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Observations on the behavior and effectiveness of three ant species (Hymenoptera|Formicidae) attacking the western spruce budworm, Choristoneura Occidentalis (Lepidoptera|Tortricidae) in western Montana

Oakford George Bain
The University of Montana

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OBSERVATIONS ON THE BEHAVIOR AND EFFECTIVENESS OF THREE ANT SPECIES (HYMENOPTERA:FORMICIDAE) ATTACKING THE WESTERN SPRUCE BUDWORM, CHORISTONEURA OCCIDENTALIS (LEPIDOPTERA:TORTRICIDAE) IN WESTERN MONTANA

By
Oakford G. Bain
B.S., University of Montana, 1972

Presented in partial fulfillment of the requirements for the degree of Master of Science
UNIVERSITY OF MONTANA

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Approved by:

[Signatures]
Chairman, Board of Examiners
Dean, Graduate School

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CHAPTER I

INTRODUCTION

The western spruce budworm (*Choristoneura occidentalis* Freeman) is one of the most destructive forest pests in the United States and Canada. The larvae of this lepidopteran caused aerially visible defoliation in excess of four million acres in the Northern Rocky Mountains during 1971 (Ciesla *et al.*, 1972). This was the fourth consecutive year that defoliation of Douglas-fir (*Pseudotsuga menziesii*), true fir (*Abies* sp.), and spruce (*Picea* sp.) forests by the spruce budworm exceeded the four million acre figure. The spruce budworm continued to be a serious pest of Douglas-fir cone crops in Montana, with infestations being reported also in spruce and subalpine fir (*A. lasiocarpa*) cones (Ciesla *et al.*, 1972).

The spraying of chemical insecticides remains the most feasible method of effecting "quick" control of the spruce budworm. Recently, however, the public health and environmental safety of insecticides has come under considerable attack. The use of DDT for the control of the spruce budworm was discontinued for the most part in 1963 after it was shown to produce undesirable effects in the target environment (USDA, 1972). Several compounds are currently being tested for use against the budworm. Yet, insecticides are only short term controlling agents at best and must be applied repeatedly in most cases. Increased application of pesticides can lead to resurgence of pest populations,
outbreaks of secondary pests and the development of genetic resistance
of the target pest to the insecticide.

A suitable alternative to insecticides for management of the
spruce budworm may be biological control. Although parasitic forms
have been released against the budworm in the past with little success
(McGugan and Coppel, 1962), they may be of considerable benefit in in­
tegrated programs utilizing biological control methods. The predator
complex of the spruce budworm has received little attention and only
limited attempts have been made to assess the effectiveness of predators
in budworm population management. Parasites and predators alike have
long been recognized as significant factors in the decline of spruce
budworm populations under natural conditions (Mathers, 1932; Heimburger,
1945; Dowden and Carolin, 1950). Ironically, these natural enemies
may be endangered by the spraying of insecticides (USDA, 1972).

Clearly, an evaluation of forest spraying of insecticides for budworm
management as it affects these beneficial species is called for. Before
an effective evaluation can be made, certain baseline information must
be gathered regarding the importance and fate of predaceous and para­
sitic arthropod forms that may be adversely affected by forest spray­
ing operations.

Extensive studies in the East by Morris (1963) have shown that
spiders are the most important arthropod predator of budworm larvae.
Morris feels, however, that spiders may be replaced in importance by
forest ants in the West because of differences in climate and topography.
Indications are that ants may be important predators in the West although
documentation has been lacking.
Considering the need for information on the predaceous ant complex attacking the spruce budworm, this investigation was designed with the following objectives:

1. To collect and identify the forest ant species present on a study plot located in a typical budworm infested Douglas-fir forest in western Montana and to survey the same area to determine the abundance of these species.

2. To determine the location of ant predation of spruce budworm i.e. whether on the ground or in the foliage.

3. To determine the fate of budworm larvae falling from the foliage of Douglas-fir and to study the behavior of these larvae as related to foraging ants in and around Douglas-fir trees.

4. To study the foraging behavior of forest ants preying on budworm, the influence of weather conditions upon their foraging activity, the types of food gathered by foraging workers and their relationship with aphids as it affects their foraging behavior in the foliage of Douglas-fir.

5. To study the attack behavior of forest ants with regard to the spruce budworm.
CHAPTER II

LITERATURE REVIEW

Spruce Budworm

The spruce budworm is a native forest pest. Growth ring comparisons have shown that budworm outbreaks occurred in the 1700’s (Kulman, 1971). Other evidence suggests that widespread outbreaks occurred in the 1810’s and 1870’s in the Northeastern States and eastern Canada (Swaine and Craighead, 1924). The budworm was first named in 1865 by Clemens from specimens collected in Virginia (Freeman, 1953). The first recorded outbreak in eastern Canada occurred in 1910 (Balch, 1946). The budworm was first detected in the West around 1914 (Carolin and Coulter, 1959).

The spruce budworm was first placed in the genus Tortrix but was later moved to the genera Harmologa, Caecia and then Archips (McKnight, 1968). Freeman (1947) moved the budworm to the genus Choristoneura where it remains today. Of the several budworm species known today, two have received the most attention; the eastern spruce budworm (C. fumiferana Clem.) and the western spruce budworm (C. occidentalis Freeman).

The budworm larva is responsible for feeding damage to host trees, primarily Douglas-fir, the true firs, and Engleman spruce (Picea engelmannii) in the West. The buds, cones and needles are mined
during the early stages of larval feeding. In the later stages, feeding is confined principally to present year's foliage and may extend to older foliage if the supply of younger needles is exhausted (Prebble and Carolin, 1967).

Defoliation caused by the budworm may range from light to severe, resulting in loss of height and increment growth, and damage to rootlets (Mott, et al., 1957; Kulman, 1971; Williams et al., 1971). Top kill commonly occurs during prolonged outbreaks (Kulman, 1971). Other damage resulting from budworm feeding includes the severing of terminal leaders of young western larch (Larix occidentalis) (Fellin and Schmidt, 1967, 1971) and the destruction of Douglas-fir cones (Dewey and Honing, 1969).

Biological Control of the Spruce Budworm

Predators and parasites have been recognized as contributing factors in the decline of budworm outbreaks (Tothill, 1922; Mathers, 1932; Heimburger, 1945; Dowden and Carolin, 1950). Heimburger (1945) was one of the first researchers to suggest biological control of the eastern spruce budworm. He felt control should be approached from the population genetics of the budworm, making use of related parasites along with specific interactions with the host, balsam fir. McGugan and Coppel (1962) report that 16 parasites were released in eastern Canada against the eastern budworm between 1944 and 1956; however, little success was realized. By 1959, there were 92 parasites of the budworm (both eastern and western species) known, the major ones consisting of nine species of hymenopterans and six species of dip-
The record of budworm predators is extensive and ranges from "hordes of dragon flies..." (Liscombe and Lejeune, 1949) to birds and small mammals (George and Mitchell, 1948; Mitchell, 1952; Dowden et al., 1953; Mook, 1963). Thomson (1957) observed several species of beetles preying upon budworm larvae. Hamre (1963) and Fye (1962) observed extensive predation of budworm larvae by solitary wasps. Warren (1954) described predation of budworm pupae by the spruce coneworm (Dioryctria reniculella). Neilson (1963) found mites to be the principal predators of budworm eggs in New Brunswick. Morris (1963) and Loughton et al. (1963) also working in New Brunswick, found spiders to be the principal invertebrate predators of budworm larvae.

The principal work with budworm pathogens has centered around Bacillus thuringiensis, a bacterium, (Denton, 1960; Yamvrias, 1970; Smirnoff, 1972), and two types of viruses (Stairs and Bird, 1962; Bird, 1969, 1970). Other principal research in the area of biological control of the budworm includes the work done by Retnakaran (1970a,b, 1971), Sanders (1971) and Weatherston et al. (1971) concerning the use of budworm pheromones and sterilants. Research in this area is continuing through the efforts of these workers and others.

Predaceous Ants

Ants (Hymenoptera: Formicidae) have been long recognized as predators important in protecting crops from certain insect pests. Doutt (1964) in quoting McCook (1882) reports the use of ants for control of agricultural pests can be traced back to ancient times when
Chinese citrus growers purchased and placed nests of predaceous ants (Oecophylla smaragdina F.) in mandarin orange trees to reduce the number of foliage eating insects. Doutt (1964) also cites Forsakal (1775) and Botta (1841) who reported the practice of Arabian date growers of making yearly trips to the mountains to collect beneficial ant species which they would place on their date palms for the control of harmful insects.

Many scientists in the United States and Canada have noted the effects of predaceous ants upon pest species and have recorded casual observations of their predatory activity. However, few specific studies have been conducted to measure the effectiveness of predaceous ants. Mathers (1932) stated that ants were among those important control factors present in natural budworm populations in the West. Graham (1935) noted ants preying upon dislodged budworm pupae. Dowden and Carolin (1950) also regarded ants as important control factors in budworm populations.

Recently, Dr. James Lowe observed ants repeatedly carrying off dislodged budworm larvae. Observations by Dr. David Fellin demonstrated that ants also prey on budworm egg masses.

Workers in North America have made similar observations of ant predation on other forest pests. Green and Sullivan (1950) observed workers of Camponotus herculeanus ligniperdus and Formica fusca preying

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1/ Associate Professor of Forestry, University of Montana, Missoula. Personal Communication, Feb. 1972.

heavily upon larvae of the forest tent caterpillar, *Malacosoma disstria*. Allen et al. (1970) listed *Camponotus noveboracensis*, *Formica exsectoides*, and *F. pallidefulva nitidiventris* as the ant species preying upon the larvae of the jack-pine budworm, *Choristoneura pinus*.

Smirnoff (1959) noted ants, especially *C. herculeanus*, carrying off dead and dying larvae of the jack-pine sawfly, *Neodiprion swainei*. Ilnitzky and McLeod (1965) recorded ten species of ants (*F. fusca* the most abundant and aggressive) preying upon pupae and adults of this sawfly but never eggs or larvae.

Bradley (1972) performed the latest (if not the first) research on transplantation techniques of predaceous ants in North America. Ants of the species *Formica obscuripes* and *Dolichoderus taschenbergi* were successfully transplanted into a jack-pine plantation from neighboring stands. The author concluded that transplantation of these species was feasible and may be instrumental in removing large quantities of forest pests from plantations.

Many European entomologists have long regarded ants as important predators of many forest defoliator species. Many of these forest pests have similar counterparts in North America and for this reason, attention has been drawn to the feasibility of employing predaceous ants for the control of such North American pests as the spruce budworm.

The genus *Formica* contains the principal species of predaceous forest ants. Adlung (1966) reports there are five species of forest ants in the genus *Formica* that have been involved extensively in observations as pest control agents in Europe. *Formica polyctena* is
generally regarded as the most important.

Forest ants of the genus *Formica* differ in the locations they choose for nest building. Some species prefer the cool dark interior of spruce forests while others prefer the open sunny pine forests (Adlung, 1966). Some species may inhabit an area in harmony while others are antagonistic. Adlung (1966) in quoting Lange (1957) mentions that *F. rufa* and *F. polyctena* are quite antagonistic species and can not be colonized in the same area.

The effective hunting range of forest ants varies considerably. Behrmdt (1934) as quoted by Cotti (1963) reported that a *F. rufa* nest protected a forest area of 1000 to 1600 square meters. Cotti (1963) noted that Wellenstein (1954) summarized data from several sources and concluded that the influence of red forest ants extended over a distance of 25 to 35 meters from the nest.

A survey of reports in the European literature indicates that approximately 15 separate forest pests have been reportedly controlled or greatly influenced through the action of predaceous ants. Wellenstein (1957) reported ants feeding upon the larvae and adults of *Cephalcia abietis* (Hymenoptera: Pampphilidae), a sawfly attacking spruce. He measured 81 percent and 100 percent reductions in the number of cocooned larvae at a distance of five meters from two nests.

Schwerdtfeger (1957) as noted by Cotti (1963) studied the influence of forest ants on the smaller spruce sawfly, *Pristophora abietina* (Christ.) (Hymenoptera: Tenthredinidae), and found that eight ant nests per hectare reduced larval numbers 22-35 percent over similar areas with no ant activity. Schwerdtfeger (1970) reported the success-
ful colonization of \textit{F. polycetna} and \textit{F. rufa} into two areas—and the resulting control they exerted over the smaller spruce sawfly population. Cotti (1963) summarized the work of several researchers investigating the effect of forest ants upon the smaller spruce sawfly. Bruns (1954), for instance, estimated that a nest of 50,000 workers gathered between 10,000 and 1,000,000 larvae daily. Bruns (1958) also measured the influence of forest ants over a smaller spruce sawfly population and found that it extended to 40 meters from the nest. Cotti (1963) reviewed the work of Ruppertshofen (1955, 1958) who also reported the successful colonization of ants for the control of the smaller spruce sawfly.

Adlung (1966) studied \textit{Epinotia tedella} (Clerck.) (Lepidoptera: Olethreutidae), another pest of spruce which causes most of its damage along sunny edges of plantations. This location is also favorable to \textit{F. polycetna} habitation. It was found that the larvae of this pest feed openly on the spruce twigs during a time of the year when temperatures are too low for normal \textit{F. polycetna} hunting activity. These observations point out the importance of coincidence between ant activity and periods of pest vulnerability.

Cotti (1963) reviewed the work of Goesswald (1954) and Wellenstein (1954) who investigated the effect of red forest ants upon \textit{Diprion pini} (L.) (Hymenoptera: Diprionidae) a pest of spruce. A reduction in the number of cocoons was measured up to a distance of 39 meters from the nest.

Adlung (1966) summarized work done by Weckwerth (1952) on \textit{Dendrolimus pini} (L.) (Lepidoptera: Lasiocampidae) a pest of pine. Ob-
servations indicated that a forest area within a 50 meter radius of a forest ant nest was protected from defoliation while trees outside this area were severely damaged. Pavan (1951, 1960) reported the successful transplantation of F. rufa rufopratensis into a pine wood to control Thaumetopa pityocampa (Schiff.) (Lepidoptera:Thaumetopoidea). Bupalus piniarius (L.) (Lepidoptera:Geometridae), another defoliator of pine, is reportedly attacked in all life stages by F. rufa and F. polyctena (Adlung, 1966).

Adlung (1966) reviewed the work of Behrmdt (1933, 1934), Sinderberger and Marcus (1937) and Wellenstein (1957) investigating the effect of forest ants upon Panolis flammea (Schiff.) (Lepidoptera: Phalaenidae) an important pest of pine. It was found that ants were instrumental in disturbing ovipositing adults thus reducing the number of eggs laid. It was also observed that more than 50 percent of the pupae of this pest were destroyed within 29 meters of a forest ant nest resulting in "green islands" around ant nests in outbreak areas.

Work by Ambros (1938, 1954, 1958), Wellenstein (1957), and Zoebelein (1957) as summarized by Adlung (1966) indicates that forest ants are extremely effective in controlling the nun moth, Porthetria monacha (L.) (Lepidoptera:Lymantriidae). Pupae of the nun moth reportedly have no chance of surviving in areas of high ant populations.

Voute (1951) observed that F. polyctena destroyed nearly 100 percent of the Pachynematus scutellatus (Htg.) (Hymenoptera: Ten-thredinidae) larvae as they descended the boles of larch to pupate. Pavan (1961) observed workers of F. lugubris destroying pupae and adults of the larch casebearer, Coleophora laricella (Hb.) (Lepidoptera:
Coleophoridae). Adlung (1966) in reporting a study by Schwenke (1957) indicated that 22-38 percent of the casebearer larvae on trees infested with larch aphids were destroyed by *F. nigricans* during endemic population levels.

Ceballos (1966) reported on initial attempts to transplant *F. nigricans* and *F. lugubris* in Spain. Scientists in the Soviet Union have also shown interest in predaceous forest ants. Dobrachev (1964) found a close relationship between ant nest density and population density of *Bupalus piniarius* and *Lymantria monacha*. Dimtrienko (1964) found that 80 percent of the insect prey brought into a medium size nest of *F. polyctena*, *F. nigricans*, or *F. lugubris* consisted of forest pests, 30-50 percent of which were lepidopteran larvae.

Smirnov (1964) compared the predatory efficiency of forest ants to that of insectivorous birds and found that birds carry off only one-thirtieth as many larvae of the winter moth, *Operophtera brumata* (L.), than a single ant nest. Malysheva (1964) reported success in the colonization of forest ants to control the pine looper, *Bupalus piniarius* and the pine moth *Dedrolimus pini*. Petrenko and Dimtrienko (1964) concluded that forest ants are more effective against forest pests when pest numbers are diminishing, especially between outbreaks, when ants help to prevent renewed increases in pest numbers.
CHAPTER III

METHODS

Field Investigation

The primary study plot was located on the Lubrecht Experimental Forest of the Montana Forest and Range Experiment Station, University of Montana, thirty miles northeast of Missoula. The plot was established in the southwest quarter of Section 14, Range 15 west, Township 13 north and was approximately ten acres in size. This location was selected for the following reasons:


(2) The stand supported a large spruce budworm population.

(3) The location was easily accessible from bordering roadways.

(4) The location was easily accessible from Missoula.

Plates 1 and 2 illustrate the varying stand structure of the primary study plot.

A second study plot was located approximately two miles east of the first plot. The second area consisted of a 20,000 tree plantation of twenty year old Douglas-fir located in a mixed stand of lodgepole pine (Pinus contorta) and Douglas-fir. Because of the large number of Formica ant nests found on the second plot, it was selected to serve as a point of comparison with the primary study plot.
Random foliage sampling using the beating method was conducted to give an indication of ant abundance in the foliage. An intensive survey was made of the study areas to assess the number of ant species present and their relative abundance. The plot was divided into a grid with lines spaced approximately 100 feet apart. All ant nests found on or near these lines were located on a map, and a description of nest type was recorded. Specimen samples were taken in triplicate from each nest type and included workers, brood and reproductives. Representative samples were later sent to a taxonomist for identification.

Observations of ant-budworm relationships in the foliage of Douglas-fir were made at all levels in six trees short enough to be viewed from a sixteen foot orchard ladder. Special attention was paid to confrontations between foraging ants and budworm larvae.

Fourteen trees were selected for study and labeled "larval fall" trees. Ranging in height from six to thirty feet, the trees were selected on the basis of their apparent budworm population, and their size and location. A population index was established for the test trees by clipping two fifteen inch branch tips from each of three height zones in the tree crowns. Labeled samples were placed in plastic bags and later all larvae were removed from the branch samples and counted. This sampling method, which followed a similar procedure outlined by Carolin and Coulter (1972), was repeated three times during the larval fall season beginning when the first larvae began to fall from the trees. Similar sampling was done on sixteen nearest neighbor trees, bringing the total number of trees from which sample data were collected to thirty.
The area under each test tree was fitted with a catch device consisting of rectangular pieces of muslin sheeting. The strips were cut to a length that would encompass the tree crown at its widest point. The widths were adjusted to a similar size by adding strips to the sides. The sheets were supported four inches off the ground by wooden stakes placed at each corner. The two inner muslin strips were pulled tightly around the tree bole and fastened with tacks. Adjoining strips were fastened together with staples. The tree bole immediately above the sheet "collar" was coated with Tanglefoot* or Tacktrap* to prevent larvae from escaping up the tree. Plate 3 illustrates the arrangement of the catch sheets.

The "larval fall" trees were visited on a daily basis beginning when the first larvae appeared on the sheets and continuing through the life cycle until most of the larvae had pupated. The sheets were checked hourly over a five or six hour time span beginning between eleven A.M. and twelve noon. At each check all larvae and other insects were recorded and removed from the sheets.

Four Douglas-fir trees ranging in height from eight to fifteen feet and supporting a sizable budworm population were selected for study into the fate of those larvae which fall from the foliage. Two of the trees were located near ant foraging areas and two were located completely away from areas of ant activity. Several budworm larvae were dislodged from the foliage of each "larval fate" tree by shaking or tapping the branches with a pole. The number of larvae dislodged was counted and a record was made of their actions and eventual fate.

* Brand names of sticky trap material
The number of foraging ants present beneath the tree, the time of day, and the length of the observation period were also recorded. Ant attacks on budworm larvae were closely observed and a record was made of each attack occurring within each observation period.

Feeding tests were conducted in the field to observe ant attack behavior as well as fate of falling larvae. Known numbers of budworm larvae collected from surrounding trees were offered to foraging ants at varying distances from Test Nest I and the time required for the ants to discover and destroy the larvae was recorded.

Observations of the main foraging trails leading from Test Nest I were made to determine what food stuffs were being gathered by the ants and what proportion budworm larvae comprised of the total insect material brought to the nest. Numbers and types of insect prey were recorded during each fifteen minute observation period. Similar observations were made around several ant nests in different locations.

**Laboratory Investigations**

A series of laboratory experiments were designed and conducted to supplement the field investigations. Emphasis was placed on the study of the behavior of the spruce budworm larvae and particularly the predaceous ant species present on the field study plots. Two artificial ant nests were constructed to house one colony each of *Formica obscuripes* and *F. criniventris*. A series of feeding experiments was conducted utilizing the two laboratory ant colonies and budworm larvae collected in the field and larvae reared in the laboratory on nutrient agar.
Ant nests of two types were constructed. Lab Nest I consisted of a plywood platform measuring two feet wide and four feet long supported by six inch steel bolts placed one in each corner (refer to Plate 4). Each leg was set in a shallow pan filled with water to act as a catch for ants escaping down the legs. The entire nest platform was painted with brown water proof paint.

A colony of *F. obscuripes* was collected in the field and placed in a plastic bucket along with nest material to be transported to the laboratory. A small stump collected in the field was placed upright in the middle of the platform and the nest material together with the ants poured slowly around it. Water was provided continuously in small dishes placed upon the platform.

Lab Nest II was patterned after a nest described by Peterson (1964). It consisted of a platform equal in dimension to Lab Nest I, however, the platform was partitioned in half with one half becoming the brood chamber and the other the foraging area. Several circular chambers with interconnecting pathways were etched into the cork bottom of the brood chamber. A sheet of glass covered with several layers of red cellophane was placed over the brood chamber to provide darkness for the brood and easy observation of nest activities without disturbance of the inhabitants. The entire platform was painted with white water proof paint (see Plate 5).

A colony of *F. criniventris* was collected in the field and placed together with nest material into a plastic bag for transport to the laboratory. Only a small amount of nest material was placed on the platform of Lab Nest II as per the instructions of Peterson (1964).
The ants were carefully placed on the platform and soon they began to carry the brood into the brood chamber through a small opening provided in the partition. Water was provided in small dishes placed in the foraging area.

Following suggestions of Peterson (1964) and Sudd (1967), the ants in both nests were offered a wide variety of foods ranging from bread crumbs, dried cereal, turkey, chicken, and beef crumbs, to dog food, cat food, nutrient agar and honey. The most widely accepted food was honey although everything offered was fed upon occasionally.

The need for budworm larvae in feeding tests and observations conducted in the laboratory prompted a rearing program involving the collection of overwintering second instar larvae from the field, forcing their emergence in the laboratory and introducing them to specially prepared nutrient agar. The shortness of the field season made collection of developed larvae from the field for the laboratory experiments impractical.

The nutrient agar was provided through the cooperation of Dr. David Fellin and Dr. Robert Lyons. The agar, prepared in inch thick sheets, was cut to size and placed in sterile petri dishes. The surface of the agar was scarred slightly with a teasing needle to allow the introduced larvae to become established. The larvae were induced to emerge prematurely from their overwintering sites under the bark scales of western larch bole sections gathered from the field during March. As the tiny larvae emerged from the bole sections heated by

3/Research Entomologist, Pacific Southwest Forest Experiment Station, Berkley, California.
150 watt light bulbs, they were collected and introduced onto the agar plates. Tight fitting lids were placed on each plate containing from twenty to thirty second instar larvae.

As the larvae developed in the agar plates, they were periodically transferred to fresh plates as the agar dried or became contaminated. Larvae were selected from the rearing plates as they matured to fifth and sixth instars and were utilized in feeding experiments and behavioral tests.

Feeding tests consisted of offering a pre-determined number of larvae to laboratory ant colonies by placing them randomly in the feeding arena. The number of ants foraging at the beginning of each test was recorded and their numbers were monitored throughout each test. Time measurements were made using a stop watch and record was kept of the time required for foraging ants to discover the larvae, subdue the larvae and transport them to the nest interior. Observations were made of the reactions of ants to budworm larvae and larvae to ants, ant attack behavior, method of transport used by the ants, the presence or absence of a signalling behavior or other means of communication between foraging ants and the variations of all these things with time of day and nest conditions.

The number of larvae offered to a nest at a time varied from one to fifteen and the time of day in which the tests were run varied from early morning to evening. Tests were conducted at two day intervals or longer to minimize the accumulation of larvae within the nest and the possibility of a test induced feeding pattern.
CHAPTER IV

RESULTS - FIELD AND LABORATORY INVESTIGATIONS

Description of Ant Species Encountered

Seven species of ants were collected on the study plot during the field investigation. Representative samples of each collection were sent to Dr. Paul Kannowski for identification. Species identified included: Manica hunteri, Camponotus modoc, Lasius crypticus, Formica montana, F. obscuripes and F. criniventris. Of the seven ant species collected on the study plot, six were observed preying upon spruce budworm larvae. Manica hunteri, a small subterranean species, was the only ant species not observed preying upon budworm larvae. Three of the remaining six species most commonly observed preying upon budworm larvae and receiving the most attention were: F. obscuripes, F. criniventris, and C. modoc.

Formica obscuripes and F. criniventris are commonly referred to as "thatching ants" because of the structure of their nest. Both species build domed type nests, although in this locality, F. criniventris is more prone to building its nest in rotten logs or stumps with the thatched dome piled up against the supporting object (Plate 6). Formica obscuripes often uses a dead shrub such as snowberry (Symphorocarpus albus) or Ceonothus sp. as the base for the nest.

4/ Professor of Entomology, University of North Dakota, Grand Forks.
piling thatch material (conifer needles and twigs) on top so that the dead branches of the shrub protrude from the base of the dome like spokes of a wheel (Plate 7). Both species prefer to build their nests on warm sunny slopes, or in sunny meadows, avoiding the darker, cooler forest areas.

Both Formica species are active foragers and may range some distance from the nest. Workers from Test Nest I (F. obscuripes) were observed foraging up to 25 meters from the nest. The two Formica species are comparable in size and aggressiveness. They forage for food both in the foliage and on the ground. These species are commonly found tending aphid colonies in the foliage of Douglas-fir to obtain honeydew and preying on other insect types.

Camponotus modoc (carpenter ant) builds its nest at the base of large trees (commonly Douglas-fir) and often constructs galleries within the tree. This species is found throughout this region in nearly all stands containing mature and overmature trees. Nests of this species were numerous on the study plot.

Camponotus modoc was observed foraging in trees and was occasionally observed tending aphids. Work by other scientists has demonstrated that workers of this species are often associated with root feeding aphids and tend them for the purpose of collecting honeydew. Many of these aphid species spend part of their life cycle in the foliage and C. modoc workers pursue them. Observations indicated that C. modoc forages for insect prey as well as honeydew and may be quite an efficient predator.
Camponotus workers are considerably larger in size than either Formica species. Their larger size and aggressive nature make them well suited as predators of spruce budworm larvae. Although C. modoc was quite abundant on the ten acre study plot, a thorough survey revealed only three nests each of F. obscuripes and F. criniventris.

Budworm Vulnerability to Ant Predation

Observations completed during this investigation suggested a relationship existing between budworm development and the subsequent vulnerability of budworm larvae to ant predation. Overwintering second instar larvae emerge in late April and early May and climb to the tree crown where they may be dispersed by wind. Once on the host material, they mine buds, needles or cones until the young buds burst exposing the much preferred new foliage. The larvae begin feeding on the new foliage by webbing several needles together to form a protected feeding site (Plate 8). Foraging ants are unable to penetrate the foliage web to attack the larvae. As temperatures rise and the larvae mature, they gradually leave the web to feed more openly on the foliage. Now well into the fourth and fifth instars, the larvae spin entirely silken feeding tubes on the branch tips (Plate 9).

Larvae often leave these silken feeding tubes to feed openly on other branch tips, spinning another tube or returning to an old one during daily periods of inactivity or during times of adverse weather (Plate 10). While exposed openly, budworm larvae are subject to the action of wind, birds and small mammals all of which act to dislodge the larvae from the foliage. Foraging ants are able to capture larvae in the foliage or act to cause their dislodgement. Larvae are quite
sensitive to disturbances and react by wiggling backwards off the end of the branch tip.

Observations made during this investigation pointed out the occurrence of larval fall beginning midway in the period of larval development and continuing to the pupal stage. The commencement of larval fall was closely associated with the movement of larvae from the protected foliage tubes to more open feeding activity. Foraging ants and weather conditions appeared to be related to the number of larvae falling during this period.

During the 1973 season the first larvae were found on the catch sheets on July 3rd. Larvae ranged in size from third instar to fifth instar with fourth instar predominating. Previous to this date most of the catch sheets contained a considerable amount of frass (fecal material) indicating that larval feeding was occurring, yet prior to July 3rd not one larva was collected from the sheets. Examination of weather records (Table 1) listing daytime maximum temperatures and relative humidities show that larval fall commenced on a day with the highest maximum temperature and the second lowest relative humidity in the previous eleven days. The weather previous to this day had been cool, partly cloudy and rainy. These conditions correspond to subdued larval feeding with the larvae being webbed up tightly in the foliage. On June 30th, three days prior to the commencement of larval fall, most of the larvae were loosely webbed up and on July 2nd a few had begun to feed openly. Maximum larval fall occurred on July 10th, the hottest day of the season (101 degrees Fahrenheit) with the lowest relative humidity (12%). Larval fall on
**TABLE 1**

WEATHER DATA COLLECTED AT GREENOUGH MONTANA - 1973

<table>
<thead>
<tr>
<th>Date</th>
<th>Maximum Temp. F</th>
<th>Percent Relative Humidity</th>
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</thead>
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* those dates that larval fall data was recorded. July 3 marked the first day larvae fell on the catch sheets.
this day was some two times greater than on the day with the next
greatest value, suggesting that weather conditions influence larval
fall (see Figure 1). Observations indicated that daily larval fall
reached a peak during the hottest part of the day. This time coincides
with peak ant foraging activity (in this area) and the period of
greatest budworm vulnerability.

During the summer of 1973, 220 larvae were caught on the
fourteen catch sheets over an eight day period from July 3rd through
July 12th (July 5th and 7th excluded). Figure 1 shows the total
number of larvae caught per tree on each of the eight days. Eighty-two
percent (82%) of all larvae collected on the sheets fell from eight of
the fourteen trees. Only two trees (numbers three and four) of the
fourteen exhibited no ant foraging in the foliage or on the catch
sheets. Ants were observed in the foliage of five trees and were
observed foraging only on the sheets of seven trees. Those trees
with ants in the foliage also had ants on the sheets. All three
predominant ant species were observed in or around those trees with
ant activity.

Sixty-one percent (61) of the total 220 larvae caught in 1973
fell from those five trees in which ants were observed in the foliage.
Twice as many larvae fell from those trees in which ants were observed
in the foliage than fell from those with ants on the sheets only.
This value was nearly seven times greater than the number of larvae
falling from trees with no ant activity at all.

Population sample data was gathered in conjunction with the
larval fall data and reflect the corresponding changes in the relative
Figure 1. Total larvae falling to the catch sheets during eight days of observation.
budworm population of the fourteen test trees as the larvae progressed toward the pupal stage. Samples were taken on July 4th, 10th, and 13th of 1973 and the number of larvae collected per sample per tree are listed in Table 2. These figures help to describe the rate of larval population decline beginning with the commencement of larval fall on July 3rd. Those trees with the highest rates of population decline did not necessarily correspond to those trees having the greater numbers of larvae falling to the catch sheets. Of those five trees with ants observed in the foliage, numbers six, seven and twelve were among the trees exhibiting the highest rates of decline. However, tree number nine displayed the lowest rate of decline of all fourteen trees and yet was observed having ants in the foliage. Factors not measured i.e. parasitism, predation by birds and insect forms other than ants, and losses to ants not accounted for are presumed to have contributed to this inconsistency in results. Sampling error, too, likely contributed to discrepancies in data. The time of day and the manner in which samples were taken, the position on the tree from which branch samples were clipped and the distribution of larvae within the tree crown are all factors contributing to sampling error.

The rates of decline of all fourteen trees grouped by their relationship to foraging ants are depicted in Figure 2 a-c. Generally speaking, the greatest rates of decline were shown by those trees with ants in the foliage, followed by those trees with ants appearing on the sheets but not in the foliage, with two trees showing no ant activity having the lowest rates of decline. The five trees with ants in the foliage and showing the largest number of larvae falling to the catch
TABLE 2
BUDWORM LARVAE AND PUPAE COUNTS TAKEN FROM FIFTEEN INCH DOUGLAS-FIR FOLIAGE SAMPLES - 1973

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<th>July 4th Pupae</th>
<th>July 10th Larvae</th>
<th>July 10th Pupae</th>
<th>July 13th Larvae</th>
<th>July 13th Pupae</th>
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</table>

Totals: 915 Larvae, 19 Pupae, 532 Larvae, 189 Pupae, 263 Larvae, 276 Pupae, 1720 Larvae, 484 Pupae

* Refers to trees with (a) designation. These trees were selected as nearest neighbor trees for sampling purposes.
sheets show an overall decline in larval population of 72 percent while those trees with ants only on the sheets showed a 64 percent overall decline. Those trees with no ant activity showed only a 22 percent decline in larval population.

Figure 2. Decline of larval population on fourteen test trees as determined by total larvae per six branch samples per tree on three sample dates. (a) those trees with ants only on the sheets; (b) those trees with ants in the foliage and on the sheets; (c) those trees with no ant activity.
Ant Foraging Behavior

Field observations indicated that ant foraging activity is closely regulated by temperature and other weather conditions. Daily nest activity seemed to be controlled largely by temperature. Test Nest I (*F. obscuripes*) was located on the sunny side of a slight swale. The east side of the swale supported many mature trees which tended to shade the west side from the morning sun. Direct sunlight did not touch the nest until 9:30 A.M. to 10:30 A.M. during the month of July. Each morning of observation found foraging activity very slow and sluggish before the nest dome has been warmed by the sun.

Thousands of ant workers covered the entire dome in these early hours. At this time, very few workers could be seen along the foraging trails or in the foliage of nearby trees. As ant activity increased with rising temperatures, workers could be seen moving down the foraging trails. By 10:45 A.M. or 11:00 A.M., there were very few workers left on the dome surface and foraging activity was in full operation, sometimes lasting well into the evening depending upon temperature. Cool or cloudy weather greatly affected this timing. On rainy days, for instance, foraging activity was almost nil even though the dome might be covered with ants.

Careful observations of the foraging trails leading to several *Formica* nests verified that predation of budworm larvae and other insect forms was considerable. Insects being brought to Test Nest I by way of one trail were identified and recorded during fifteen minute
observation periods. These data, listed in Table 3 below, clearly show the emphasis placed upon budworm larvae, indicating the reaction of *Formica* ants to a budworm outbreak.

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  <tr><th>Insect</th><th>Length of Observation Period</th></tr>
  <tr><td>6 budworm larvae</td><td>15 min.</td></tr>
  <tr><td>6 budworm larvae, 1 pupa</td><td>"</td></tr>
  <tr><td>4 budworm larvae</td><td>"</td></tr>
  <tr><td>4 budworm larvae, 1 pupa</td><td>"</td></tr>
  <tr><td>2 budworm larvae, 1 pupa, 1 geometrid larvae</td><td>"</td></tr>
  <tr><td>4 budworm larvae, 1 diptera larva</td><td>30 min.</td></tr>
  <tr><td>5 budworm larvae, 1 pupa</td><td>"</td></tr>
  <tr><td>several dead or injured ants</td><td>15 min.</td></tr>
  <tr><td>1 moth (unknown), 2 budworm pupae, 1 diptera larva</td><td>"</td></tr>
  <tr><td>1 budworm larva, 5 pupae, 1 diptera larva</td><td>"</td></tr>
  <tr><td>1 budworm pupa, 1 diptera larva</td><td>"</td></tr>
  <tr><td>4 budworm larvae, 1 diptera larva</td><td>"</td></tr>
  <tr><td>2 budworm pupae, 1 geometrid larva</td><td>"</td></tr>
  <tr><td>2 budworm larvae, 1 adult fly</td><td>"</td></tr>
  <tr><td>3 budworm larvae</td><td>"</td></tr>
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Food habits of *Formica* ants have received considerable study in North America and Europe. Observations made in this investigation tended to support the work of Oakland (1932), Wellenstein (1952) and Zoebelein (1956) as summarized by Cotti (1963) and Sudd (1967) which demonstrated that honeydew secreted from aphids and related plant sucking insects constituted a major portion of the *Formica* ant diet. Workers of the two *Formica* species studied in this investigation were observed tending aphids even when budworm numbers were considered to be
Several workers (Flanders, 1951; Bartlett, 1961; Way, 1963; and Bradley and Hinks, 1968) have found that aphid colonies tended by ants flourish because they are protected by the ants from their natural enemies. Observations made during this study indicated that ants were by far more numerous in Douglas-fir trees containing aphid colonies than in those trees without aphid colonies.

Aphid colonies were not found to be numerous in Douglas-fir trees on the study plot. Damage to branch tips and terminal leaders was negligible. Observations made in the Douglas-fir plantation provided some basis for comparison of ant, aphid and budworm relationships. Aphid populations were high in the twenty year old plantation and damage to branch tips and terminal leaders had occurred with some distortion in growth. Interestingly, the more open, sunny plantation supported a Formica nest population three times greater than found on the study plot. Samples taken from the foliage by beating indicated that budworm populations were considerably lower than on the study plot with only negligible defoliation apparent in 1973. Similar sampling in the mixed Douglas-fir - lodgepole pine stand immediately surrounding the plantation revealed budworm populations considerably greater than on the plantation.

**Predatory Behavior of Ants**

Results of feeding tests and observations conducted both in the field and in the laboratory verified the predation of spruce budworm larvae by forest ants both in the foliage of Douglas-fir and on the ground beneath the trees. Ants of all three species foraging in the
foliage of Douglas-fir would readily attack feeding larvae exposed on the branches and twigs and would actively roust larvae from their silken feeding tubes. Foraging ants often worked on a confined larva for an hour or longer. *Camponotus modoc* was best adapted for this activity because of its greater size and longer appendages. During one twenty minute observation period, a *C. modoc* worker dislodged three budworm larvae from their tubes. The two *Formica* species were equally persistent predators but were somewhat restricted by their smaller size.

The structure of the feeding tubes often impeded efforts of foraging ants to force larvae from them. The tubes are constructed from fine sticky silk spun by glands located in the head of budworm larvae. While crawling about the feeding tubes, foraging ants would sometimes become entangled in the sticky silk and would require one or two minutes of vigorous activity to free themselves.

Foraging ants would crawl from top to bottom and around all sides of the feeding tubes, reaching first in one end with front legs and head, and then the other end. The larva would usually move from one end of the tube to the other keeping just out of the ant's reach. Eventually, the ant would reach far enough into the tube to touch the larva, causing it to wiggle out the other end. The ant would then either make a successful capture by pinning the larva against a twiglet and grasping it, or force the larva to fall or spin from the foliage. Often times a dislodged larva would spin down on a silken thread and dangle from the branch tip. Ants were observed as though waiting on the branch above dangling larvae. As a larva climbed back up the thread to the branch an ant would again attack. In the struggle
of an attack, both the ant and the larva often tumbled to the ground where the ant made the capture.

Ants were rarely seen feeding on larvae in the foliage. More often a capture was made and the larva was taken down the bole to the nest. However, observations made around one tree with a strong foraging population of C. modoc indicated that this species was particularly aggressive in its attacks in the foliage. Workers descending the bole were collected and were found to be carrying bits and pieces of budworm larvae captured in the foliage.

Several attacks were observed along the boles of trees. Foraging ants were continuously ascending and descending the boles and would often encounter budworm larvae which had fallen to the ground and had managed to crawl safely back to the tree bole. The larva was invariably confronted by one or more ants and attacked. The ants were often successful in capturing the larva on the bole and carrying it down to the nest. Plates 11 and 12 describe such a capture. In other instances the larva was dislodged from the bole and the ants made the attack and capture on the ground. Ants are continuously foraging in the area beneath the trees and are responsible for heavy predation of fallen larvae.

Attack behavior of ants on the ground was closely related to their foraging patterns. Hundreds of attacks were observed during the study, both in the field and in the laboratory. Two principal behavior patterns associated with prey finding were observed. In one, attack was merely a response to touch. During the course of foraging, the ant simply bumped into the larva and reacted by attacking it. The larva was
grasped behind the head by the ant and the struggle lasted until the larva succumbed (usually one to five minutes). This pattern was most commonly observed in laboratory feeding tests. The restricted foraging area in the artificial nests increased the chances of foraging ants bumping into larvae.

In another behavior pattern, a visual or olfactory response was suspected. The ant seemed to sense the presence of a larva from a distance of one half to two centimeters and deliberately changed its direction of travel to make the attack. This behavior pattern was observed most frequently in the field.

Attacks were initiated by one or more ants. The attacking ant or ants would approach the larva and make initial contact which would cause the larva to wiggle violently backwards. The attackers would then quickly flank the larva and grasp it behind the head. If several ants were involved, one would hold the head while the others would grasp the abdomen. A larve attacked in this manner would be stretched out between the ants, unable to wiggle.

Attacking ants would chew and tear at the larva's skin and would usually squirt formic acid from their gaster into the wounds. After ants made an attack, the larva was seldom abandoned until it had been deposited in the nest. It was noted, however, that ants in laboratory nests would often become disinterested in the attack and leave the larva for a while returning later to continue. This behavior was never observed in the field.

The number of available prey directly affected the number and activity of foraging ants. The discovery of many larvae in an area
would soon result in frenzied activity of other foraging workers. Within minutes there was a sudden influx of additional workers into the area. Once all larvae were under attack, additional workers aided in transporting the larvae to the nest. Many workers would continue to forage in the area for quite some time. This behavior was observed in the field and in the laboratory.

Transporting of larvae back to the nest represented a major portion of ant foraging activity and predatory behavior. Obstacles that had to be crossed or circumvented and temporary loss of nest location were the primary problems encountered by ants returning to the nest with prey. Most Formica ants do not leave scent trails and must rely largely on eyesight and their ability to determine direction by utilizing the force of gravity and the angle of the sun. Occasionally nest location was lost by returning ants and in these cases the ant would drop the larva for a moment and appear to scout ahead as though to determine the correct direction of travel. The ant would then retrieve the larva and continue on towards the nest.

The method of carrying a larva also varied. A single ant might carry a larva to the nest by simply straddling the larva, grasping it by the thorax and walking towards the nest with the larva suspended between its legs. By another method, the ant would grasp the larva by the thorax and turn backwards to the direction of travel. The ant would then twist around quickly, lifting and flinging the larva in the direction of the nest. The ant, turning backwards, would repeat the flipping procedure. Sometimes both methods were employed by an ant depending upon the condition of the return pathway.
Two ants were considerably more efficient at transporting a larva than one ant. The ants would grasp the larva at opposite ends and the trio would travel towards the nest in a looping fashion, each ant spinning the other around with the larva stretched between them. Observations demonstrated that when three or more ants were engaged in transporting a single larva, the efficiency of the procedure was greatly diminished. With several ants holding the larva, no direction of travel could be maintained because each ant was pulling in a different direction.

**Response and Fate of Larvae Attacked by Ants**

Dislodged larvae either fall to lower branches, to the ground or spin down from the branch by a silken thread. During observation periods, it was not uncommon to see eight or ten larvae dangling from the branches of one tree. Crown configuration of the tree has some effect on the number of larvae falling to the ground. Those trees with narrow upper crowns and wide spreading lower branches often retain many larvae falling from upper branches. Other factors such as wind and distribution of larvae within the crown also affected larval fall.

The backward wiggling described earlier is a common response of tortricid larvae upon being disturbed. The wiggling action proved to be an effective means of escape from foraging ants in the foliage. However, once the larva was dislodged and fell to the ground, the wiggling was of little consequence since an ant could easily overpower the larva and the ground offered the larva no means of escape.

When the skin of a larva was punctured by an attacking ant,
greenish fluid (haemolymph) exuded from the wound. In some cases, an attacking ant would become coated with this fluid and appeared to be repelled from the wounded larva. The ant would stagger about in a disoriented fashion, sometimes collapsing, appearing to be dead or dying. The ant might remain debilitated for 45 minutes or longer before it recovered and resumed normal activity. The larval haemolymph was not a primary deterrent to ant attack. Attacking ants were observed feeding on this fluid as it exuded from wounds on larvae.

Larvae were seldom observed to recover from an ant attack. On those occasions during laboratory feeding tests when a wounded larva was abandoned by an ant affected by the haemolymph, the larva usually died or was captured and carried to the nest by another ant or ants. Wounded larvae were never observed to be abandoned under field conditions.

Dislodged larvae reaching the ground would begin swinging their heads from side to side. This behavior is presumably associated with the functioning of photoreceptors located in the head region of the larva which act to distinguish light intensity. Soon the larva would begin crawling and would generally climb the first obstacle it came to, including twigs, grass, shrubs and other non-host material. The larva would remain on such an obstacle from a few minutes to several hours. Larvae appeared to react to the intensity of sunlight. Once full sunlight reached the larva, it would often climb down from its perch and begin crawling (not always in the direction of shade) until it confronted another obstacle which it would then climb. Many times the new location was in a more shaded area, but the larva's ability to
seek out shade appeared to be limited. Ants foraging on the twigs and grass beneath the trees also forced stranded larvae to seek out a new perch.

Dislodged larvae falling in areas of shade beneath a tree would invariably begin crawling towards the bole of the tree from which they fell. Their success in reaching the bole depended upon the density of non-host material beneath the tree and the density of foraging ants beneath the tree. Larvae falling in areas of strong ant foraging stood very little chance of surviving. Ants also were observed foraging on the grass and shrubs beneath trees, thus decreasing the chance of a larva surviving by crawling non-host material.

The sun often becomes an important factor in the survival of fallen larvae. During hot periods of the day, temperatures at ground level become extremely high. When a larva falls into an area of direct sunlight and the nearest shade is some distance away, observations demonstrated that the larva was often overcome by the heat before reaching a shaded area. A larva falling into an area of full sunlight would often begin crawling away from the nearest shade and in a few minutes its movements would slow and soon cease. Prodding with a small stick would not elicit a response and if removed to a shaded area the larva would not recover.

**Verification of Ant Predation**

The process of verifying ant predation began by counting the number of attacks made by ants on budworm larvae under one test tree. Larvae attacked included those on the ground at the beginning of each observation period as well as those which fell from the foliage during
that period. The results listed below in Table 4 show the number of attacks counted during three observation periods. Each attack resulted in the elimination of one larva. These data serve only to illustrate the variability in the number of attacks that can occur under natural conditions.

**TABLE 4**

OBSERVED NUMBER OF BUDWORM LARVAE KILLED BY ANTS UNDER ONE TREE ON THREE SEPARATE OBSERVATION PERIODS

<table>
<thead>
<tr>
<th>Number of Attacks</th>
<th>Length of Observation Period</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>45 minutes</td>
</tr>
<tr>
<td>12</td>
<td>45 &quot;</td>
</tr>
<tr>
<td>37</td>
<td>45 &quot;</td>
</tr>
</tbody>
</table>

The results of three feeding tests conducted under field conditions utilizing a total of 136 budworm larvae are listed in Table 5. These tests, designed to observe ant attack behavior and ant reaction to varying prey density, provided data which suggest a relationship between the number of larvae available and the time required for foraging workers to discover and capture them.

The results of eight feeding tests conducted in the laboratory with colonies of *F. obscuripes* augmented results obtained in the field. Larvae were placed in the foraging arena of the artificial nest as far from the dome as possible. The number of larvae offered during a particular test varied from two to fifteen. The shortest period of time required for an ant to find a larva was one minute (four larvae
offered), and the longest period of time required was eighty minutes (one larva offered).

<table>
<thead>
<tr>
<th>Number of Larvae Offered</th>
<th>Distance Dish Placed From Test Nest I</th>
<th>Time Elapsed—All Larvae Removed From Dish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Test 1</td>
<td>10</td>
<td>4-4½ feet</td>
</tr>
<tr>
<td>Test 2</td>
<td>10</td>
<td>4-4½ feet</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>7-8 feet</td>
</tr>
<tr>
<td>Test 3</td>
<td>20</td>
<td>4 feet</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>6 feet</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>8 feet</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>10 feet</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>12 feet</td>
</tr>
</tbody>
</table>

Two larvae were offered in each of two tests conducted with Lab Nest I (E. obscuripes). In both tests it took foraging ants four minutes to find the first larva and thirty-eight minutes to find the second. The average number of foraging ants in both tests was fifteen and this number did not change appreciably throughout the tests. Results from a test in which three larvae were offered to ants in Nest I showed that four and one half minutes were required for the first larva to be found and thirty-one minutes for the third. The number of foraging ants (average 17) remained fairly constant during this test also.

When four larvae were offered to ants in Nest I, the first larva was attacked within one minute and the last larva was attacked
within two and one half minutes. The number of foraging ants increased from 20-25 at the beginning of the test to 55-60 after one hour and forty-five minutes.

In another test with Nest I utilizing four larvae, all larvae were under attack within two minutes and the number of foraging ants increased from 20-25 at the beginning of the test to 70-80 after thirty-five minutes, and increased further to 120-130 after one hour and thirty minutes. When fifteen larvae were offered, all were under attack within one and one half minutes. The number of foraging ants increased from 25-30 at the beginning of the test to 60-80 after fifteen minutes, to 180-200 after seventeen minutes, and finally to 280-300 after thirty minutes.

The time required for a larva to be subdued once attacked was extremely variable and depended upon the number of larvae available and the foraging pressure. If only two or three larvae were present and the number of foraging ants did not increase appreciably, an attacking ant might require up to an hour to prepare a larva for transport to the nest. A large number of larvae in the foraging area greatly increased the ant foraging pressure and each attacking ant or group of ants tended to move each larva to the nest more quickly.

The time required for the ants to carry all larvae to the nest also varied with the number of larvae offered. Three hours or more were required to move three or four larvae into the nest. However, in a test utilizing fifteen larvae, all were deposited in the nest in fifty-five minutes. Just how the time required for attack, capture and transport of larvae to the nest varied under field conditions is not fully known.
Table 6 lists the results of nearly 18 hours of observation designed to study the fate of larvae falling from the foliage of Douglas-fir. This data serves to strengthen the assertion that budworm larvae falling into areas of ant foraging activity stand little chance of surviving. The importance of heat from the sun as a mortality factor affecting fallen larvae is also pointed out.

Other Budworm Life Stages Attacked by Ants

Observations of budworm pupae and adults demonstrated that these forms too are attacked by all three principal ant species studied. The budworm pupa is attached to the branch tip by silken threads, sometimes completely webbed up among needles and sometimes attached only at the tip or anal end (cremaster), dangling freely from the branch (Plate 13). Ants were not observed dislodging pupae from the foliage. Wind and other disturbances result in a number of pupae falling to the ground where they are readily gathered by foraging ants. Pupae were observed being taken into Test Nest I and were observed being carried by ants in other areas of the plot.

Budworm moths also come under attack by foraging workers of all three ant species, but to a lesser degree than pupae or larvae. Moths are generally less active during the daylight hours and stay sheltered on the interior portion of Douglas-fir branches (Plate 14). The moths, especially the females, are quite sluggish in their movements and although they are easily disturbed, their reactions are slow. Ants moving to and from aphid colonies often came into contact with moths resting on the branches and would readily attack them. Usually the
### TABLE 6

RESULTS OF NATURAL PREDATION OBSERVATIONS DESIGNED TO STUDY FATE OF FALLEN LARVAE

#### Under Trees With No Ant Activity

<table>
<thead>
<tr>
<th>Length of Observation Period</th>
<th>Number of Larvae Falling</th>
<th>Fate</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 hours</td>
<td>5</td>
<td>3 succumbed to heat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2 on shrubs at end of period</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>3 hours</td>
<td>10</td>
<td>4 succumbed to heat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1 back to bole</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5 stranded on shrubs</td>
</tr>
<tr>
<td>2½ hours</td>
<td>8</td>
<td>3 succumbed to heat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2 back to bole</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3 stranded on shrubs</td>
</tr>
<tr>
<td>3½ hours</td>
<td>5</td>
<td>1 succumbed to heat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4 stranded on shrubs</td>
</tr>
</tbody>
</table>

#### Under Trees With Ant Activity

<table>
<thead>
<tr>
<th>Length of Observation Period</th>
<th>Number of Larvae Falling</th>
<th>Fate</th>
</tr>
</thead>
<tbody>
<tr>
<td>1½ hours</td>
<td>10</td>
<td>5 attacked by ants</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3 succumbed to heat</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2 stranded on shrubs</td>
</tr>
<tr>
<td>1 hour</td>
<td>4</td>
<td>4 attacked by ant</td>
</tr>
<tr>
<td>2 hours</td>
<td>5</td>
<td>5 attacked by ant</td>
</tr>
<tr>
<td>2 hours</td>
<td>12</td>
<td>1 back to bole</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11 attacked by ant</td>
</tr>
</tbody>
</table>
disturbed moth would flutter away unharmed. Occasionally, a moth would be too slow in reacting and one or two ants would grasp the moth by the legs or wings and subdue it. The moth was then taken down the tree bole and carried to the nest.
CHAPTER V

DISCUSSION AND CONCLUSION

This study has succeeded in providing considerable background information concerning the behavior of predaceous ants associated with the western spruce budworm. Without a doubt, the data collected and the observations made during this investigation have conclusively demonstrated that in western Montana at least three species of forest ants prey on budworm larvae, pupae and adults and that budworm larvae comprise a substantial proportion of the insect prey collected by these species when budworm numbers are high. The actual or numerical effect of ant predation upon the budworm population as a whole was not clearly shown by this study or was it a primary objective.

The effectiveness of predaceous ants in "controlling" a spruce budworm population is an interesting problem and a discussion of effectiveness in terms of the results presented in this paper is in order. For purposes of discussion an effective predator would be considered one that causes through its actions a measurable effect on a pest population. Effectiveness may be thought of in terms of a one on one situation where the effectiveness of one ant or a small group of ants in capturing one or several budworm larvae is considered. The effect of ants as a population on budworm as a population is, of course, measured under the full definition of predator effectiveness.
A consideration of the effectiveness of forest ants as predators of western spruce budworm must begin with a look at the development and behavior of the budworm itself. In its early stages on the foliage of Douglas-fir, the spruce budworm larva is well protected by its tightly woven web of needles and silk. Foraging ants have little effect on the budworm population at this time. It has been speculated that spruce budworm and other related tortricid larvae are rather immune from attack by predators such as ants because of the feeding tubes which they construct. Evidence collected in this study shows that this is not the case, at least with the western budworm.

Several factors act to induce the budworm larva to replace its tightly woven foliage web with a more mobile and loose silken tube and encourage the larva to leave the confines of the tube to periodically feed openly on the foliage. Weather and climatic conditions are in large part responsible for this transition. The actual development of the larva is also involved, but to a lesser extent than might be imagined. Third through fifth instar larvae make the transition from the foliage web to the silken tube within the same time period and this would cast some doubt on the need for them to move strictly because of their increasing size. Increasing appetites and decreasing food supply are important in inducing the larva from the silken tube to search for fresh foliage. Temperature and humidity also exert an effect on this move. Such larval behavior is tied directly to the question of predaceous ant effectiveness because each developmental step makes the larva increasingly more vulnerable to ant attack.
Behavioral aspects of the predator must also be considered. Where the predator seeks its prey is important as related to budworm larvae because it was originally felt that ants only captured larvae that fell to the ground. This investigation has shown that ants attack budworm larvae both in the foliage and on the ground. Consider, however, the decrease in total effectiveness of predaceous ants were they restricted to larvae that had fallen to the ground. Ant predation would be directly dependent upon larval fall. However, because of their ability to capture larvae in the foliage, the effectiveness of ants as predators is greatly increased.

There is a period in the larval cycle of the budworm in which larvae begin to fall or spin by silken threads from the foliage. This larval fall is quite distinct from and totally unrelated to the dispersal of tiny first and second instar larvae which occurs each fall and spring. The beginning of larval fall corresponds closely with the movement of the third through fifth instar larvae from the tight foliage webs to more open locations. Weather factors are presumed to be important in dislodging larvae from the foliage. However, because of the larva's increased vulnerability, foraging ants play a primary role. Ants act by attacking and capturing exposed larvae in the foliage and dislodging larvae through missed captures and rousting larvae from feeding tubes. Those trees with ants foraging in the foliage nearly always have ants foraging in the area beneath the tree that successfully capture the majority of larvae falling from the foliage. When the actions of predaceous ants are considered in total, the effectiveness of any given group of ants in an area of budworm infestation appears to be
Where are ants most effective as budworm predators? They are able to complete more captures on the ground because the larva has little chance of escape. However, perhaps they are most effective in their contribution to dislodgement. In this study, nearly seven times more larvae fell from those trees with ants foraging in the foliage than from those without. On still days the wind contributes little to dislodgement. Evidence indicates that more larvae fell on hot, still days than on days with wind. Ants foraging in the foliage certainly contribute greatly to larval fall on these days.

The effectiveness of ants as predators is closely related to their distribution within the forest habitat. Because of the sparse density of *Formica* nests, the primary study plot represented a poor location for studying the effectiveness of ant predation on the total budworm population. The plantation, however, was densely populated with the two *Formica* species. Because of the lack of information regarding the development of the budworm outbreak around the plantation, one can only speculate about the effectiveness of the ants in protecting the plantation trees from budworm damage. Yet, the fact remains that budworm numbers were few within the plantation at the time of the study and trees showed no significant defoliation attributable to budworm.

Of the several environmental factors affecting the establishment and distribution of ants throughout a forest area, available food supply is certainly a primary one. Ants, like predators in general, are not specific in their food requirements. Their very survival depends upon
their ability to utilize several food sources. Budworm larvae, for example, are available for only a comparatively short time during the ant's foraging season. Aphids are widely sought after by foraging ants for their sweet honeydew exudations. Aphids are present early in the season and remain active on Douglas-fir for a large part of the summer. It is understandable why aphids are a first priority with foraging ants and insect prey, while collected in quantity, is of secondary importance.

The mutualism between ants and aphids appears to be an important factor inducing ants to foraging in the foliage of Douglas-fir. Ants are seldom seen in trees without aphid colonies. The presence of aphid colonies may be responsible for encouraging the growth of ant colonies. This could explain the high density of Formica nests (nearly three times that on the study plot) in the plantation and the corresponding damaging numbers of aphids in the trees. Whatever the relationship, aphids seem to induce ant foraging in the foliage and ants in this situation do not normally pass up an opportunity to attack whatever insect pests they may encounter, including budworm larvae.

One might conclude that by allowing aphids to inhabit Douglas-fir, the establishment of Formica ant nests will be encouraged with a resultant suppression of defoliator pests through the foraging activity of the ants. This may not be an incorrect assumption. One difficulty with this approach is that aphids have long been considered pests. High aphid numbers can cause terminal leader distortion, branch twisting and other growth deformities. In many cases, however, young trees thus afflicted by aphids will recover with little noticeable
damage. More research is required into the affects of aphid feeding on coniferous tree growth. Perhaps the damage done by even high aphid populations is insignificant when compared to that done by a pest such as the western budworm.

The concept of "significant damage" is very critical when considering the use of predaceous ants for management of such pests as the budworm. It has been recognized that aphid colonies tended by ants flourish and multiply rapidly. If the presence of aphid colonies is required to encourage ant foraging activity in the foliage then the damage done by the aphids compared to that done by the pest must be insignificant for the management program to be successful.

While considerable quantitative data is needed to determine the actual "degree" of predator effectiveness demonstrated by forest ants, this investigation has supplied considerable evidence showing that the three ant species studied are effective budworm predators in those situations where ants and budworm exist together. It is felt their effectiveness as a group in managing budworm populations depends largely on their distribution within the pest's environment. The problem of distribution was beyond the scope of this study.

The utilization of predaceous ants for the management of forest insect pests is entirely possible in North America. Transplantation of ant colonies offers a method of overcoming distribution problems within a particular environment. Effective management of budworm by transplanting nests of predaceous ants may be accomplished best in plantation situations because of easy access and a more controlled environment. With natural stands of timber being quickly con-
sumed, it is quite conceivable there will be an increasing interest in plantation type forest management. It is in these situations that forest ants can contribute the most to a biological or integrated pest management program.
Plate 1. Dense Douglas-fir reproduction typical of much of the study plot.

Plate 2. Areas with open grown trees also found on the study plot.
Plate 1. Catch plates supported on stakes and fastened tightly around tree boles.
Plate 3. Catch sheets supported on stakes and fastened tightly around tree bole.
Plate 4. Lab Nest I with "natural" ant dome in the center.

Plate 5. Lab Nest II patterned after a nest described by Peterson.
Plate 6. Nest of *Formica criniventris* - note dome piled against stump.

Plate 7. Nest of *Formica obscuripes* - note dead branches protruding from base of dome.
Plate 8. Tight needle web of young budworm larvae protects them from ant attack.

Plate 9. Foraging ants are able to roust larvae from these silken webs.
Plate No. Sugar rusting closely and must be removed to get victory.
Plate 10. Larvae feeding openly are most vulnerable to ant attack.
Plate 11. Ants attacking budworm larva on tree bole.

Plate 12. Captured larva on ground being transported to the nest.
Plate 13. Budworm pupa dangling by cremaster - often dislodged by wind, ants and other disturbances and collected by ants foraging on the ground.

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