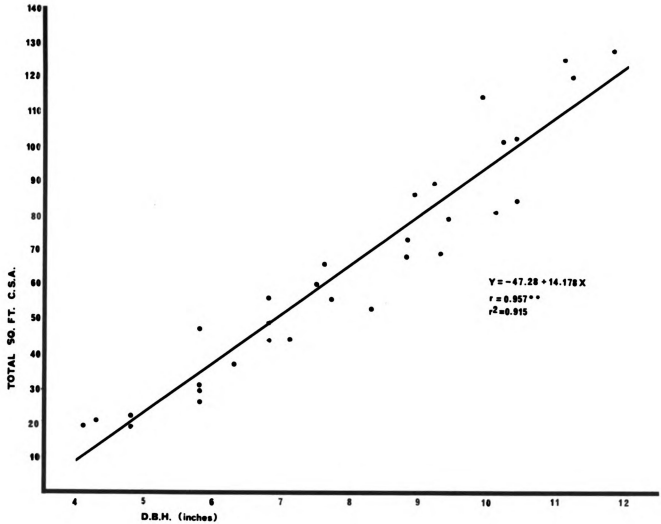


Figure 20.--Relationship between DBH and total cambial surface area for closed grown American elm.

TABLE 8.--Average total ft^2 C.S.A. for each branch diameter within a given DBH closed grown American elm (average four trees per DBH increment)

DBH Increment (inches)	Branch Diameter (inches)									
	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12
4-5	6.0	8.7	5.6							
5-6	5.0	8.5	9.7	10.4						
6-7	5.8	9.1	10.1	10.5	11.0					
7-8	6.4	7.4	9.7	13.6	11.1	8.3				
8-9	9.1	7.6	5.8	10.8	10.8	13.8	11.9			
9-10	15.1	10.9	10.5	8.0	7.1	17.2	9.2	8.9		
10-11	11.3	12.6	7.7	8.2	7.5	14.4	13.4	9.9	7.5	
11-12	17.3	11.1	15.6	11.1	3.5	7.6	2.01	16.9	11.9	8.8

TABLE 9.--Average length of log to be cut from each branch increment to yield a 10% total sample of a given DBH closed grown American elm

DBH Increments (inches)		Branch Diameter (inches)									
		2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12
4-5	A	1.11	1.11	0.55							
	B	0.60	0.87	0.56							
5-6	A	0.93	1.09	0.95	0.82						
	B	0.50	0.85	0.97	1.04						
6-7	A	1.08	1.16	0.99	0.83	0.73					
	B	0.58	0.91	1.01	1.05	1.10					
7-8	A	1.19	0.94	0.95	1.07	0.74	0.47				
	B	0.64	0.74	0.97	1.36	1.11	0.83				
8-9	A	1.69	0.98	0.57	0.86	0.72	0.79	0.60			
	B	0.91	0.76	0.58	1.08	1.08	1.38	1.19			
9-10	A	2.79	1.40	1.03	0.63	0.47	0.99	0.47	0.40		
	B	1.51	1.09	1.05	0.80	0.71	1.72	0.92	0.89		
10-11	A	2.09	1.61	0.75	0.65	0.50	0.83	0.68	0.44	0.30	
	B	1.13	1.26	0.77	0.82	0.75	1.44	1.34	0.99	0.75	
11-12	A	3.19	1.42	1.52	0.88	0.23	0.44	1.01	0.76	0.48	0.32
	B	1.73	1.11	1.56	1.11	0.35	0.76	2.01	1.69	1.19	0.88

A = 10% total log length (feet).

B = 10% total cambial surface area (ft^2).

Sampling Method Development

In developing a sampling method for studies of this nature where some precision in population estimation is desired, an intensive sampling method is desirable. To adequately assess the survival of Scolytus after the action of all mortality factors, a stable segment of the population had to be accurately sampled, for use as a reference point in determining initial population density. With bark beetles this is a relatively simple task as the initial population density is permanently recorded on the sapwood in the form of egg-galleries. Thus this sampling method was developed to accurately determine the egg-gallery distribution and density within a given elm tree. The gallery information along with data on mating habits can then be used for a comparison with the emerging adult population, with the difference between the two providing an estimate of within-generation survival.

The six trees selected for sampling were felled in early Spring 1969 and by using Table 9, two 20% samples were removed from each branch increment. The 20% sample was selected primarily by considering length of log in the sample. In reference to Table 9, in the larger trees a 10% sample yields a very short log section with a large diameter. It was possible that these short logs would dry too rapidly, thereby affecting the insects survival, so sample size was doubled.

To determine the number of samples that had to be removed from a given increment a linear regression was calculated between the number of galleries per ft^2 C.S.A. estimated by each of the two samples. If no difference existed between samples we would expect a one to one relationship (i.e. b = 1.0) with a high correlation coefficient (r). This was

the result, in that the regression analysis yielded a b = 0.83 with a significant r = 0.960** indicating that between sample variation was very low. The accuracy of the samples in predicting the total population per ft^2 C.S.A. within each increment could also be determined directly in the same manner because the total gallery population was also known for each increment. The linear regression, calculated as a measure of the ability of one 20% sample to predict the total galleries per ft^2 C.S.A., is shown in Figure 21. Although there is greater variation, r = .937, the relationship is also significant and shows that one 20% sample will give reliable estimates of total increment gallery density over an entire tree.

The data above suggests that egg-galleries are quite uniformly distributed within a given increment and good density estimates are possible with a single sample. The size of the sample as stated previously was arbitrarily set at 20%. However, the actual size in terms of ft^2 C.S.A. varied for each increment depending on DBH of the tree (Table 9). By using these different sample sizes in relation to the standard deviation calculated between the sample and total galleries, within each branch increment, it was possible to determine if size of sample is related to variance in estimation of total population size. A plot of the data is given in Figure 22. There is no apparent relationship, indicating that size of sample is not related to the error in estimating the total gallery population within an increment. The regression line shown was calculated to provide a least squares estimate of the slope b = -1.32, which for all practical purposes can be considered zero at a mean SD = $\pm$ 3.0 over all sample sizes considered.

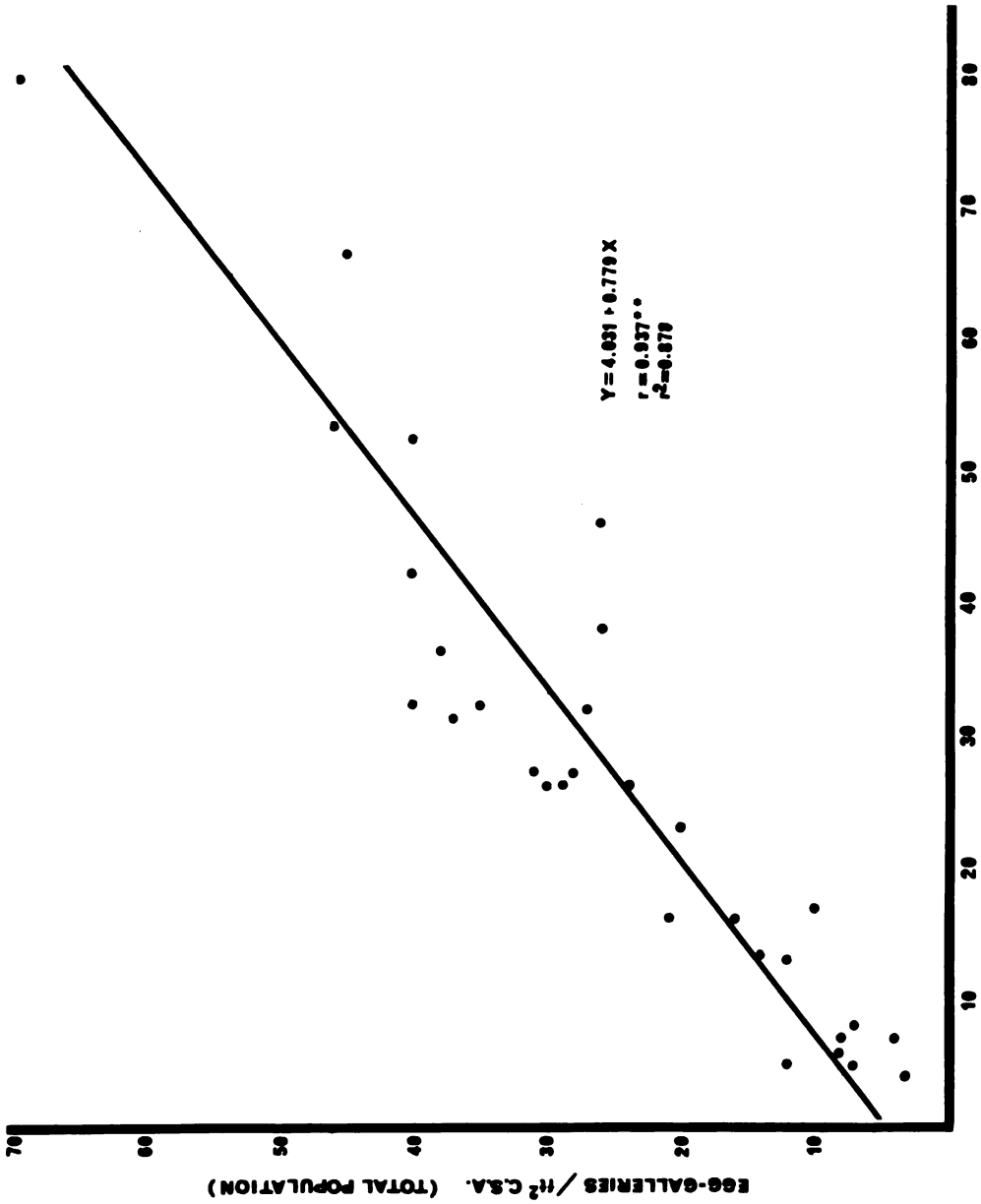


Figure 21.--Relationship between gallery density estimates from one 20% sample to the total gallery density within a branch increment.

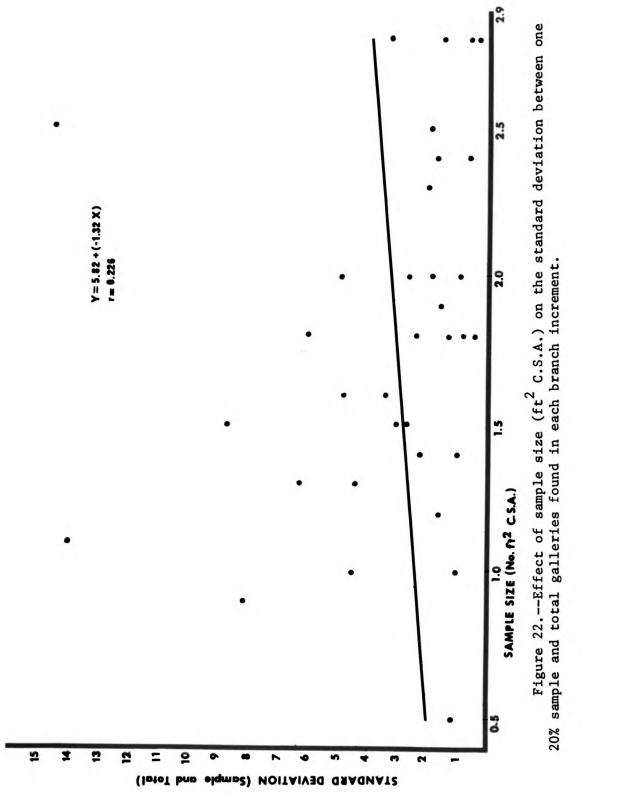


Figure 22.--Effect of sample size (ft^2 C.S.A.) on the standard deviation between one 20% sample and total galleries found in each branch increment.

Either method of sample selection can be used reliably--the one using weighted stratified sampling of a constant percentage of each increment and the other unweighted using a constant unit of cambial surface area. If the latter method is used, it is suggested that between one and two square feet be used as a sample size. Table 10 gives the length of log needed from each branch diameter to equal one square foot of cambial surface area. Multiplication of the table values by the size of sample desired will give the length of log needed.

TABLE 10.--Length of log needed from each branch diameter increment to equal one square foot of C.S.A. for closed grown American elm

Branch Diameter Increment (inches)	Log Length (feet) Needed to Equal One ft^2 C.S.A.
2-3	1.85
3-4	1.28
4-5	0.98
5-6	0.79
6-7	0.67
7-8	0.57
8-9	0.50
9-10	0.45
10-11	0.41
11-12	0.37

The test of a sampling method is in its ability to predict with accuracy the population being sampled. It has already been demonstrated

that the 20% samples taken from each increment will accurately predict the segment of the gallery population within that increment. However, it must be known how well the total number of galleries within a given DBH tree is predicted from the samples. The gallery data from one of the 20% samples in each of the branch increments for the six trees samples, was multiplied by the average total square feet of C.S.A. found in that increment for each tree (Table 8). These totals for predicting galleries in each increment were then added together giving a calculated total number of egg-galleries for each tree. This total was then compared with the actual total, the difference noted, and the percent error calculated. The results are given in Table 11. The errors ranged from 6 to 22% with five trees underestimating the true population and only one giving an overestimate.

TABLE 11.--Percent error between actual and calculated total tree *Scolytus* egg-gallery populations

DBH Increment (inches)	Total Galleries per DBH Tree		A-C Difference	$\frac{D}{A}$ % Error
	Actual	Calc.		
4-5	987	1190	+203	+21
5-6	660	632	-28	-4
6-7	665	524	-131	-20
8-9	2438	1910	-528	-22
9-10	1943	1620	-323	-17
10-11	2468	2311	-157	-6

Considering the amount of actual variation in total galleries evident between trees, the maximum 22% error is acceptable with the calculated estimates also tending to be somewhat conservative.

In conjunction with the intensive sampling method just presented, an attempt was made to develop a survey sampling method that would require a minimum number of samples. Tables were developed (not presented) proportioning the total galleries within each tree back into the proper branch increments. By taking one sample from any branch and knowing the tree DBH, it should have been possible to reproportion the sample back into the total tree. However, the method was unreliable when tested. A possible explanation is that the diseased trees do not die uniformly causing the proportion of attacks in each branch increment to be somewhat different for each tree.

The Scolytus egg-gallery density and distribution within the six trees sampled intensively is presented in Figure 23. Means and standard deviations are given for each branch diameter. The decreasing trend in the number of attacks evident for the larger size branches, agrees with biological observations noted from the literature. Analysis of this data in relation to Scolytus survival will be presented in the next section.

Within-Generation Survival Analysis

From a standpoint of regulation the important features of mortality factors are their dependence or independence of population density and their spatial and temporal variation (Morris, 1957). This study was initiated to examine the density relationships between Scolytus and its parasites, Spathius and Entodon within one generation of the beetle.

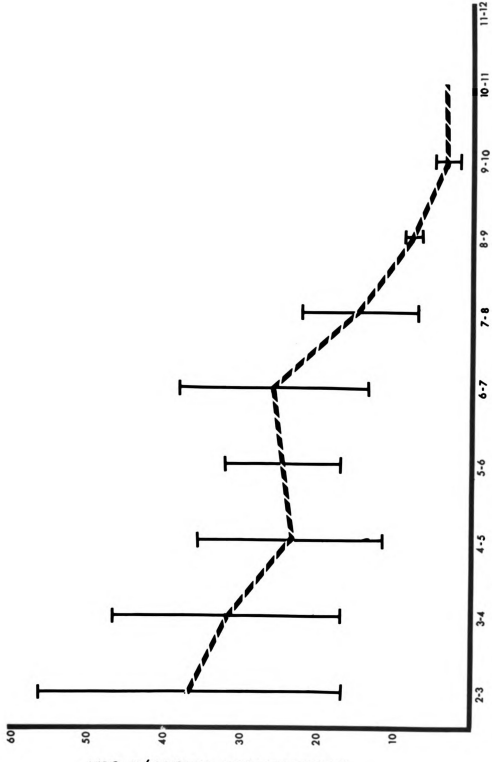


Figure 23.--Average density, standard deviation and distribution of Scolytus egg-galleries in closed grown American elm.

From the standpoint of regulation it is important to determine if Scolytus is under the influence of density-dependent constraints, and to what extent parasitism is a contributing factor at the various host densities.

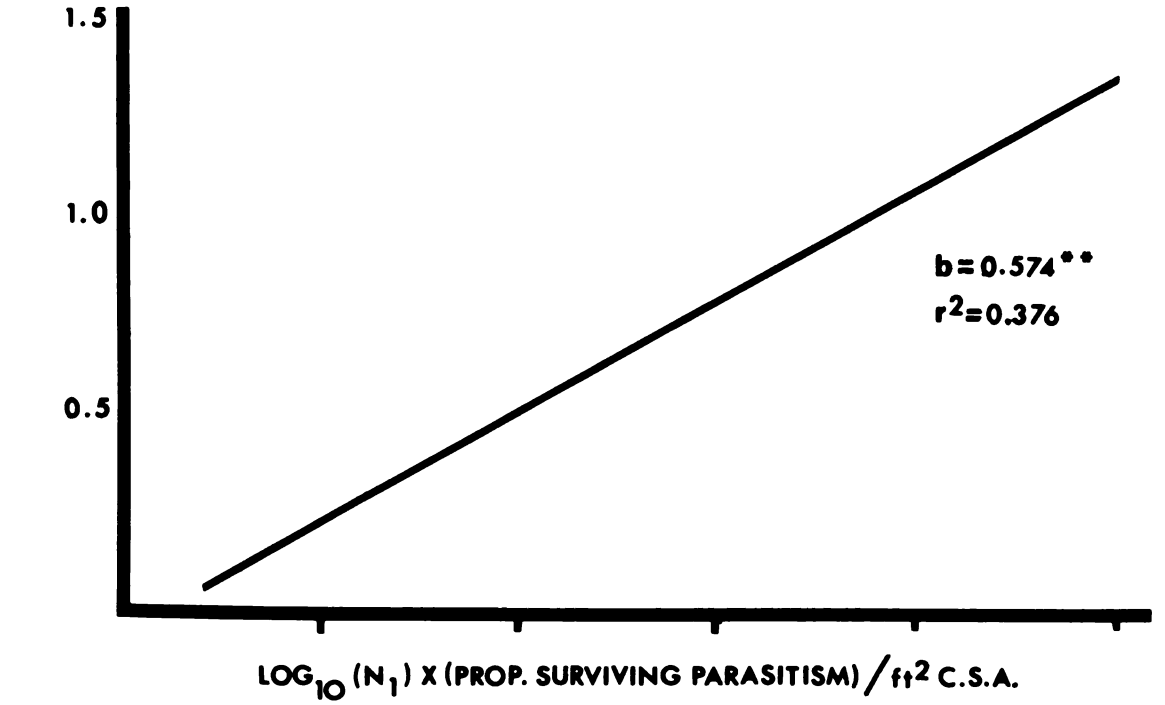
To obtain a range of population densities it is not necessary to obtain results from different locations during different years. In each of the branch increments, of the six trees considered previously, the total population was determined, so each branch increment can be taken to represent a unit beetle population. The only error associated with the estimates is due to extraction or tabulation. The density of attacks represented by density of egg-galleries within the various branch increments was illustrated previously (see Figure 23). By multiplying egg-galleries X 69 (the average fecundity), the number of beetle eggs initiating the generation within each increment can be determined.

Southwood (1966) has presented methods used by various authors for analysis of survival data. Most of these methods are suitable primarily for life-table studies which have a detailed separation of mortality factors operating on the various stages through time. One method presented, Morris' key factor analysis, is ideally suited to the type of data collected here in that it requires a precise population measurement for only one stage in each generation, with information on the proportion destroyed by parasites predators, and environmental factors also required. Morris (1959) presented the idea that although numerous mortality factors operate on a population, only a few, the key factors, cause the main fluctuations from one generation to the next. Although

the method was originally developed to detect the key factors responsible for changes between successive generations it can also be modified to detect changes within a generation (Beaver, 1967b.).

The method consists rather simply of calculating a linear regression of adult survival (N_2) on initial egg density (N_1) and testing whether the slope (b) is significantly different from one. A slope less than one indicates the action of density-dependent factors which operate to maintain the population around a given level, over all densities. A slope b = 0 indicates perfect regulation at all densities while a slope of b = 1 indicates no density-dependent regulation. The above method assumes a linear relationship between N_1 and N_2 so a log-log transformation is necessary to increase linearity and help stabilize the variance (Morris, 1959). The r^2 value measures the size of population fluctuations from one increment to the next. The extent to which the various mortality factors contribute to this fluctuation in population size is given by changes in r^2 as each factor is incorporated into the regression equation. A measure of the density-dependent action of each factor is given by changes in slope toward b = 1.

The test for overall density-dependent regulation in the Scolytus populations from the six trees is presented in Figure 24 (lower graph). The slope was tested using the formula presented in Snedecor and Cochran (1967), and found to be significantly different from b = 1 at the 1% level. The significance of this slope indicates that the beetle populations within the branch increments, are being regulated in a density-dependent manner. To determine if parasitism was causing the major portion of this regulation, the proportion of the beetle



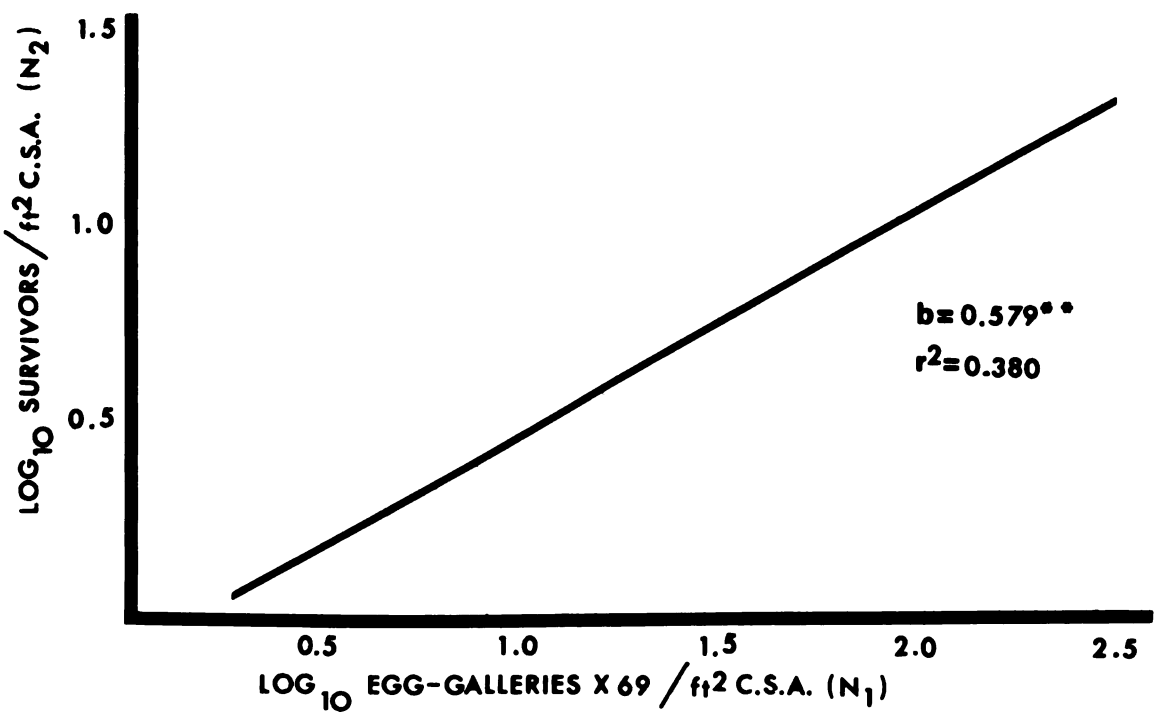


Figure 24.--Density relationship of the total mortality of S. multistriatus before (lower) and after (upper) including parasitism by Spathius and Entodon.

populations surviving the action of both Spathius and Entodon was multiplied by the initial population (N_1), and the regression recalculated. Both parasites were entered simultaneously as their distribution and densities were similar when plotted over branch diameter. The resulting regression is also plotted in Figure 24 (upper graph). The slope was found significantly different from b = 1. However, the important aspect is that the value did not increase at all. This consideration indicates that parasitism is not influencing the size of the surviving beetle generation. The r^2 values reflect this same point in that the addition of parasitism did not increase the value and therefore is not accounting for any of the observed variation around the line. This situation is a bit unusual and could only have occurred if the parasites were responding to the beetle density in a constant manner. If this is true then the distribution of beetle survival over branch diameter would be parallel before and after the action of parasites. Figure 25 illustrates that this is indeed what is happening. Although neither regression is significantly different from b = 0 the trend toward greater survival in the larger size branches is evident. The constant effect of parasitism is represented by the area between the two regression lines. This area is accounting for about a 2% reduction in the bark beetles survival. This is a rather low mortality when considering that on the average, in each increment, 96.1% of the beetles died before emergence. (Data presented in Appendix A.) Parasitism is therefore accounting for only a small part of the total mortality observed.

From Figure 25 any other density-dependent mortality cannot be recognized because the branch diameters do not adequately represent the

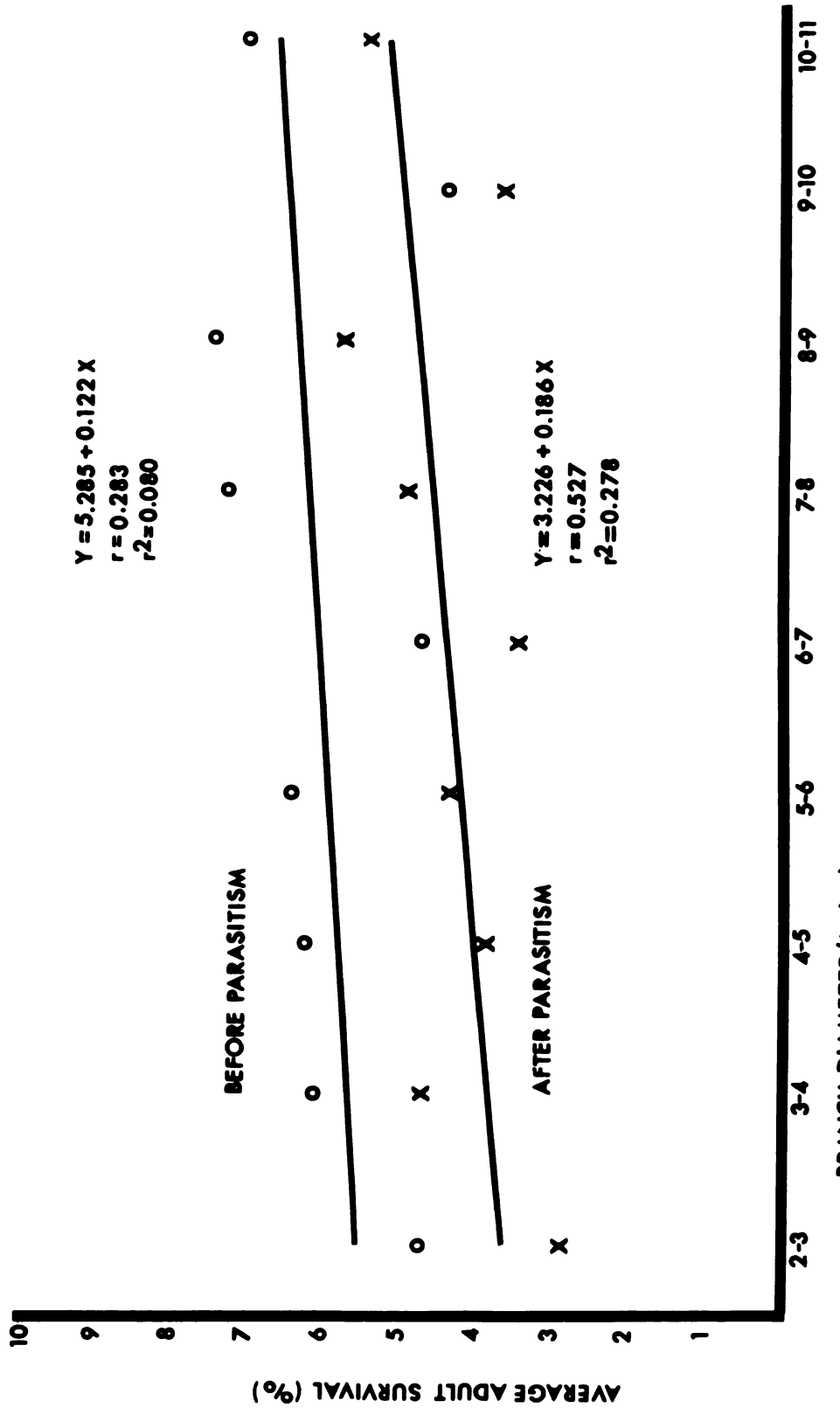


Figure 25.--Average Scolytus adult survival before and after the effect of parasitism.

initial population density. By calculating the relationship between egg-gallery density and adult survival, the density-dependent mortality shown previously to be operating on the beetle populations would be evident. Figure 26 presents this relationship giving the average percent beetle survival over mean gallery density both before and after parasitism. Standard deviations are only presented on one side of each mean value, for clarity. Although considerable variation is present, the decreased survival at high gallery densities is evident before and after the effect of parasitism. The relatively constant percent survival is again evident between the two plots. Above a mean gallery density of 25 a plateau in percent survival is evident. The mortality factor or factors responsible for this trend appear to be operative above a mean gallery density of 25, and are responsible for removing equal proportions of both bark beetles and parasites in an apparent density-dependent manner.

There are three related mortality factors that were not measured which could account for the evident mortality at high gallery density; intraspecific competition, woodpecker predation and dessication. Looking at the distribution of surviving adult beetle and parasite density plotted over branch diameter (Figure 27) suggests that the density-dependent mortality is occurring within the 2-6 inch diameter branches. In view of this relationship, looking first at competition we can get an estimate of the effect of this factor alone by examining Figure 13. Both trees used were contained in barrels throughout the winter months, this excluded woodpeckers and prevented dessication. The distribution for Scolytus shows no pronounced decrease in the smaller branch

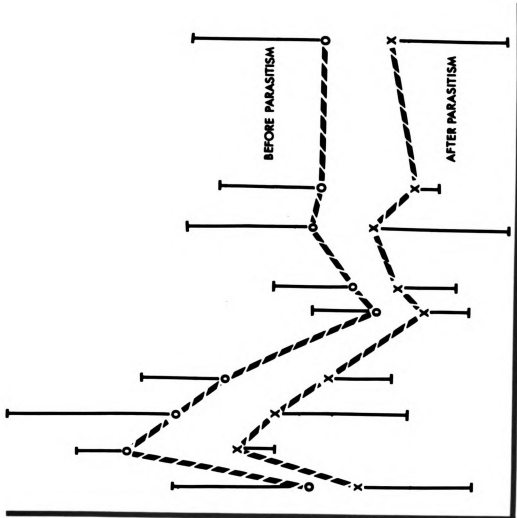


Figure 26.--Average adult survival for Scolytus over initial egg-gallery density.

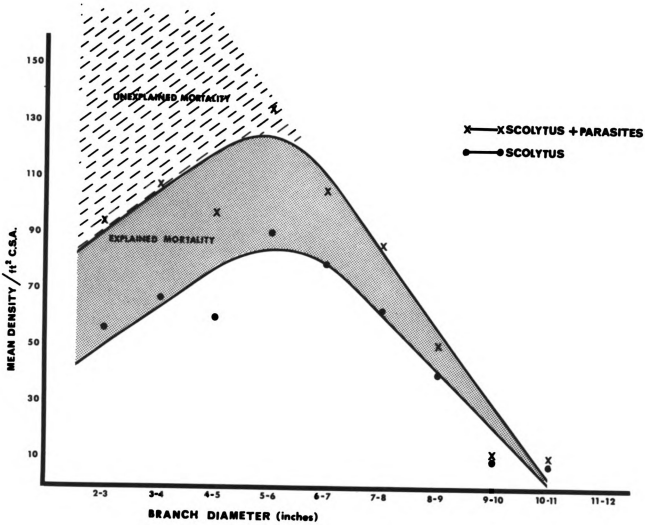


Figure 27.--Mean Scolytus and parasite density within each branch increment from six closed grown American elms.

increments, thus competition probably does not cause a large amount of the observed mortality. No direct evidence is available on the remaining two factors. However, the slope of the two curves suggests the action of a non-selective mortality factor operating on both the parasites and the beetle contemporaneously. Woodpeckers by their habit of stripping the bark expose the underlying insects to greater dessication, so the two factors cannot be separated, in effect, both being non-selective. Three species of woodpeckers, the Red-Headed, the Downy and the Hairy, were observed working on infested elms in the plots. The latter two species have been reported previously, feeding on Scolytus larvae. It was also noted that the majority of damage occurred in the crown area in the smaller diameter limbs. This is not unusual in that woodpeckers commonly respond to a given prey density threshold, and are very effective in reducing the prey population above this threshold density (Knight, 1958).

From the above evidence it can be assumed that woodpeckers operating contemporaneously on both the beetle and parasite populations, are causing the observed density-dependent mortality. These predators operating sequentially after the action of the previous mortality factors completely obliterate any possible regulatory capability of either parasite.

SUMMARY AND CONCLUSIONS

The ability of Dendrosoter to survive Michigan winters has been demonstrated by both supercooling and actual field releases. Tree influence on actual temperature exposure, indicates greater potential survival of the parasite and its host in the south facing branches of standing trees. The northern distribution for Dendrosoter and Scolytus potentially occurs throughout Michigan's lower peninsula, but increased winter mortality is probable in areas with extremely cold temperatures. Hylurgopinus a possible freezing-tolerant species could become the more important vector in these northern areas.

Biologically Dendrosoter starts emergence in early April and two generations per year are indicated on natural Scolytus populations. Following the initial field release at St. Charles, Michigan, the parasite was collected both in trap-logs and logs from standing trees. After these initial collections only one specimen of Dendrosoter was collected the same fall, and no further recoveries were made in the rotary traps or in logs from standing trees. The rotary traps were found to be less efficient in sampling Entodon flight activity and the same could be true for Dendrosoter. The tree crown area was also sampled with rotary nets to detect activity, but with negative results. Several possible explanations offered for this lack of parasite success are: inability to locate host material under field conditions,

competition with native parasites and severe bark thickness limitations. No data were collected on the parasites ability to locate an infested tree or the beetle larvae within it. Bark thickness was measured and Dendrosoter was found to be very severely limited in effectiveness by increasing bark thickness and tree DBH. In the smallest branches the parasites' ovipositer can only reach 50% of the cambial area with the percentage decreasing with increasing branch size. Spathius was shown to have approximately the same length ovipositor, suggesting that possible interspecific competion was occurring. This competition for the same host resource may account for the lack of success in establishing the new parasite in the study areas. Temperature accumulations necessary for the initiation of flight activity by Scolytus, Spathius and Entodon were presented. The 50°F threshold predicts flight of the first two species while a base of 40°F was found to be more reliable in predicting Entodon activity. These data could be very useful in timing control operations using the new short-lived insecticides.

A method of sampling closed grown American elms was determined and found to be reliable in giving estimates within 20% of the total Scolytus egg-galleries present. This method is applicable only for research studies in that it requires intensive sampling of each tree. A method useful for survey work requiring only one sample per tree, was tested and found unreliable due to large between-tree variation.

The analysis for possible density-dependent regulation of Scolytus by the native parasites revealed, that both Entodon and Spathius were having no effect in causing the observed beetle density-dependent regulation. Both parasites together accounted for 2% of the observed

96.1% total beetle mortality. No increase in parasitism with increasing host density was observed. The operation of other non-selective mortality factors completely masked any regulatory properties of the parasites. Intraspecific competition, woodpecker predation and dessication were examined as to their role in causing the observed regulation. Competition was shown to be of little importance. The remaining two mortality factors, woodpecker's and dessication, are interrelated and their effects were not quantified in this study. However, the action of these two non-selective mortality factors operating contemporaneously during the winter months could have caused the observed density-dependent beetle regulation.

Due to the action of non-selective density-dependent mortality factors operating with equal intensity on both beetles and parasites, any possible regulatory effect of the native parasites was not apparent in this study.

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LITERATURE CITED

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APPENDIX A

APPENDIX A

WITHIN-GENERATION SURVIVAL DATA
ST. CHARLES, MICHIGAN 1968-69

Emergence, mortality and survival data from the six trees of various DBH cut for analysis of within-generation Scolytus survival at St. Charles, Michigan.

Percent Mortality Scolytus

$$\text{A. After Parasitism} = \frac{(\text{egg-galleries X 69}) - (\text{No. adults})}{(\text{egg-galleries X 69})} \text{ X 100}$$

$$\text{B. Before Parasitism} = \frac{(\text{egg-galleries X 69}) - (\text{No. adults} = \text{No. parasites})}{(\text{egg-galleries X 69})} \text{ X 100}$$

Percent Survival Scolytus

After Parasitism = 1 - A X 100

Before Parasitism = 1 - B X 100

Emergence Data From The Dendrosoter Field Release
And Evaluation Study 1968-69

DBH	Branch Diameter	Total ft^2 C.S.A.	Scolytus		Hylurgopinus		Total Entodon	Total Spathius	Total Dendrosoter
			Total Galleries	Total Adults	Total Galleries	Total Adults			
Spring 1968									
7-8	2-3	3.32	127	181	3	0	29	7	7
Plot C	3-4	7.92	220	388	5	2	76	46	4
	4-5	8.73	158	405	40	161	53	18	0
	5-6	11.65	154	460	153	1076	127	42	0
	6-7	10.58	116	48	112	2526	13	6	1
	7-8	6.29	44	0	94	465	0	0	1
7-8	2-3	5.93	69	260	36	5	54	96	4
Plot W	3-4	3.76	90	343	101	51	64	93	8
	4-5	7.96	247	660	302	677	276	100	7
	5-6	3.84	158	184	165	697	95	13	1
	6-7	3.84	187	77	152	260	80	4	2
	7-8	3.48	77	2	81	165	5	0	1
Spring 1969									
6-7	2-3	4.81	135	370	19	0	41	5	0
Plot C	3-4	9.69	163	872	75	22	103	17	0
	4-5	14.11	82	664	216	726	53	22	0
	5-6	9.60	31	85	230	155	1	0	0
	6-7	7.52	10	27	141	368	1	0	0
6-7	2-3	4.87	108	1745	42	25	341	18	0
Plot W	3-4	6.02	59	846	36	121	106	56	0
	4-5	11.04	72	959	79	570	90	55	0
	5-6	12.13	150	1285	160	1267	263	3	0
	6-7	4.66	39	113	91	203	4	0	0
Fall 1968									
6-7	2-3	..	..	26	..	0	31	78	1
Plot C	3-4	..	..	229	..	392	66	49	0
	4-5	..	..	59	..	4248	13	35	0
	5-6	..	..	4	..	905	1	3	0
	6-7	..	..	7	..	191	0	0	0
6-7	2-3	..	..	37	..	366	35	28	0
Plot W	3-4	..	..	41	..	714	5	25	0
	4-5	..	..	27	..	1182	2	26	0
	5-6	..	..	53	..	352	0	3	0
	6-7	..	..	27	..	128	0	2	0

APPENDIX B

APPENDIX B

EMERGENCE DATA FROM THE *DENDROSOTER* FIELD RELEASE AND EVALUATION STUDY 1968-69

Emergence data from the four trees cut from the *Dendrosoter* field release and evaluation study 1968-69. The data presented for fall 1968 goes with the spring 1969 trees. The spring 1968 trees were standing all winter while the spring 1969 trees overwintered in the emergence barrels.

Within-Generation Survival Data St. Charles, Michigan 1968-69

DBH	Branch Diameter	Total ft^2 C.S.A.	Scolytus		Parasites		% Mortality Scolytus		% Survival Scolytus	
			Total Galleries	Total Adults	Total Spathius	Total Entodon	After Parasitism	Before Parasitism	After Parasitism	Before Parasitism
4.8	2-3	4.81	338	383	3	285	98.35	97.12	1.65	2.88
	3-4	10.16	462	265	13	232	99.16	98.40	0.84	1.60
	4-5	7.26	187	81	0	81	99.37	98.74	0.63	1.26
5.8	2-3	6.22	151	244	65	67	97.65	96.39	2.35	3.61
	3-4	5.63	66	382	62	52	91.61	89.10	8.39	10.90
	4-5	7.05	72	349	13	89	92.97	90.92	7.03	9.08
	5-6	11.11	343	343	0	234	98.55	97.56	1.45	2.44
6.8	2-3	9.08	105	512	124	198	92.93	88.48	7.07	11.52
	3-4	12.04	236	980	60	450	93.98	90.84	6.02	9.16
	4-5	11.35	87	427	69	182	92.88	88.70	7.12	11.30
	5-6	7.70	108	197	5	195	97.35	94.67	2.65	5.33
	6-7	9.77	119	91	0	75	98.89	97.97	1.11	2.03
8.8	2-3	16.82	621	679	479	176	98.41	96.88	1.59	3.12
	3-4	16.88	687	1241	1010	311	97.38	94.59	2.62	5.41
	4-5	4.40	176	403	343	145	96.68	92.66	3.32	7.34
	5-6	5.05	296	598	446	84	97.07	94.47	2.93	5.53
	6-7	8.72	303	282	363	121	98.65	96.33	1.35	3.67
	7-8	13.61	288	956	300	263	95.18	92.35	4.82	7.65
	8-9	8.14	67	356	43	47	92.29	90.35	7.71	9.65
9.2	2-3	19.52	749	1225	419	159	97.62	96.51	2.38	3.49
	3-4	8.52	243	816	223	110	95.13	93.14	4.87	6.86
	4-5	16.36	449	1033	243	284	96.66	94.96	3.34	5.04
	5-6	4.04	188	926	106	108	92.86	91.21	7.14	8.79
	6-7	3.61	132	776	46	56	91.48	90.36	8.52	9.64
	7-8	22.33	151	570	82	238	94.52	91.45	5.48	8.55
	8-9	9.13	61	106	11	38	97.48	96.31	2.52	3.69
	9-10	10.02	20	7	0	1	99.49	99.42	0.51	0.58
10.4	2-3	18.01	722	1056	481	254	97.88	96.40	2.12	3.60
	3-4	12.50	564	740	145	159	98.09	97.31	1.91	2.69
	4-5	10.12	284	455	74	131	97.67	96.63	2.33	3.37
	5-6	9.97	258	463	51	137	97.39	96.34	2.61	3.66
	6-7	7.82	236	448	38	50	97.24	96.70	2.76	3.30
	7-8	13.61	218	650	56	126	95.67	94.46	4.33	5.54
	8-9	7.15	92	452	36	78	92.87	91.08	7.13	8.92
	9-10	13.13	52	241	11	38	93.28	91.91	6.72	8.09
	10-11	16.77	42	158	6	40	94.54	92.96	5.46	7.04