DISSERTATION

BIRD DISSEMINATION OF

ARCEUTHOBIUM VAGINATUM SUBSP. *CRYPTOPODUM*

Submitted by

George W. Hudler

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY GEORGE W. HUDLER ENTITLED BIRD DISSEMINATION OF ARCEUTHOBIUM VAGINATUM SUBSP. CRYPTOPODUM BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Adviser

Head of Department

ABSTRACT

BIRD DISSEMINATION OF ARCEUTHOBIUM VAGINATUM SUBSP. CRYPTOPODUM

Long distance dissemination of *Arceuthobium vaginatum* subsp. *cryptopodum* (Engelm.) Hawksworth and Wiens was studied at the Manitou Experimental Forest, Teller County, Colorado. Specifically, the role that birds play in disseminating the parasite over long distances was examined.

Dwarf mistletoe occurrence in an 0.8 km x 4.3 km area was plotted on 1:7920 aerial photographs. Thirty two infection centers (satellite centers) were found in 128 h of healthy timber. They were judged to have originated by some means other than or in addition to explosive seed discharge. Satellite centers were 0.1 m^2 to 3000 m^2 in size and up to 458 m from the nearest inoculum source. They occurred on various topographical sites but never in gulches or similar confined drainages. All but two centers originated from seeds yielding female flowers. In 27 satellite centers, original infections were found. They ranged in age from 17 to 120 years.

Birds were mist-netted in or near infection centers during seed dispersal in 1974-1976. A total of 411 birds representing 21 species was trapped. Birds were examined for dwarf mistletoe seeds on feathers and in fecal material. Seeds were found on feathers of mountain chickadees (*Parus gambeli* Ridgway), pygmy nuthatches

(Sitta pygmaea Vigors), gray-headed juncos (Junco caniceps (Woodhouse)), a chipping sparrow (Spizella passerina (Bechstein)), and a Williamson's sapsucker (Sphyrapicus thyroideus Cassin). Seeds were found rarely in fecal material and were not viable.

Dwarf mistletoe seeds were fed to gray-headed juncos, chipping sparrows, pygmy nuthatches, and mountain chickadees. Whole seeds were voided by the latter two species but were not viable. Tests of seed survival at pH levels and temperatures similar to those encountered in birds' digestive tracts suggest that both factors act to render passed seeds nonviable.

Observations made during dwarf mistletoe seed dispersal suggest that birds are struck by explosively discharged seeds and seeds are transferred to pine foliage during subsequent foraging. Mountain chickadees and pygmy nuthatches were the only species observed foraging, apparently for insects, in dwarf mistletoe shoots. Both species were suspected to be important long-distance vectors of the parasite.

Populations of pygmy nuthatches were regulated, at least in part, by cavity tree frequency and distribution. One quadrant of the study area had 1 cavity tree per 2 h, and 1 breeding pair of pygmy nuthatches per 4 h. An adjacent quadrant had 1 cavity tree per 0.6 h and 1 breeding pair of pygmy nuthatches per 2.4 h.

George W. Hudler
Department of Botany and Plant Pathology
Colorado State University
Fort Collins, Colorado 80522
Fall, 1976

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Cont'd)

CHAPTER I

INTRODUCTION

Dwarf mistletoes, Arceuthobium sp., are the most serious disease agents in coniferous forests of the western United States. Annual losses through growth reduction and mortality are estimated to be as high as 3.2 billion board feet (Shea and Howard, 1968). In the southwestern states, Arceuthobium vaginatum subsp. cryptopodum (Engelm.) Hawksworth and Wiens occurs on 2.5 million acres (36%) of ponderosa pine (Pinus ponderosa Laws.) (Andrews and Daniels, 1960). In Colorado, New Mexico, and Arizona, annual losses of ponderosa pine may exceed 150 million board feet (Flake et al, 1972). In Colorado, dwarf mistletoe occurs on an estimated 46% of ponderosa pines east of the Continental Divide (Johnson and Minnemeyer, 1976).

In addition to losses caused through the direct effect of dwarf mistletoe on its host, the presence of the parasite poses several other threats to the longevity of a tree and/or stand. Infected trees usually have more dead limbs and needles, thereby greatly increasing potential fire danger. Of particular concern to the forest manager is the fact that infected trees provide avenues by which ground fires can be elevated to tree crowns. Since infected trees are less vigorous than healthy trees, they are less able to survive barkbeetle attack.

When heavily infected branches succumb and break from the bole, they leave excellent infection courts for heart rot fungi.

Dwarf mistletoe, once established, slowly expands from tree to tree into irregularly-shaped infection centers. In ponderosa pine, radial disease spread is documented at 0.37 m per year in dense stands and 0.52 m per year in open stands (Hawksworth and Gill, 1960). Infections from a single overstory tree encompassed 0.12 h over a 35 year period (U. S. Forest Service, 1955).

Presently, dwarf mistletoe is controlled by eradication or sanitation. Clearcutting is used to achieve this goal on large areas, and pruning of infected branches on lightly-infected, high-value trees in small areas is also effective. Meyers et al. (1974) constructed tables which aid in predicting yields from infected areas at rotation age with prescribed levels of thinning at stand assessment. In any case, the potential for reintroduction of the parasite to sanitized areas is of concern.

The purpose of this investigation was to determine if birds are important vectors of _A. vaginatum_ subsp. _cryptopodum_ over long distances. Specifically, the following questions were asked:

1. Do birds play a role in disseminating seeds of _A. vaginatum_ subsp. _cryptopodum_? If so, which bird species are most important? How often does such dissemination occur?

2. Is the activity of avian vectors related to stand characteristics?

3. Can bird dissemination of A. vaginatum subsp. cryptopodum be alleviated through stand and/or habitat management?

CHAPTER II

LIFE CYCLE OF A. VAGINATUM SUBSP. CRYPTOPODUM

The mature fruit of *A. vaginatum* subsp. *cryptopodum* is a one-seeded berry suspended from the shoot on a recurved pedicel. The seed is surrounded by mucilaginous cells termed "viscin." The hygroscopic nature of viscin permits it to imbibe water. Consequently, great pressures develop within the semi-elastic exocarp of the fruit. Concurrent with fruit maturation, which occurs between mid-July and mid-August in Colorado, an abscission layer forms at the fruit-pedicel junction. When the abscission layer ruptures, internal pressure is relieved, and the seed is expelled. Seeds so discharged leave the fruit at velocities up to 2540 $\pm$ 40 cm per second and travel up to 20 m (Hinds and Hawksworth, 1965). Hudler and French (1976) found that explosive seed discharge of *A. pusillum* Peck in Minnesota occurred primarily in the morning, when fruits were first warmed by the sun. Hourly fluctuations in seed discharge of *A. vaginatum* subsp. *cryptopodum* have not been reported, but it is assumed that most seeds are discharged in the morning (F. G. Hawksworth, unpublished data). The viscin coating on seeds permits them to stick to any substrate they encounter; however, needles are the primary receptors of discharged seeds (Hawksworth, 1965). Viscin dries shortly after seed discharge, but when rewetted by subsequent rain, it becomes slippery and allows the seed to slide down the needle to the twig.

Unlike most other species of Arceuthobium, seeds of A. vaginatum subsp. cryptopodum germinate several days after discharge. The parasite, however, does not penetrate the host and establish the parasitic relationship until the following spring. Aerial shoots of A. vaginatum subsp. cryptopodum are not reproductively functional until at least four years after infection. Anthesis of mature flowers occurs in May and June. The Arceuthobia are dioecious, having an approximate male:female ratio of 1:1 (Hawksworth, 1961). Insects and wind are both considered effective agents for pollen dispersal (Penfield et al., 1976). Fertilization immediately follows pollination and fruits are mature 14 months thereafter (Hawksworth and Wiens, 1972).

Dwarf mistletoe shoots may survive and reproduce for up to 7 years. Young plants consist of only a few shoots, each less than 8 cm tall. As plants mature, new shoots emerge and form dense clumps of 20 or more shoots, each 10 to 15 cm tall.

As branches infected with A. vaginatum subsp. cryptopodum grow, new host buds and branches are produced at the site of infection. The resulting dense masses of negatively geotropic twigs may reach 2 m in diameter and weigh a kilogram or more. Such growths, witches grooms, are symptomatic of all dwarf mistletoe-host relationships in the U.S.

Several potentially significant variables in a study of bird dissemination of dwarf mistletoe are minimized by restricting the investigation to *A. vaginatum* subsp. *cryptopodum*. Seed dispersal usually occurs from mid-July to mid-August and germination occurs shortly thereafter. Most, if not all, birds have completed nest-building by that time, and the possibility of birds transporting seeds on debris used for nest building is negligible. Under normal circumstances, viscin loses its ability to be rewetted and adhere to additional substrates by late August which is prior to most bird migration. Thus, potential dissemination by migrants is minimized.

CHAPTER III

REVIEW OF THE LITERATURE

Leafy or true mistletoes in genera closely related to Arceuthobium (i. e., Viscum, Phoradendron, Korthalsella, etc.) lack an explosive seed dispersal mechanism and are almost entirely dependent on birds for inter- and intrahost spread. The literature on bird transmission of those mistletoes was reviewed by Ridley (1930), Doctors van Leeuwen (1954), Kuijt (1969) and others. In some cases, only one or a few bird species are responsible for the bulk of seed dispersal of a given species. In those cases, seed dispersal is effected by birds ingesting and voiding viable seeds, sometimes through unique digestive tract modifications which promote highly efficient seed dispersal (Desselberger, 1951; Walsberg, 1975). With other true mistletoes the association between vector and parasite is more haphazard, and seed dissemination is a result of seeds adhering to birds' feathers, beaks and feet (Ridley, 1950).

Long distance dissemination of dwarf mistletoes is subject to much speculation but little definitive research. Most observations of associations between birds and dwarf mistletoes provide only circumstantial evidence that birds may serve as vectors of the parasite. Arceuthobium campylopodum Engelm., A. laricis (Piper) St. John, and *A. douglasii* Engelm. are reported as components of diets of blue grouse (*Dendragapus obscurus* (Say)) in Montana (Martinka, 1970) and the Pacific Northwest (Boag, 1963; Beer, 1943). Wicker (1967) found *A. douglasii* seeds in crops of ruffed grouse (*Bonasa umbellus* (L.)), and Weir (1916) observed house sparrows (*Passer domesticus* (L.)) feeding on seeds of *A. campylopodum*.

Warren (1899) found gray jays (*Perisoreus canadensis* (L.)) nesting in a black spruce (*Picea mariana* (Mill.) B.S.P.) witches' broom caused by *A. pusillum*. Hudler et al. (1974) trapped birds in dwarf mistletoe-infected black spruce stands in Minnesota and found gray jays were potential vectors. Although birds were lured into witches' brooms in the Minnesota study, the authors expressed confidence that mist-netting was a satisfactory technique for catching birds with dwarf mistletoe seeds on their feathers.

Zilka and Tinnin (1976) studied bird dissemination of several species of *Arceuthobium* in Oregon. By combining habitat preference and frequency of observation, they determined that 10 bird species representing 7 families were potential vectors. They postulated that birds could disseminate dwarf mistletoe seeds by using debris with seeds on it for nest material or by picking up sticky seeds on their plumage. However, they never observed birds feeding on dwarf mistletoe seeds or aerial shoots.

A black-headed grosbeak (*Pheuticus melanocephalus* (Swainson)) (Marshall, 1957) and an evening grosbeak (*Hesperiphona vespertina*

(Cooper)) (Hawksworth, 1961) were observed eating seeds of _A. vaginatum_ subsp. _cryptopodum_. Bailey et al. (1953) photographed a red crossbill (_Loxia curvirostra_ L.) nest in a ponderosa pine witches' broom caused by the same parasite.

The digestive tracts of birds have high temperatures and high hydrogen ion concentrations. A dwarf mistletoe seed eaten by a bird would have to tolerate both of those factors in addition to mechanical action of the gizzard if it were to be infectious upon excretion. Baldwin and Kendeigh (1932) found body temperatures of a variety of passerines to be slightly more than 44C. Norris (1958) cited thirteen records of pygmy nuthatch (_Sitta pygmaea_ (Vigors)) body temperatures ranging from 38.4C to 42.2C and averaging 41.3C.

Hydrochloric acid is secreted in the proventriculus and reaches its highest concentration in the gizzard where pH values of 2.0 to 3.0 are common. The environment becomes more alkaline in the small intestine as the acid is neutralized by other digestive juices but never rises above pH 7 (Sturkie, 1965).

Rodents such as Abert squirrels (_Sciurus aberti_ Woodhouse), red squirrels (_Tamiasciurus hudsonicus_ Erxleben), chipmunks (_Eutamias_ spp.), and porcupines (_Erethizon dorsatum_ (L.)) frequent ponderosa pine forests and have been observed eating dwarf mistletoe plants and pine branches at infection sites. Red squirrels were observed eating branches infected with _A. americanum_ Nutt. ex Engelm. in British Columbia by Baranyay (1968). Broadbooks (1958) reported that chipmunks ate shoots of *A. campylopodum* in Washington. Keith (1965) and Patton (1975) both reported that young ponderosa pine branches swollen by infection with *A. vaginatum* subsp. *crypotopodum* were favorite foods of the Abert squirrel, particularly in winter. Taylor (1935) noted that shoots of *A. vaginatum* subsp. *cryptopodum* were the leading food item of porcupines in autumn in the Southwest.

CHAPTER IV

MATERIALS AND METHODS

Preliminary Research: Examination of Stomach Contents

Prior to initiation of field investigations, a collection of bird stomach contents preserved by the Zoology Department at Colorado State University was examined. The collection was made in July and August of 1962 and 1963 by a student who studied bird predation on ponderosa pine barkbeetles (Dendroctonus ponderosae Hopk.) in central Colorado. Birds were collected randomly in and near dwarf mistletoe infection centers. Initially, all contents which were noted to contain vegetation were examined by me for dwarf mistletoe seeds. Subsequently, I examined all mountain chickadee (Parus gambeli Ridgway) and pygmy nuthatch stomach contents.

Study Area Description

All of the field work for this study was done at the Manitou Experimental Forest (elevation = 240 m) located ca. 40 km northwest of Colorado Springs in Teller County, Colorado.

The climate at the Experimental Forest is classified as "dry-subhumid" (Thornthwaite, 1941). Winters are dry and often cold for long periods while summers are cool. Average annual precipitation from 1965 to 1974 was 41.3 cm, 63% of which occurred as rain between April 1 and August 31 (Figure 1). Mean monthly temperatures varied from ca. -7C in January to ca. 15C in July in the same 10-year period (Figure 2).

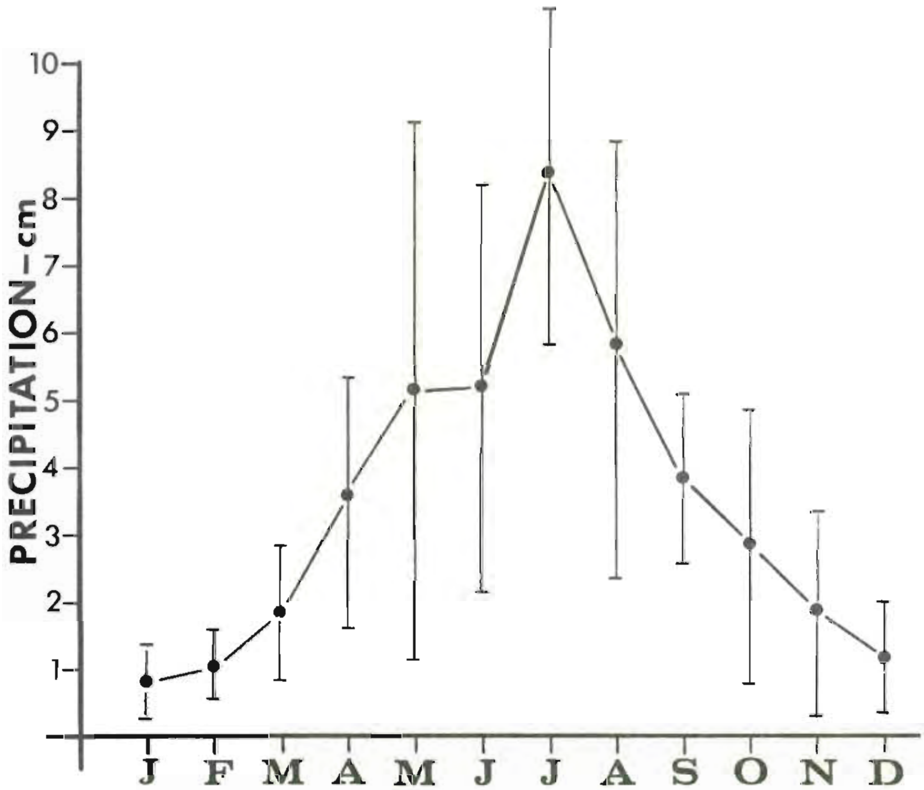
Throughout the course of this investigation, a weather station located in the north quadrant of the study area was maintained by U. S. Forest Service personnel at the Experimental Forest headquarters.

An area 4.3 km x 0.8 km was selected for study of dwarf mistletoe distribution and bird dissemination of the parasite. Preliminary observations indicated that pines on the eastern edge were heavily infected and supplied ample inoculum to be disseminated into adjacent healthy timber. A relatively large area was selected for study to insure that long distance dissemination could be assessed even if rare. The area was divided into four consecutive subunits, the first being at the north end of the area and the fourth at the south end (Figure 3). The area was on a gentle ($<5\%$) west-facing slope in the east side of a broad valley drained by Trout Creek. Two major drainages, Hotel and John's Gulches as well as several minor drainages ran from east to west through the area. In subunits 2 and 4, minor drainages were bordered by steep (ca. 30%) slopes rising as much as 30 m above drainage bottoms in some places.

Soils were uniform throughout the study area and were gravelly or sandy loams derived from alluvial deposits of Pikes Peak granite.

Figure 1. Average monthly precipitation between 1965 and 1974. Brackets denote one standard deviation from the mean value for each month.

Figure 2. Average monthly temperature between 1965 and 1974. Brackets denote one standard deviation from the mean value for each month.


PRECIPITATION – cm
10
9
8
7
6
5
4
3
2
1
J F M A M J J A S O N D

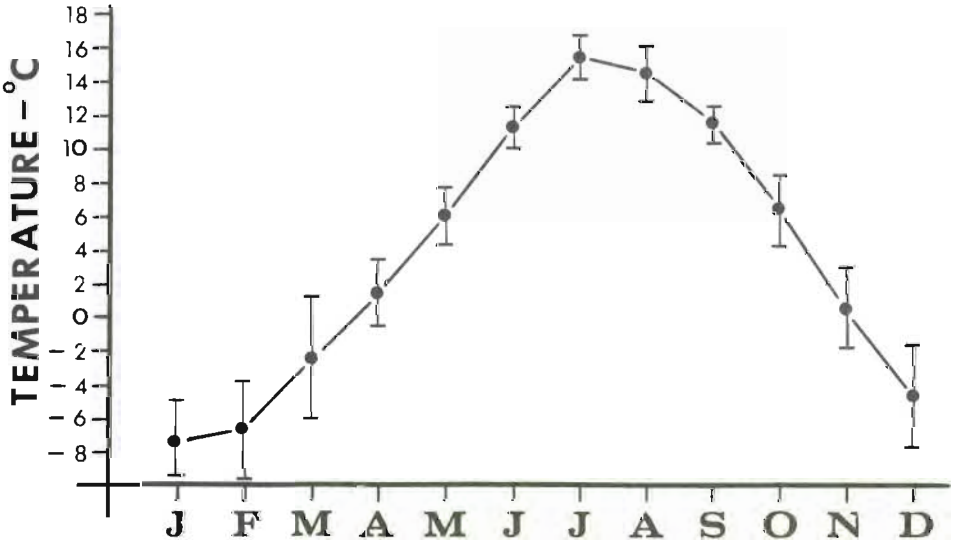
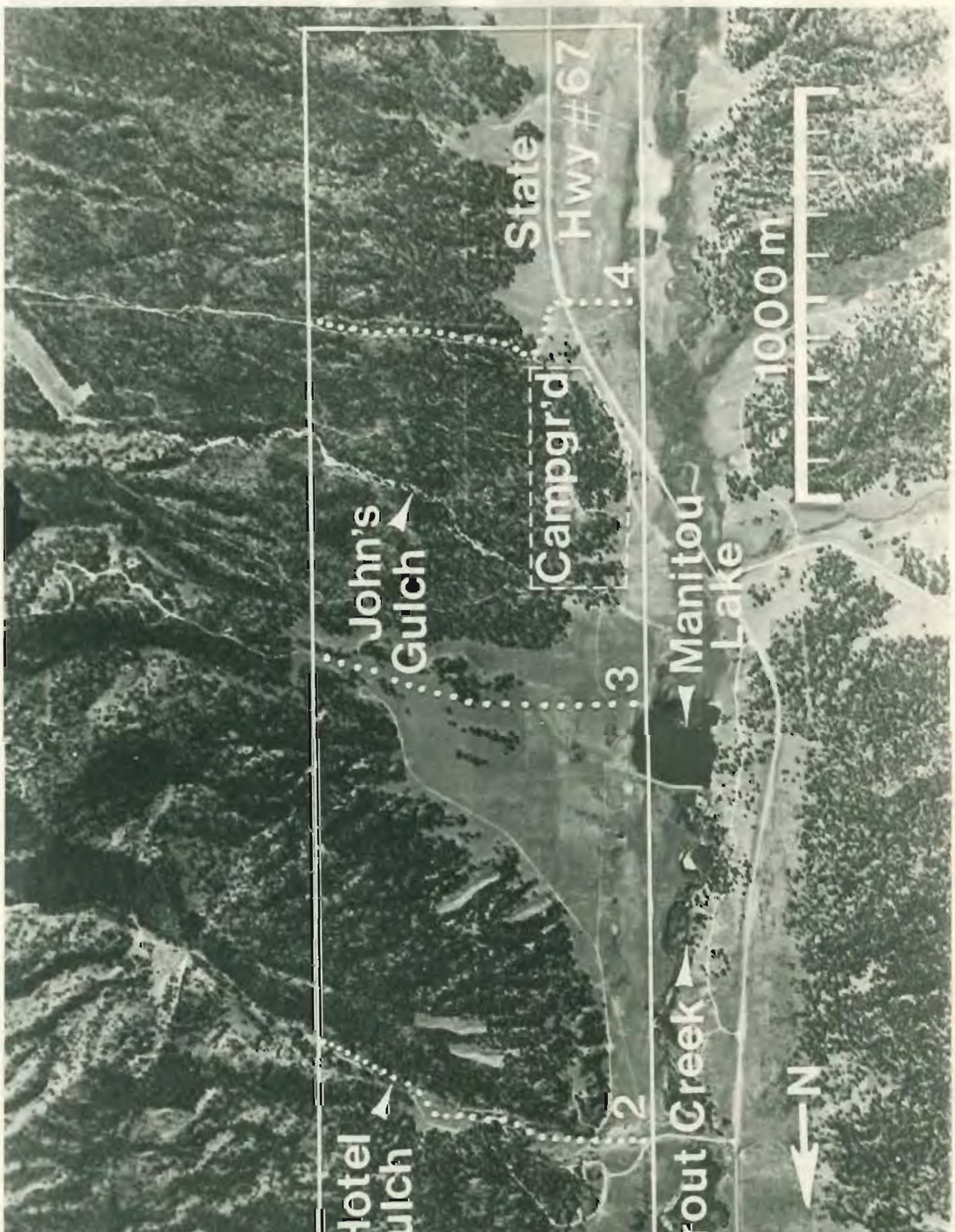

TEMPERATURE – °C
18
16
14
12
10
8
6
4
2
0
– 2
– 4
– 6
– 8
J F M A M J J A S O N D

Figure 3. Aerial photograph showing major features and boundaries of the study area. Subunits are also delineated.


State
Hwy #67
4
Campgr'd
John's
Gulch
Manitou
Lake
3
1000 m
Trout Creek
2
Hotel
Gulch
1
N

They were low in organic matter, slightly acidic (pH = 6.0 - 6.5) and moderately permeable to water (Retzer, 1949).

Three unpaved roads ran from east to west through the area. A national forest campground, Colorado Campground, occupied ca. 16 h in subunit 3 and was often filled to capacity with campers from May 31 to September 1 each year.

Ponderosa pine was the dominant tree in the study area. The species occurred in uneven-aged, multi-storied stands at a mean density of 380 $\pm$ 250 stems per hectare and a mean basal area of 8.6 $\pm$ 2.5 m^2 per hectare.[1] The oldest age group of ponderosa pine which occurred in a significant amount was ca. 125-150 years old, but trees twice that age were found occasionally. Trees in the 125-150 year age group averaged ca. 17 m high and 50 cm diameter at breast height (dbh). Aspen (*Populus tremuloides* Michx.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) occurred either singly or in small (< 0.5 h) stands, particularly on north-facing slopes and in drainage bottoms.

Understory vegetation was limited to kinnikinik (*Arctostaphylos uva-ursi* (L.) Spreng.) and dwarf juniper (*Juniperus communis* L. var. *depressa* Pursh.) in most of the forested areas, but mountain mahogany (*Cercocarpus montanus* Raf.) and numerous herbs and grasses were

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[1] Stand composition data was obtained from analysis of 63 0.1 h plots located in subunits 3 and 4. In each plot, the number of trees and diameter and species of each tree were recorded. Ages and heights of the two largest trees in each plot were also determined.

present in sparsely-stocked or non-forested areas or where pine mortality from dwarf mistletoe was severe.

Dwarf mistletoe distribution in the study area

The extent of dwarf mistletoe infection in the study area was surveyed by walking along the edges of large (<1 h) infection centers and plotting the route on acetate overlayed on 1:7920 infrared, false-color aerial photographs. Additional, smaller infection centers were located by a thorough visual examination of "healthy" stands in the study area. When smaller infection centers (satellite centers) were located, they were also plotted on the aerial photographs. The areas of the satellite centers were measured, and number of infected and healthy trees recorded. Topographic position of each satellite center with respect to its immediate surroundings was noted. Where possible, the tree containing the oldest dwarf mistletoe infection, hence the original infection site in the satellite center, was located. The age, height, and dbh of origin trees and the height and age of the oldest infections were determined. The latter measurement was determined by cutting through branches at original infection points and counting rings from the outside to the oldest ring containing mistletoe endophytic tissue. Distances from sateliite center origins to the nearest inoculum source were measured. In larger and older satellite centers, distance to the nearest inoculum source of a comparable age was measured.

Explosive Seed Discharge

Dwarf mistletoe seed discharge was quantified in 1974 by a daily estimate of the percentage of seeds dispersed from 10 dwarf mistletoe plants, each with 50 to 100 ripe berries per plant. In 1975 and 1976, six 1.0 x 2.5 m muslin sheets spread out on ground beneath infected trees were used to quantify seed dispersal. Sheets were located in the same place in both years, and number of seeds found on the sheets recorded daily.

Bird Dissemination of *A. vaginatum* subsp. *cryptopodum*

Birds were trapped in or near infection centers from July 24 to August 23, 1974; August 17 to September 10, 1975; and August 1 to August 23, 1976. The trapping periods coincided with dwarf mistletoe seed dispersal and ca. 1 week thereafter each year except in 1976 when trapping ceased the same day that the last seed was found on the sheets.

Birds were trapped with black, nylon mist nets. Ten nets, each 12 m long and 3 m high were used each day between 0700 hours and 1900 hours in 1974 and 1975. In 1976, 15 nets were used. The nets were of various sizes of mesh, but those with 36 mm x 36 mm openings were most effective. Cell traps were also used occasionally.

Each trapped bird was examined externally for seeds, placed in an 0.3 m x 0.3 m x 0.3 m holding cage for three to six hours, and released. Fecal material voided in the holding cages was collected and, when time permitted, examined immediately for dwarf mistletoe seeds or was stored in 30 ml vials with 95% ethyl alcohol until examination.

To further test the possibility that birds could pass viable dwarf mistletoe seeds, each of five mountain chickadees, pygmy nuthatches, gray-headed juncos (Junco caniceps (Woodhouse)), and chipping sparrows (Spizella passerina (Bechstein)) were each fed 10 dwarf mistletoe seeds. The seeds were consumed readily by juncos and sparrows but were only ingested by the other two species when concealed within the exoskeletons of live mealworms. The technique was extremely efficient and proved the only successful means by which captive individuals of those species would eat dwarf mistletoe seeds. After eating all ten seeds, each bird was held for 4-12 hours and released. Fecal material voided during that time was examined immediately for dwarf mistletoe seeds. A seed was considered to have been passed if the endosperm and embryo were intact. Such seeds, when found were tested for viability as described below.

Dwarf mistletoe seed survival was tested in temperature and pH ranges including those encountered in birds' digestive tracts. The purpose of these tests was to identify factors which caused passed seeds to lose viability.

Seed survival was tested in solutions of HCl and water with pH values of 0.7, 1.4, 1.9, 2.8, 4.1, and 5.7. For each test, 50 fresh seeds were added to 10 ml of the desired acid solution and incubated for 3 hours at 25C or 40C. In one set of tests, entire seeds, including endocarp and viscin cells were used. In a second set, the endosperm and embryo of each seed were extracted from the endocarp prior to exposure to an acid solution. Each test was replicated once. After exposure to its respective acid solution, each lot of seeds or seed parts was rinsed for 20 minutes in each of two changes of 125 ml of distilled water and tested for viability.

Dwarf mistletoe seed survival was tested at 25C, 40C, 55C and 70C. A lot of 50 fresh seeds was placed in 10 ml of distilled water in a test tube. The tube was sealed and immersed in a beaker containing 900 ml of water at the desired temperature. Seeds were incubated for 1 hour, air dried for 2 hours, and tested for viability.

Viability of seeds obtained from fecal material or those subjected to ranges of pH and temperature was tested by exposing embryos and endosperms to an 0.2% w/v solution of 2, 3, 5-triphenyl tetrazolium chloride (TTC) for 24 hours. In instances where the endocarp and viscin were left in place, the seeds were halved longitudinally to permit inner portions to be exposed to TTC. Live tissue stained pink to red, but dead tissue remained unstained. The technique was used successfully by Scharpf (1970) to test viability of seeds of A. abietinum Engelm. ex Munz and A. occidentale Engelm.

Trapping results and observations in 1974 suggested that mountain chickadees and pygmy nuthatches were the primary vectors of A. vaginatum subsp. cryptopodum. Thus, in 1975 and 1976, those species were observed more closely and additional data on their numbers and behavior was collected. The more intensive studies were conducted in subunits 3 and 4 because they were close together and easily accessible. Satellite center occurrence was much more frequent in subunit 4 than in any other subunit. It was hoped that comparisons of chickadee and nuthatch behavior and numbers in the two subunits would help to explain the higher frequency of infections in subunit 4.

In 1975 and 1976, mist-netting of mountain chickadees and pygmy nuthatches began in early July, and continued through seed dispersal when it was coordinated with general trapping and examination of all birds. When mountain chickadees or pygmy nuthatches were trapped, they were marked with one aluminum and one or three colored plastic leg bands. Each bird was banded with a distinct color combination to aid visual identification with binoculars. When marked birds were seen, their locations were plotted on aerial photographs. Repeated sightings of marked birds permitted estimation of foraging territories.

Since both species nest in cavities in standing trees, locations of all such trees in subunits 3 and 4 were plotted on aerial photographs. The tree species and, when possible, nature of injury which permitted cavity origin were noted.

The population of breeding pygmy nuthatches in subunits 3 and 4 was determined by a complete census of those areas in June and

July, 1976. Active nests were easily located between the times of hatching and fledging because the parents made frequent trips to and from nests while feeding hatchlings.

Mountain chickadee nests were difficult to locate and the population of that species was determined in a less exact manner. During the time of nest-building and territory establishment, locations of singing mountain chickadees (presumably males) were plotted on aerial photographs. This census was undertaken in conjunction with other activities; thus, the area was not traversed in a systematic manner. However, a conscientious effort was made to cover the entire area weekly. Following fledging, each flock of mountain chickadees encountered was noted as to location and number of individuals. Most flocks had at least one banded individual and could be recognized by that bird.

Additional observations concerning foraging habits and daily movements of the two species were noted.

CHAPTER V

RESULTS

Preliminary Research: Examination of Stomach Contents

Stomach contents of 131 birds representing 15 species were examined (Table 1). Whole dwarf mistletoe seeds or seed fragments were found only in stomach contents of mountain chickadees and pygmy nuthatches. Sixteen seeds were found in one mountain chickadee stomach.

Dwarf mistletoe Distribution in the Study Area

Ponderosa pines in the eastern portion of the study area were severely and extensively infected with dwarf mistletoe. A total of 47 h were included in several large infection centers in that region. In addition, 32 satellite centers were found in otherwise healthy timber west of the main infection centers (Figures 4-7). The frequency of occurrence of satellite centers increased markedly from north to south such that there were nine times as many satellite centers in subunit 4 as in subunit 1.

Satellite infection centers ranged in size from one tree to 0.3 h (Table 2). The 32 satellite centers occupied a total of 1.2 h. Most (84%) satellite centers were located within 100 m of the nearest

Table 1. List of species from which stomach contents were collected in 1962 or 1963 and examined for dwarf mistletoe seeds in 1973.

Species	1962	1963	Total
Mountain chickadee	37(8)*	7(1)	44(9)
Pygmy nuthatch	8(1)	3	11(1)
White-breasted nuthatch	6	4	10
Red-breasted nuthatch	0	4	4
Gray-headed junco	29	0	29
Robin	6	0	6
Steller's jay	5	0	5
Townsend's solitaire	6	6	12
Solitary vireo	1	0	1
Yellow-rumped warbler	1	1	2
Brown creeper	1	0	1
Red crossbill	0	2	2
Green-tailed towhee	0	1	1
Hermit thrush	0	1	1
Ruby-crowned kinglet	0	2	2

*Numbers in parentheses are numbers of birds with whole seeds (i. e., 8 of 37).

Figure 4. Aerial photograph showing distribution of dwarf mistletoe infections in subunit 1. Two satellite infection centers are shown.


500 m
1
2
N

Figure 5. Aerial photograph showing the distribution of dwarf mistletoe infections in subunit 2. Three satellite infection centers are shown.

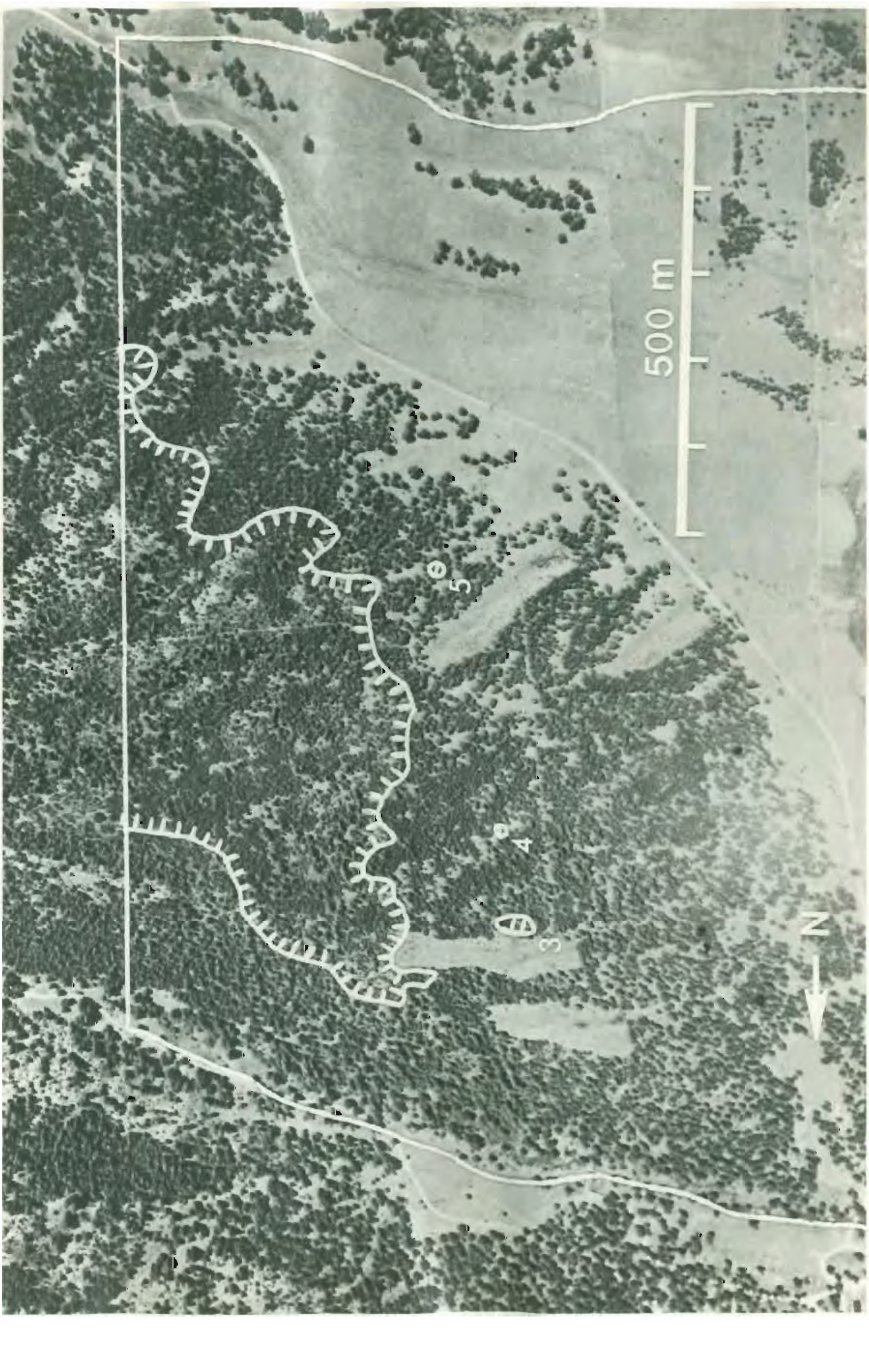

500 m
N
5
4
3

Figure 6. Aerial photograph showing the distribution of dwarf mistletoe infections in subunit 3. Nine satellite infection centers are shown.

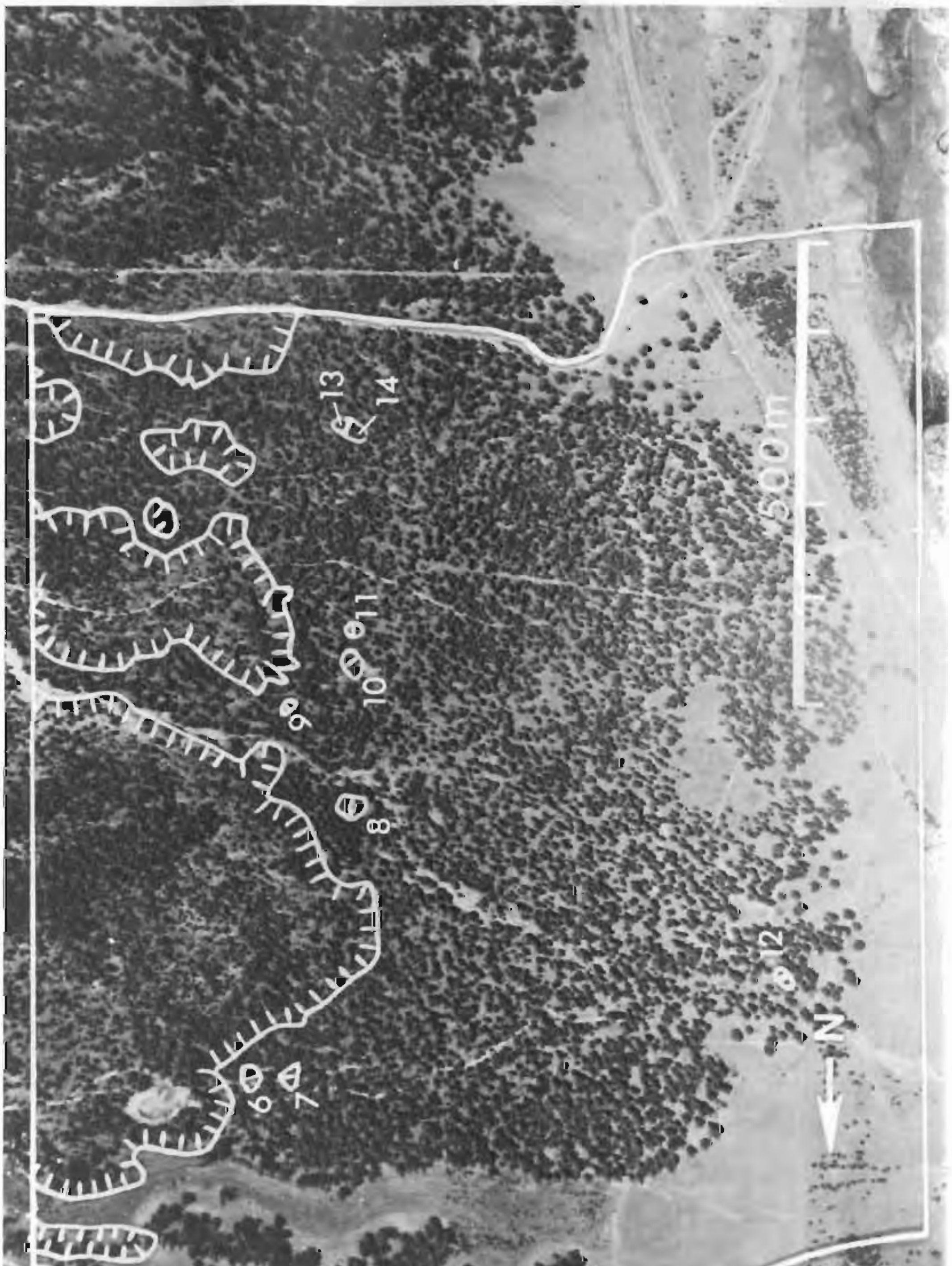

500m
N
6
7
8
9
10
11
12
13
14

Figure 7. Aerial photograph showing the distribution of dwarf mistletoe infections in subunit 4. Eighteen satellite infection centers are shown.

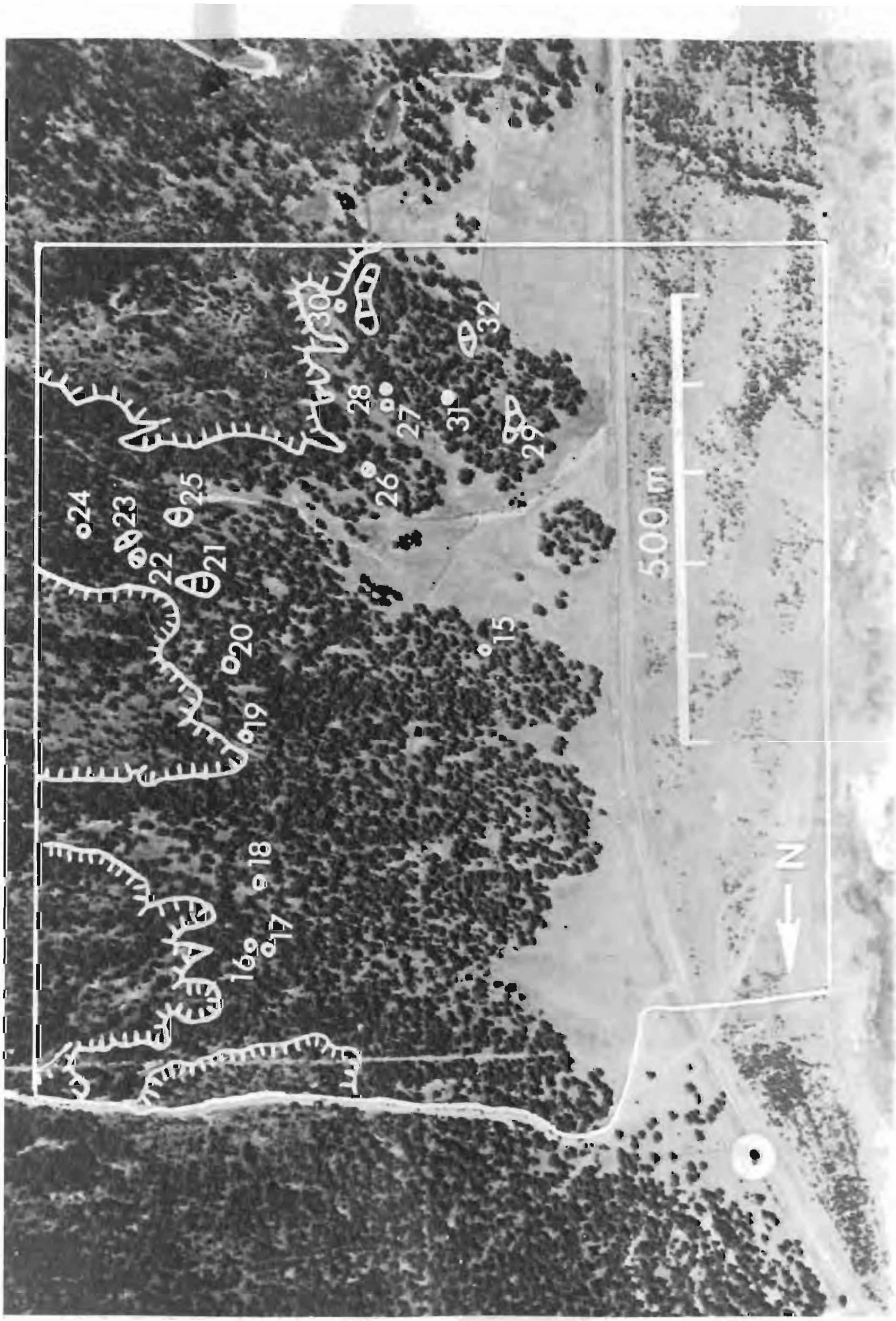

15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
500 m
N

Table 2. Characteristics of satellite infection centers. The number of each satellite center corresponds to its number on Figures 4-7.

Center No.	No. Trees Infected	No. Trees Healthy	Area m^2	Distance and Direction from Seed Source-m	Topography
1	1	--	0.1	49 E	Bench
2	1	--	0.1	150 E	Bench
3[a]	100+		1011.5	68 E	Ridge-S. slope
4	3	--	55.3	76 N	Ridge top
5	6	2	3.8	126 E	Level-low
6	7	20	131.1	47 E	Level-low
7	34	35	505.3	63 E	Level-low
8	23	35	198.2	58 E	Gulch edge
9	24	19	184.0	46 SE	Gulch edge
10	27	16	329.5	46 E	Level
11	1	--	0.1	76 E	Level
12	8	3	37.7	458 E	Level
13	42	12	489.4	76 E	Level
14	55	20	177.4	20 E	Level
15	1	--	0.1	263 S	Level
16	2	2	10.8	76 W	Ridge top

[a] Center too large for detailed analysis.

Table 2. Continued.

Center No.	No. Trees Infected	No. Trees Healthy	Area m^2	Distance and Direction from Seed Source-m	Topography
17	4	0	7.5	64 E	Ridge top
18	2	--	7.5	65 N	Level-low
19	48	15	809.7	28 NE	Bench
20	35	8	97.5	45 E	Bench
21[a]	175+	--	3000.0 +	126 NE	Ridge top
22	49	32	568.3	53 SE	Level-low
23	3	--	140.3	42 N	Level-low
24	1	--	0.1	55 N	Level-low
25	39	9	601.1	88 N	Level-low
26	21	5	201.7	41 SE	Ridge-S. slope
27	1	--	0.1	55 E	Level-low
28	1	--	0.1	55 E	Level-low
29	17	9	1789.6	84 SW	Ridge-W. slope
30	6	3	37.6	24 W	Level-low
31	1	--	0.1	22 W	Ridge top
32	11	4	768.9	79 E	Level-low

possible source of inoculum, but five were more than 100 m away. In several instances, the nearest inoculum source was another satellite center.

Satellite centers were placed in one of five categories depending on location in relation to surrounding topography (Figure 8). Distinctions between "low level" and "gulch" and between "level" and "bench" were based on visual estimates of size of the area each occupied. Designations "level" and "low level" were assigned to topographic areas greater than 150 m measured on a north-south axis. Satellite centers were found in four of the five categories but were never found in gulches or similar confined drainages.

In 27 satellite centers, original infections were located. Of those, 24 branches were still living and could be collected for infection age determination. Infections ranged in age from 17 to 120 years (Table 3). All but 2 of 24 original infections bore shoots with pistillate flowers.

Explosive Seed Discharge

Explosive discharge of dwarf mistletoe seeds began on July 25, 1974, and was complete by August 16 (Figure 9). In 1975, however, explosive seed discharge began on August 17, approximately 4 weeks later than in 1974. Freezing temperatures on August 21 damaged much of the fruit crop, and seed discharge was negligible thereafter.

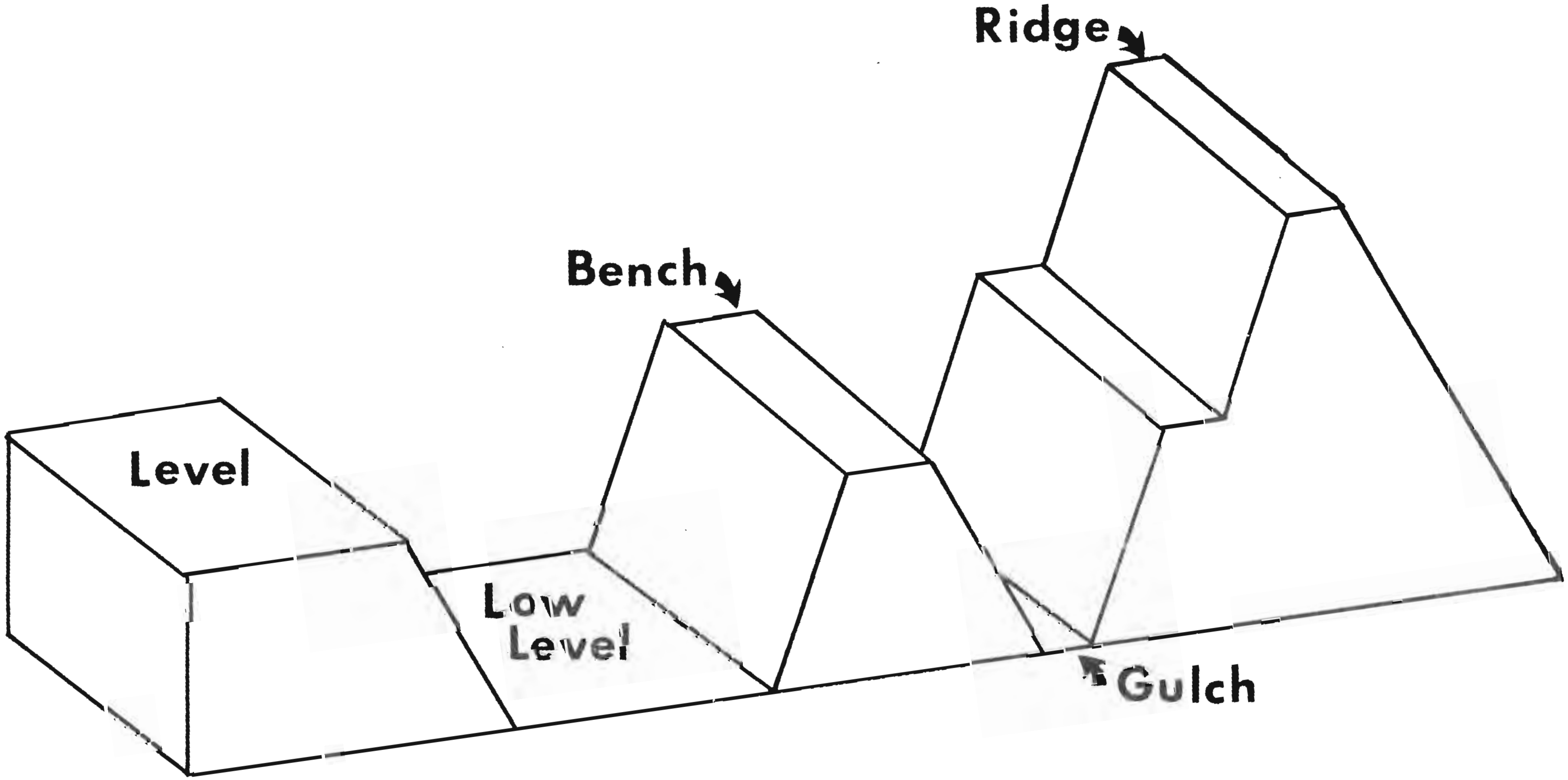


Figure 8. Schematic diagram illustrating topographic categories used to classify satellite centers.

Figure 9. Dwarf mistletoe seed dispersal during each year of the study expressed as percentage of seeds dispersed daily.

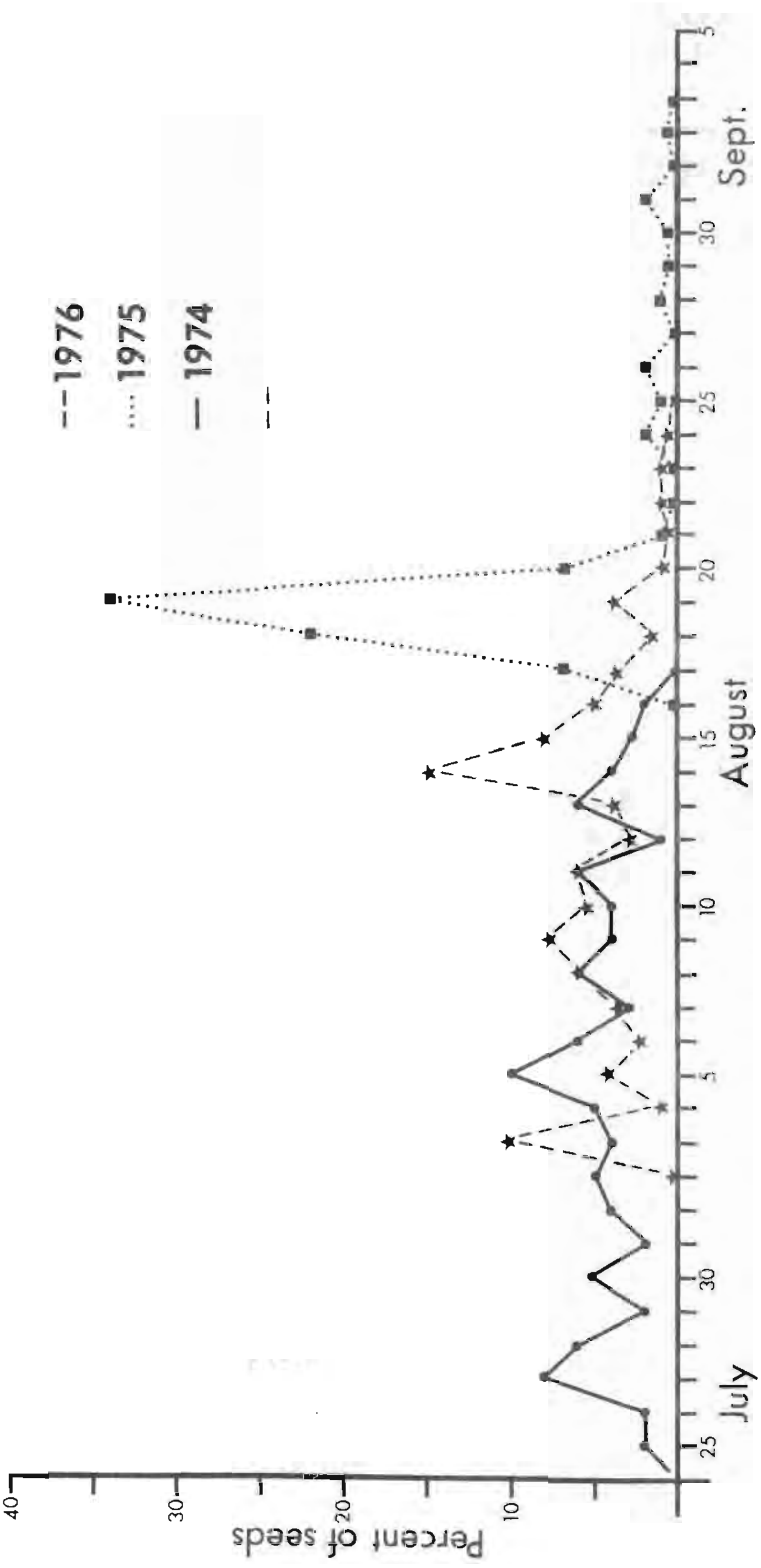

1976
1975
1974
Percent of seeds
40
30
20
10
July
August
Sept.
25
30
5
10
15
20
25
30
5

Table 3. Characteristics of trees in satellite infection centers containing oldest infections (origin trees). Ages and heights of oldest infections are also given.

Center No.	Origin Tree Hgt. m	Dbh cm	Age	DMR[a]	Origin Infection Hgt. m	Age[b]	Sex
1	7.9	13.5	59	1	2.4	33	F
2	4.3	12.8	79	4	2.0	28	F
5	11.6	18.0	75	1	2.4	36	F
6	7.2	35.6	150+	6	6.8	71	F
7	11.6	18.8	131	6	8.8	52	F
10	8.5	18.0	141	5	4.0	42	F
11	18.7	39.1	134	1	3.0	60	M
12	15.4	36.3	163	6	4.6	52	F
13	14.0	28.2	d	6	6.7	26	F
14	8.5	17.8	76	6	1.4	58	F
15	18.3	34.3	175	1	5.5	32	F
16	20.1	35.8	133	4	10.2	d	F
17	16.7	35.3	237	2	5.5	120	F
18	17.4	39.1	84	5	12.8	22	F
19	20.1	35.3	162	6	4.0	70	F
20	14.9	27.9	80	4	6.4	20	F
22	12.8	28.2	66	6	c	c	c
23	21.3	61.0	d	6	c	c	c
24	13.1	22.6	81	1	2.4	43	F
25	10.7	25.4	86	6	4.7	82	F
26	15.2	23.4	116	6	7.3	35	F
27	5.5	7.6	46	1	2.7	17	F
28	18.0	33.0	133	1	2.4	48	M
29	10.4	26.4	164	6	2.1	75	F
30	8.1	19.0	76	4	3.7	38	F
31	18.6	34.0	147	1	13.4	e	e
32	17.4	42.4	166	4	3.7	113	F

[a] DMR = Dwarf mistletoe rating--0-6: 0 = no visible infection; 6 = 100% of crown visibly infected.

[b] Age = Length of time branch has been infected.

[c] Origin infection dead and fallen from tree.

[d] Tree has heart rot--age not determined.

[e] Infection site inaccessible.

In 1976, seed discharge began on August 3 and was complete by August 26.

Climatological data recorded throughout the study showed unusually low precipitation in July, August, and September, 1975 (Figure 10). In July of that year, precipitation amounted to 3.8 cm, only 47% of the 10 year average for that month.

Bird Dissemination of *A. vaginatum* subsp. *cryptopodum*

A total of 411 birds representing 21 species was captured in 530 hours of trapping during dwarf mistletoe seed dispersal in 3 years (Table 4). Gray-headed juncos, yellow-rumped warblers (*Dendroica coronata auduboni* (Townsend)), mountain chickadees, and pygmy nuthatches most frequently were trapped.

Dwarf mistletoe seeds were found on feathers of 16 (3.4%) of the 411 birds. Seeds were found most frequently on mountain chickadees and pygmy nuthatches and occasionally on other species. All but one of the birds trapped bearing seeds carried only one seed. The exception was a pygmy nuthatch which had three seeds.

Additional information regarding birds carrying seeds on their feathers was obtained through observation. On eight separate occasions, mountain chickadees foraging on infected branches and in dwarf mistletoe shoots were observed to be struck by discharging seeds which adhered to their feathers. After flying to another branch, the chickadees either continued foraging or stopped to preen seeds

Figure 10. Monthly precipitation during 1974, 1975, and 1976 as compared to mean monthly precipitation between 1965 and 1974. Note the low precipitation recorded in July, August, and September, 1975.

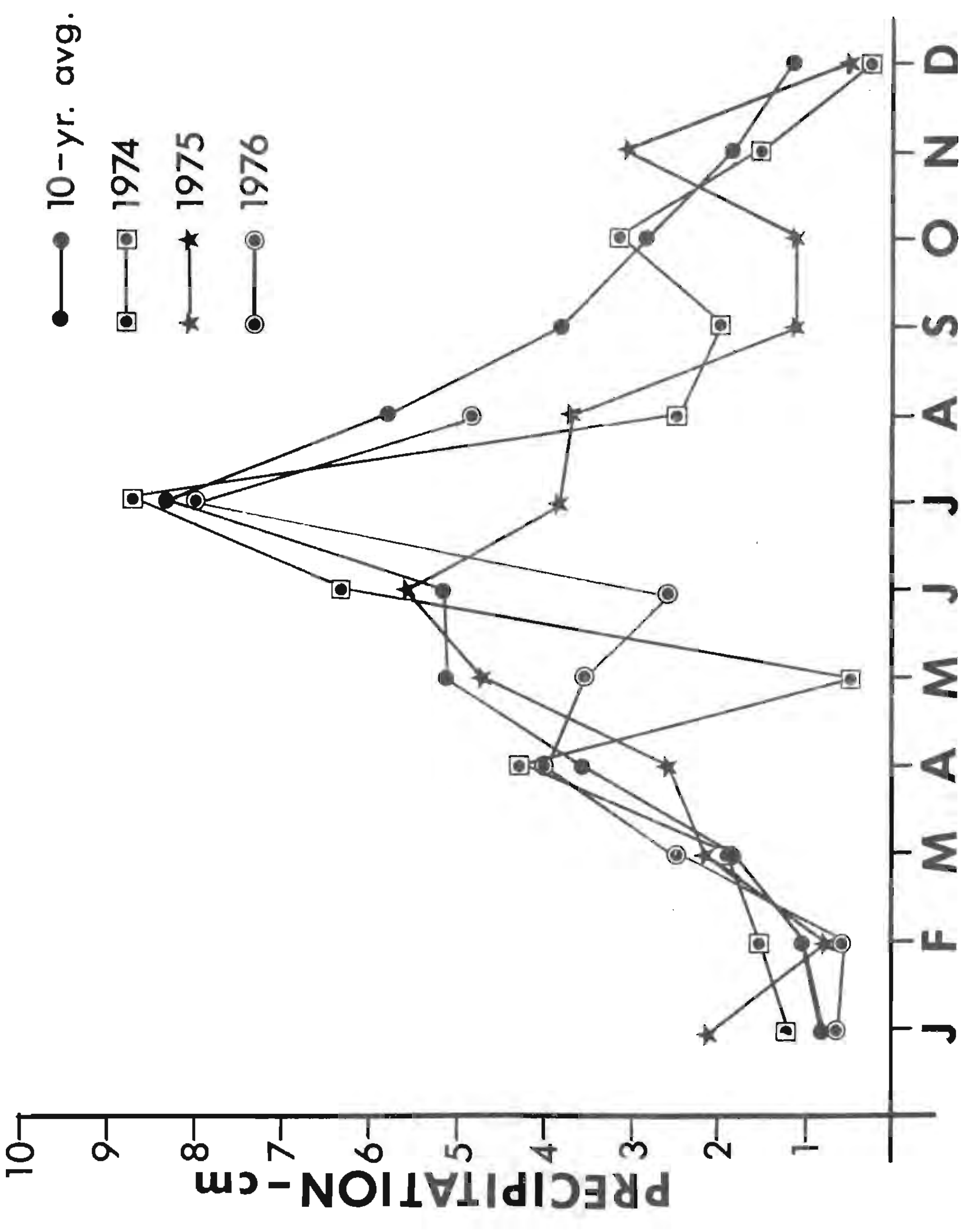

10-yr. avg.
1974
1975
1976
PRECIPITATION - cm
10
9
8
7
6
5
4
3
2
1
J F M A M J J A S O N D

Table 4. Birds trapped during dwarf mistletoe seed dispersal in 1974, 1975, and 1976. The number of each species which were trapped with seeds on their feathers are shown in parentheses.

Species	Dates and Amount of Time			Species Total
	7/24-8/23, 1974 215 hours	8/14-9/10, 1975 159 hours	8/3-8/23, 1976 156 hours	
Pygmy nuthatch	31(6)	33	41	105(6)
Mountain chickadee	11(3)	27(1)	25	63(4)
Gray-headed junco	31(3)	10	12(1)	53(4)
Chipping sparrow	20(1)	1	10	31(1)
Yellow-rumped warbler	3	5	64	72
Vesper sparrow	10	0	12	22
Lincoln's sparrow	8	1	6	15
Broad-tailed hummingbird	0	3	5	8
Western tanager	4	0	3	7
Western wood pewee	2	0	3	5
Hermit thrush	1	0	4	5
White-breasted nuthatch	3	0	2	5
Empidonax flycatcher	3	0	1	4
Williamson's sapsucker	1	3(1)	0	4(1)
Western bluebird	1	0	3	4
Steller's jay	1	1	0	2
American robin	2	0	0	2
Mountain bluebird	1	0	0	1
No. 3-toed woodpecker	1	0	0	1
House wren	0	0	1	1
Common nighthawk	0	0	1	1
Yearly Total	134(13)	84(2)	193(1)	411(16)

from their feathers. In the latter case, activities such as bill-wiping, to suggest that birds were actively placing seeds on branches were not observed. Preened seeds were presumably eaten. In five instances, chickadees hit by discharged seeds continued foraging in tips of ponderosa pine branches, and seeds were transferred from birds to pine needles. Pygmy nuthatches were also observed to be struck by discharging seeds on six occasions, although transfer of seeds from their plumage to pine needles was not observed. The habit of foraging in dwarf mistletoe shoots was not observed with chipping sparrows, gray-headed juncos, yellow-rumped warblers, Steller's jays (Cyanocitta stelleri (Gmelin)), white-breasted nuthatches (Sitta carolinensis Latham) or robins (Turdus migratorius L.).

Seeds were rarely found in the excrement of trapped birds and then only in that of pygmy nuthatches and mountain chickadees. A total of three seeds was found in feces of two pygmy nuthatches, and one seed in feces of a mountain chickadee. None of the 50 seeds ingested by captive gray-headed juncos or chipping sparrows were passed whole. Seeds fed to those birds were presumably digested. Mountain chickadees passed 12 of 50 seeds, and pygmy nuthatches passed 7 of 50 seeds. However, none of the 19 seeds were viable when tested with TTC. The endocarp and viscin of the seeds were missing, but each seed retained the yellow-green color characteristic of healthy seeds.

Viability of whole dwarf mistletoe seeds with endocarps and viscin intact was unaffected by exposure to any of the HCl solutions at 25C, but was affected adversely at 40C (Table 5). When only the endosperm and embryo were incubated in acid solutions, mortality increased with decreasing pH. Solutions of pH 0.7 and 1.4 were lethal to all seeds tested at either temperature (Table 6).

Increasing temperatures also had an adverse effect on survival of seeds of A. vaginatum subsp. cryptopodum. Seeds incubated at 40C for 1 hr lost approximately 50% viability. Incubation at 70C was lethal to all seeds (Table 7).

A total of 96 trees with bird nesting cavities was found in subunits 3 and 4 (Figures 11 and 12). Of that number, 69 were ponderosa pine, 10 Douglas fir, and 17 quaking aspen. Most of the cavities in ponderosa pine were in living trees at heights of 5-10 m. Cavities were most often located in wounds resulting from lightning strikes. Cavities in Douglas fir were in large, old decayed stumps, while those in quaking aspen were in dead or living stems with heart wood decayed by Phellinius tremulae (Bond.) Bond. et Boris.

Most of the cavity trees in subunit 3 were at the northern and southern edges of the subunit and along John's Gulch. Of 33 cavity trees, 14 were used as nesting sites by pygmy nuthatches in 1976 (Figure 13). Foraging territories estimated from observations made between hatching and fledging ranged from 1.5 to 3.4 h and averaged 2.3 h.

Table 5. Survival of whole seeds of A. vaginatum subsp. cryptopodum incubated for three hours in solutions of HCl at 25C or 40C.

pH	25C		40C	
	I	II	I	II
0.7	36/50	38/50	0/50	0/50
1.4	40/50	41/50	2/50	5/50
1.9	39/50	43/50	11/50	8/50
2.8	38/50	39/50	13/50	9/50
4.1	36/50	44/50	20/50	18/50
5.7	44/50	40/50	24/50	21/50
6.8 (water)	46/50	41/50	15/50	22/50

Table 6. Survival of seeds of A. vaginatum subsp. cryptopodum with endocarps and viscin removed, incubated for three hours in solutions of HCl at 25C or 40C.

pH	25C		40C	
	I	II	I	II
0.7	0/50	0/50	0/50	0/50
1.4	0/50	0/50	0/50	0/50
1.9	6/50	4/50	0/50	1/50
2.8	11/50	10/50	0/50	4/50
4.1	17/50	14/50	1/50	8/50
5.7	17/50	18/50	14/50	10/50
6.8	46/50	38/50	22/50	20/50

Table 7. Survival of seeds of A. vaginatum subsp. cryptopodum incubated in water for one hour at 25C, 40C, 55C, or 70C.

Trial No.	Temperature			
	25	40	55	70
I	38/50	13/50	3/50	0/50
II	40/50	18/50	0/50	0/50

Figure 11. Aerial photograph of subunit 3 showing locations of 33 cavity trees. Solid circles represent ponderosa pines, triangles represent quaking aspens, and stars represent Douglas firs.

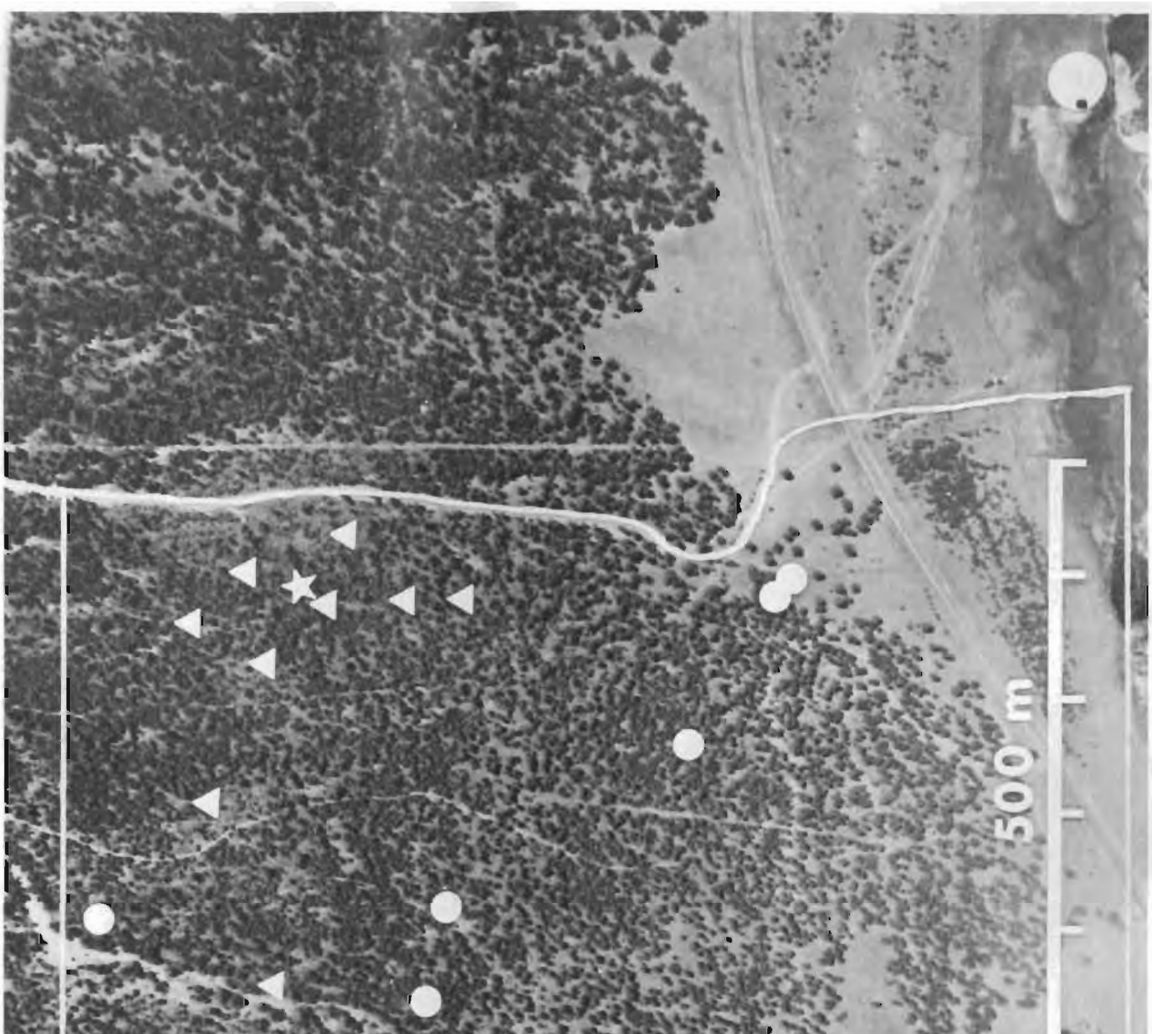

500 m
N

Figure 12. Aerial photograph of subunit 4 showing locations of 63 cavity trees. Solid circles represent ponderosa pines, triangles represent quaking aspens, and stars represent Douglas firs.

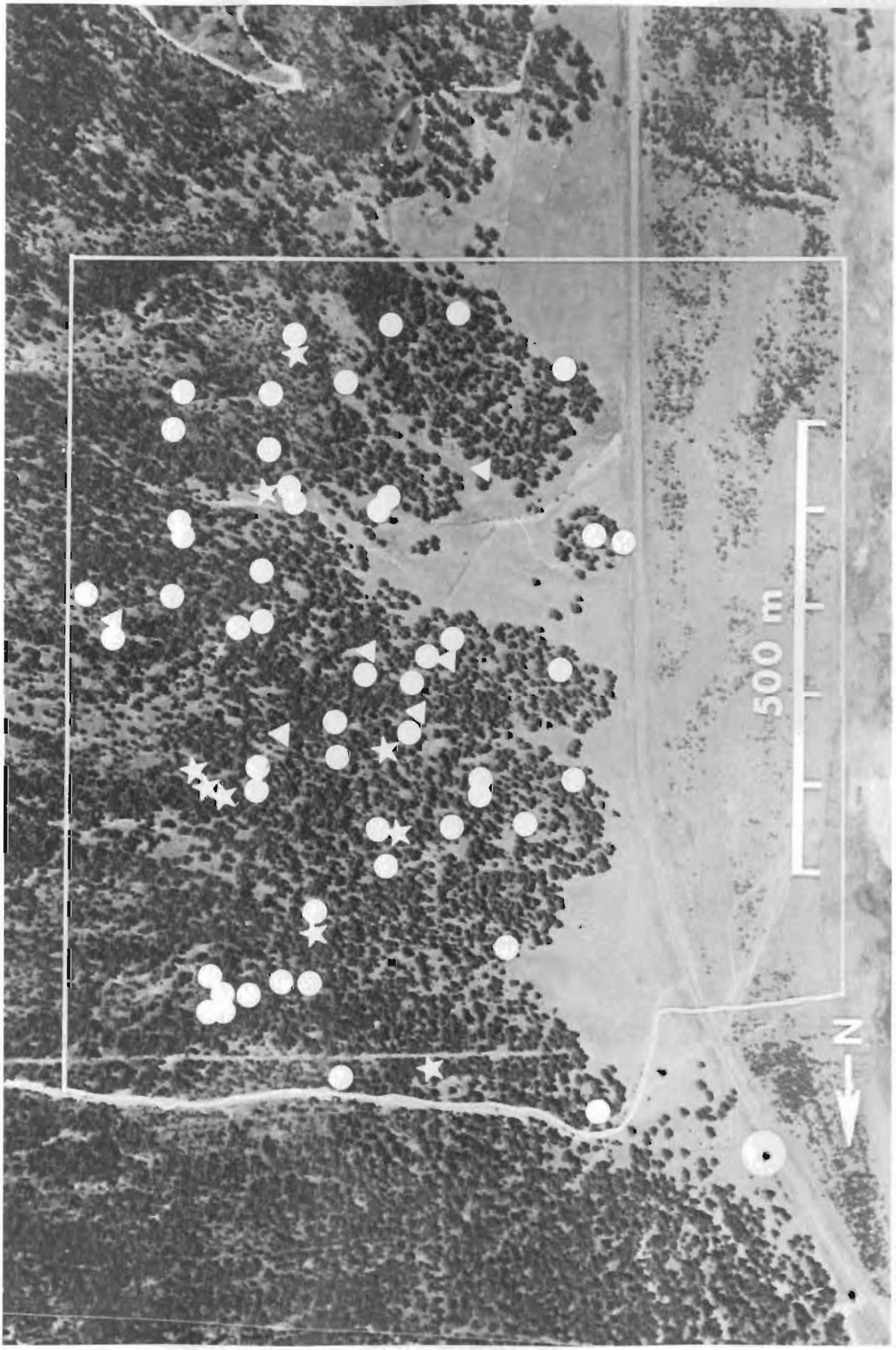
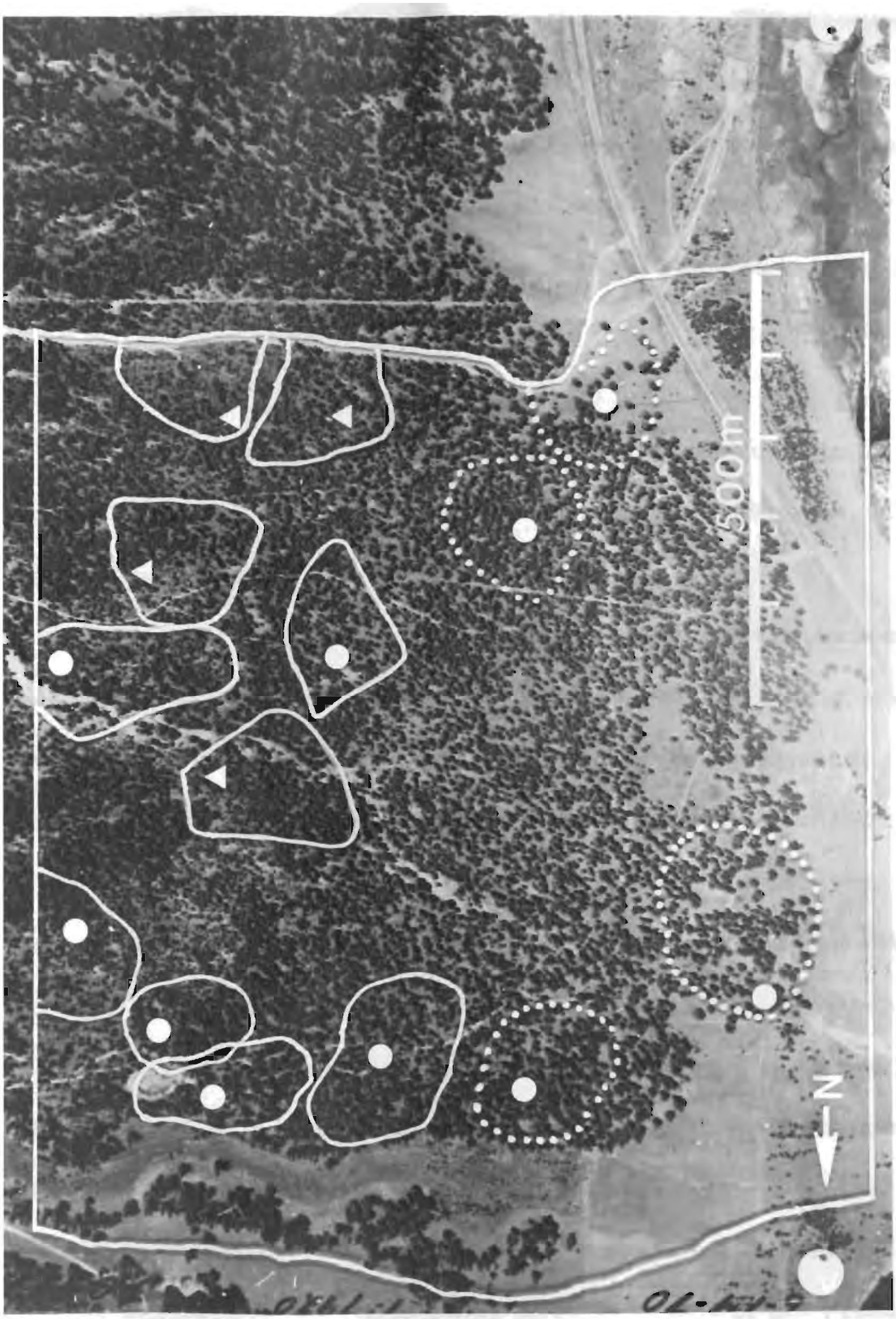

500 m
N

Figure 13. Aerial photograph of subunit 3 showing locations of active nests of pygmy nuthatches in 1976. Territory boundaries shown with solid lines are based on 10 or more observations while those shown with dotted lines are based on less than 10 observations.


500m
N

Of ten pairs of breeding mountain chickadees found in subunit 3, five pairs foraged exclusively within the subunit. They occupied areas of 2.5 to 4.0 h (Figure 14).

A total of 63 cavity trees was distributed uniformly throughout subunit 4. There were no areas larger than 4.5 h which were without potential chickadee or nuthatch nesting sites. Pygmy nuthatches nested in 17 cavity trees and had foraging territories of 0.9 to 2.8 h (Figure 15).

Of seven breeding pairs of mountain chickadees found in the subunit, only four had foraging territories exclusively therein. Territories ranged from 1.7 to 4.8 h (Figure 16).

Within one month after fledging, young pygmy nuthatches became independent of the parents and moved freely over much larger areas than those used by parents during nesting. In several instances, a flock of young birds from the same nest was trapped and banded but never observed together thereafter. Pygmy nuthatches 192-196, all from the same nest, were trapped together in the same net on July 25. Bird 192 was observed on August 9 in a flock that included members of three other families. Bird 194 was observed on the same day in a different flock with birds from two additional families. Nuthatches 193, 195, and 196 were never seen after banding.

In early morning, between 0600 and 0800 hours, pygmy nuthatches were active and conspicuous foraging in tops of tall ponderosa pines. Those locations were first to be struck by the morning sun,

Figure 14. Aerial photograph of subunit 3 showing approximate territories used by mountain chickadees in 1976.

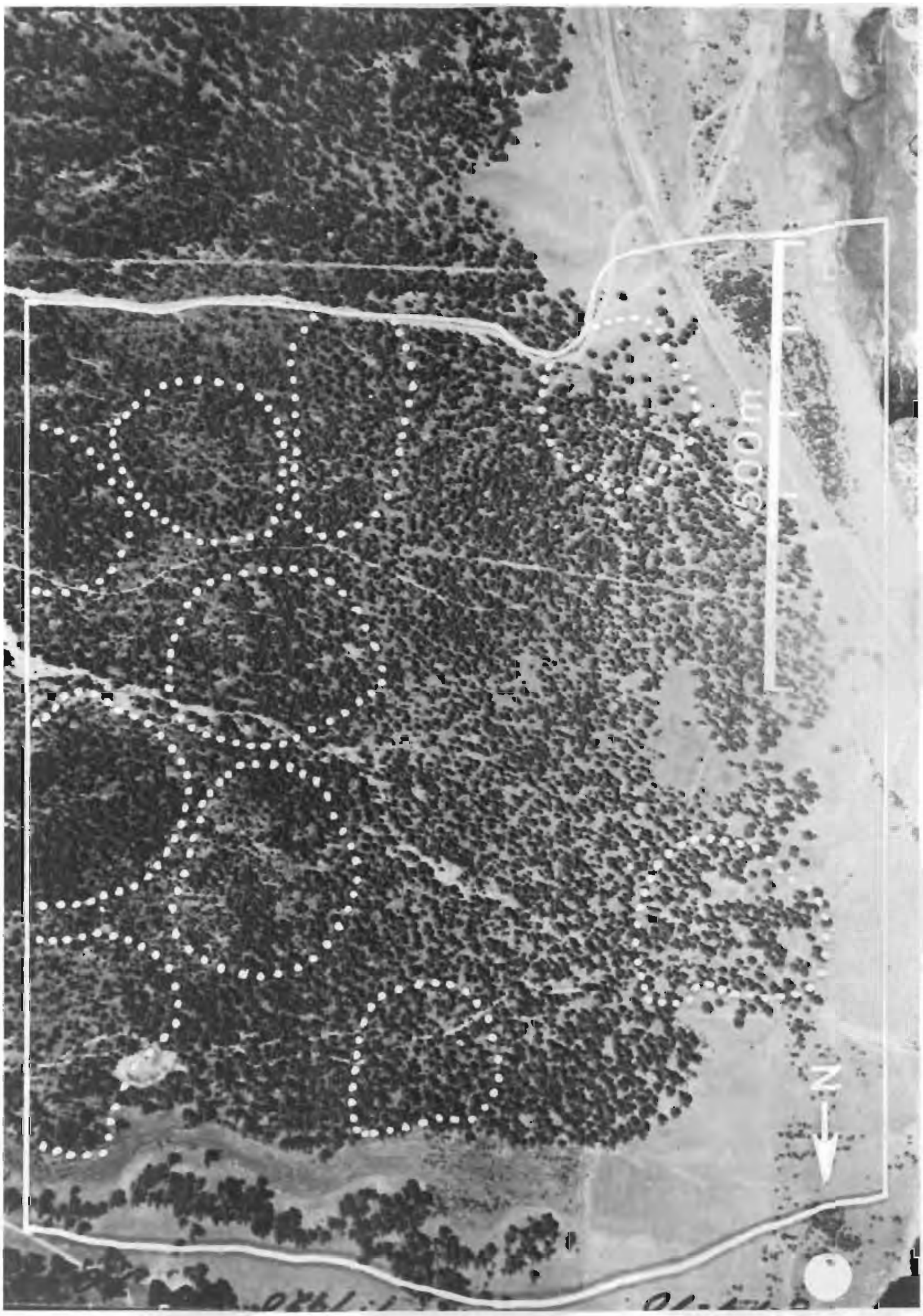

500m
N

Figure 15. Aerial photograph of subunit 4 showing locations of active nests of pygmy nuthatches in 1976. Territory boundaries shown with solid lines are based on 10 or more observations while those shown with dotted lines are based on less than 10 observations.

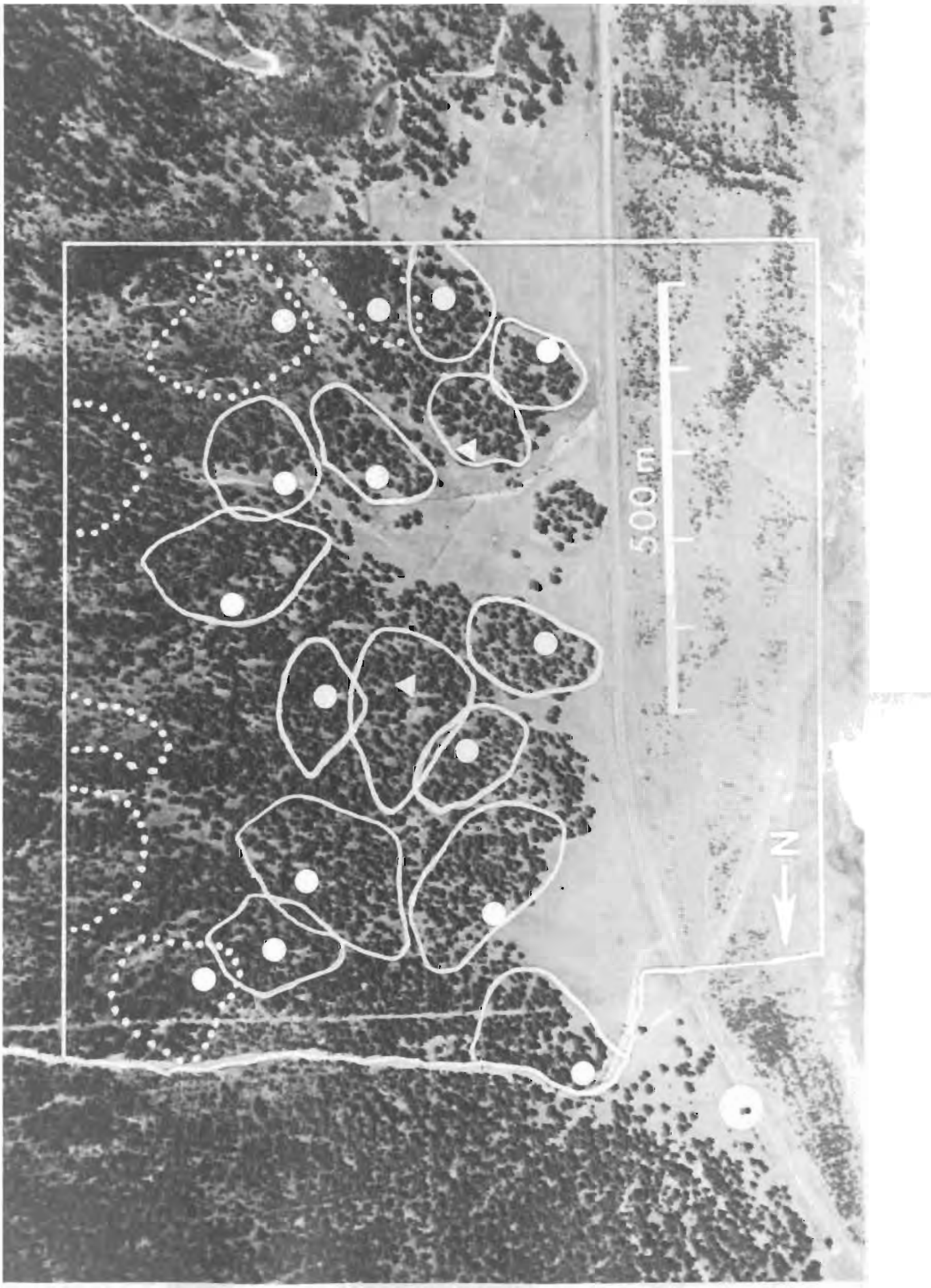
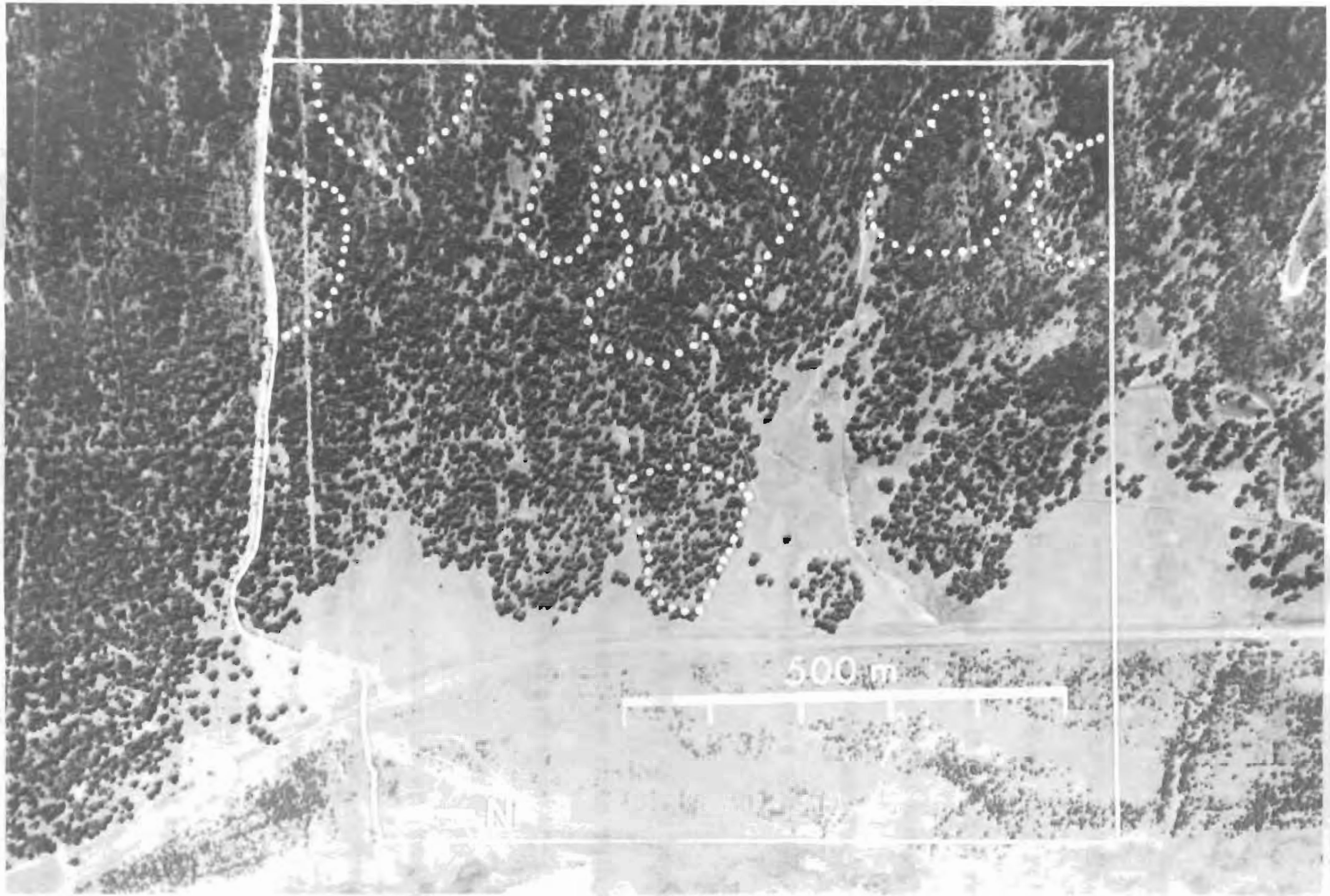

500 m
N

Figure 16. Aerial photograph of subunit 4 showing approximate territories used by mountain chickadees in 1976.


500 m
N

and birds were presumably seeking warmth as well as food when confining their activities to tree tops. As the sun continued to rise, nuthatches ventured into lower portions of crowns, and by 1100 hours they could be found at any level in the pines or on the ground. They also were more often found in smaller trees and denser stands as the temperature increased. Shortly after midday, however, they returned to stands of mature timber where they foraged at all levels but remained relatively quiet and inconspicuous except for brief bursts of activity. Foraging activities increased by 1700 hours, and the nuthatches again moved freely through various stand types until ca. 2000 hours when they roosted for the night.

Pygmy nuthatches foraged in pine foliage as well as on branches and stems, spending approximately an equal amount of time with each. They were observed occasionally foraging in dwarf mistletoe plants, but such activity amounted to less than 1% of the total effort.

Daily movement patterns of mountain chickadees were nearly identical to those of pygmy nuthatches, and the two species were almost always found together. Mountain chickadees, however, did not restrict their early morning foraging to sunlit portions of crowns as consistently as pygmy nuthatches. Mountain chickadees spent ca. 75% of their time foraging in pine foliage and usually perched on branches only to preen or eat. When chickadees foraged in dwarf mistletoe-infected pines, as much as 25% of their efforts were directed toward seeking insects within dwarf mistletoe plants. That insects, and not dwarf mistletoe seeds were their primary objective was evidenced by the fact that they always searched at the bases of shoots and not in aerial portions.

Flocks of chickadees and nuthatches encountered during seed dispersal were comprised of 10 to 30 individuals. When the two species were together, there were two to three times as many nuthatches as chickadees. The birds would forage in an area of 0.3 to 0.5 h for 10 to 30 minutes and then move as a group to a new area 50 to 200 m away.

CHAPTER VI

DISCUSSION

The occurrence of dwarf mistletoe infection centers at distances up to 450 m from the nearest potential seed source indicates that some agent other than or in addition to explosive discharge was involved in seed dispersal. However, analysis of the ages of satellite centers reflected the relative infrequent occurrence of long-distance dissemination. On the average, new infection centers were established only once every four years in ca. 150 h of healthy ponderosa pine.

Wind has only a limited effect on dwarf mistletoe seed discharge (Hudler and French, 1976; Smith, 1966; Scharpf, 1971) and was probably not a factor in establishing satellite centers. Most satellite centers are west of nearest inoculum sources in this study. Prevailing winds during seed dispersal are from the west or northwest and strong east winds are rare. Even if strong east winds were present, seeds would have to successfully penetrate a moderately dense canopy if they were to travel very far. That possibility seems remote.

Rodents are known to frequent infected trees and feed on dwarf mistletoe plants. Abert squirrels and chipmunks were seen frequently in the study area and could serve as vectors of the parasite. However, while collecting dwarf mistletoe seeds, I noted that viscin from freshly discharged seeds dried in 6 to 10 minutes on cotton cloth. Drying may take slightly longer on rodent fur because it is water repellent to some extent. In any event, it was my impression that Abert squirrels and chipmunks rarely traveled more than 30 m from one tree to another in less than 15 minutes. They may aid in intensifying infections within trees, but their ability to spread the parasite over longer distances is questionable.

Birds were the most likely agents of long-distance dispersal of A. vaginatum subsp. cryptopodum in this investigation. Their foraging habits and mobility make them excellent vectors. Trapping data and observations suggest that mountain chickadees and pygmy nuthatches were primary vectors of this mistletoe. Not only were those species found most often carrying seeds, but they also were seen foraging repeatedly, apparently for insects, in dwarf mistletoe shoots where seeds could be obtained and in tips of pine branches where seeds could be deposited most favorably.

Mountain chickadees are abundant residents in upper montane regions of the central Rocky Mountains as reported in numerous censuses (Thatcher, 1956; Winternitz, 1973). They are primarily cavity nesters and prefer old woodpecker holes in living aspen (Bailey and Niedrach, 1965). Relatively little is known of the diet of mountain chickadees, but it is assumed that insects comprise a large portion of the chickadees' daily consumption. In this study, captive mountain chickadees refused to eat commercial bird seed or suet and would only eat live mealworms. On the basis of feeding habits, mountain chickadees are classified as "timber searching" (Salt, 1957) or "timber-foliage searching" (Bock and Lynch, 1970). Winternitz (1973), in an area ca. 20 km south of the Experimental Forest, documented seven complete foraging territories ranging from ca. 1.4 h to 1.9 h. Dixon (1964) noted that the birds rarely visited points more than 1.3 km apart in an area of discontinuous woodland in Utah. Mountain chickadee territories documented in this study ranged from 1.7 h to 4.8 h, areas substantially larger than that reported previously.

Pygmy nuthatches are abundant and frequently encountered in Colorado ponderosa pine forests (Thatcher, 1956; Winternitz, 1973). They nested most often in standing ponderosa pines with rotten heartwood. Norris (1958) estimated that pygmy nuthatches in California ate mostly pine seeds but showed a strong preference for insects in May and late August. Observations in this study suggest that insects were preferred throughout the summer, and pine seeds were taken only rarely. The terms "timber gleaning" (Bock and Lynch, 1970) and "timber searching" (Salt, 1953) are used to describe their foraging habits. Winternitz (1973) documented seven pygmy nuthatch foraging territories ranging from ca. 1.6 h to 2.0 h. Norris (1958) found six territories ranging from 0.8 h to 1.3 h in California forests. He further noted that nest sites were often near territory centers, and territory boundaries stayed more or less constant throughout the year. The sizes of pygmy nuthatch territories documented in this study (0.9 h to 3.4 h) more closely agree with those of Winternitz (1973) and were usually of ample size to include the distance between satellite centers and nearest inoculum source. Contrary to Norris' (1958) observation, however territories of pygmy nuthatches did not remain constant throughout the year. Shortly after fledging, when young birds achieved independence from their parents, they and their parents roamed over far greater areas than those used by the parents while tending young.

Other less-easily trapped species or those which were less abundant in the study area could also function as vectors of *A. vaginatum* subsp. *cryptopodum*. Several gray-headed juncos, a chipping sparrow, and a Williamson's sapsucker (*Sphyrapicus thyroideus* Cassin) were trapped with seeds on their feathers.

Most birds caught in mist nets struggled only slightly until they were untangled. It is possible that birds with seeds on their feathers flew into mist nets, and the seeds fell off or stuck to nets. Hudler et al. (1974) tended mist nets constantly in their study and watched numerous gray jays bearing seeds get caught. They expressed confidence that seeds did not fall off of gray jays. Small passerines caught in this study struggled much less than gray jays, and it is suspected that few if any seeds were lost. Seeds were never found stuck to portions of nets holding birds.

Although mountain chickadees and pygmy nuthatches were found to eat dwarf mistletoe seeds and void them intact, voided seeds were not viable. Viability was probably lost due to combined effects of temperature and acidity in birds' digestive tracts. Incubation of seeds in a variety of temperatures and acidic environments including those found within birds caused significant losses in viability and suggests that birds rarely if ever disseminate viable seeds by eating and voiding them.

If it is assumed that birds only disseminate dwarf mistletoe when seeds adhere to their feathers and are transferred to pine needles in subsequent foraging, the small number of seed-bearing birds trapped is understandable. Seeds would most likely be picked up during morning hours when the majority of explosive seed discharge takes place. However, in morning hours, pygmy nuthatches and mountain chickadees foraged high in pine trees and above mist-netting range. When birds finally did forage at catchable heights, much of a day's seed discharge was complete. Infected trees near mist nets were usually less than 5 m high and not used for foraging until later in the day.

Unusually dry weather in 1975 had a direct effect on explosive seed discharge. Lack of moisture slowed fruit maturation and prevented ripe fruits from attaining turgor pressure necessary to rupture the abscission layer and discharge seeds normally. Thus, activities of birds foraging near dwarf mistletoe fruits did not stimulate seed discharge.

By the time adequate precipitation and atmospheric moisture were available in 1975, many non-resident birds had begun their southward migration. Species such as mountain (Sialia currucoides Bechstein) and western (S. mexicana Ridgway) bluebirds, vesper (Pooecetes gramineus Baird) and chipping sparrows, robins and yellow-rumped warblers were observed in large flocks of 20 or more individuals. The flocks were observed for only a short time, usually less than one day, in any one area, before continuing south and east to lower elevations and more favorable weather. In years such as 1975, when seed discharge occurs during bird migration, it is conceivable that migratory species could disseminate dwarf mistletoe over distances far greater than those reported in this study. Satellite centers 12 and 15, 484 m and 252 m, respectively, from nearest inoculum sources may have originated in such years.

Damage to dwarf mistletoe fruits by freezing is reported for A. laricis and A. americanum (Baranyay and Smith, 1974) in British Columbia, A. americanum and A. douglasii in Montana (Tunnock et al., 1966) and A. pusillum in Minnesota (Hudler and French, 1976). This is the first report of freeze damage to fruits of A. vaginatum subsp. cryptopodum. Seeds oozed from frozen berries and remained attached to the pedicel rather than being forcibly discharged. Although viscin on such seeds was still sticky, the chances of birds contacting seeds diminished with loss of explosive discharge capability.

If bird dissemination of _A. vaginatum_ subsp. _cryptopodum_ is as haphazard as results of this study suggest, then frequency of satellite center occurrence in a given area should be a function of the number of birds in that area. Subunit 4 contained almost twice as many satellite centers per hectare as subunit 3. The density of pygmy nuthatches was also much greater in subunit 4. In 1976, there was one breeding pair per ca. 5.0 h of forested land in subunit 3 as opposed to one breeding pair per 2.0 h in subunit 4. Differences in densities of pygmy nuthatches between subunits could be attributed to a variety of factors, but cavity tree frequency and distribution seemed major contributing factors.

There was one cavity tree per ca. 2 h in subunit 3 and one cavity tree per 0.6 h in subunit 4. Cavity trees were evenly distributed in subunit 4 while in subunit 3 they were concentrated in definite areas. Grouping of cavity trees in subunit 3 had the consequence of lowering the actual number of cavity trees available for nesting. If one of a group of cavity trees was used for nesting, the surrounding area, including nearby cavity trees, was guarded against trespass by the nesting pair. Pygmy nuthatches only defended their territories from other pygmy nuthatches and nested in the same trees as white-breasted nuthatches, violet-green swallows (_Tachycineta thalassina_ Mearns), and Williamson's sapsuckers. Groups of cavity trees were also found in subunit 4, but because there were many more cavity trees and they were well-distributed, the overall effect was probably not as detrimental to population density as was the apparent case in subunit 3.

Two reasons for the relative scarcity of cavity trees in subunit 3 were evident. Dead, potential cavity trees around the campground are utilized by campers for firewood since none is provided. Also, there were few mature aspens in subunit 3 except in John's Gulch and a narrow drainage near the southern edge of the subunit. Aspens greater than ca. 20 frequently have heartwood decayed by _Phellinius tremulae_. Thus, they are easily excavated by woodpeckers, sap-suckers, and flickers. These trees were used in subsequent years as nesting sites by mountain chickadees and pygmy nuthatches.

Balda (n. d.) addressed the problem of cavity tree availability as a limiting factor of bird density in southwestern ponderosa pine forests. Areas with all snags removed were devoid of mountain chickadees and had only two pairs of pygmy nuthatches per 40 h. Nearby, undisturbed areas had 7 pairs of mountain chickadees and 15 pairs of pygmy nut-hatches per 40 h. Balda estimated that pygmy nuthatches needed a minimum of 66 cavity trees per 40 h to maintain "natural densities." Mountain chickadees needed 15 cavity trees. Frequency of cavity trees in subunit 4 approximated Balda's estimates but subunit 3 had less than half the minimum required.

Admittedly, attempts to relate frequency of satellite centers, some of which originated over 100 years ago, to bird populations in

1976 is a gross oversimplification of the situation. Cavity tree development and longevity are little-studied factors in avian ecology and more information on these points is needed. However, wood deterioration is a relatively slow process in southwestern ponderosa pines, and cavity trees may remain standing and functional as nesting sites for 25 or more years. The lack of debris or stumps in subunit 3 suggests that there have never been many cavity trees in that subunit.

Results of satellite center analysis pose several interesting problems concerning biology and epidemiology of A. vaginatum subsp. cryptopodum. Since dwarf mistletoes are dioecious, development of satellite centers requires that after a seed yielding pistillate flowers becomes reproductively functional, there must be an adequate supply of pollen available for fertilization. Such a supply of pollen could come from nearby infection centers or a staminate plant could be introduced at the time of original infection, perhaps by the same bird. Fertiliation of pistillate flowers of A. vaginatum subsp. cryptopodum located ca. 4 km from the nearest pollen source is documented (F. G. Hawksworth, personal communication). Penfield et al. (1976) trapped pollen 91 m from the nearest male flower. Hawksworth (1961) reported that 1% of A. vaginatum subsp. cryptopodum seeds contained two embryos. He speculated on the possibility of such seeds yielding both sexes, but that has not been observed. However, Showler (1974) observed development of both sexes from seeds of Viscum album L. with two embryos.

In addition to the problem of pollination, per se, one might also question differences in intensification and expansion among satellite centers with respect to their ages and distances from pollen sources. Satellite center 1, for instance, consists of one branch with pistillate shoots which has been infected for 33 years and is only 44 m from the nearest source of pollen. The single tree in satellite center 2, however, has been infected for 29 years, is 150 m from a pollen source and has separate infections in 66% of its crown. Similar instances of old, pistillate infections apparently reproducing at low levels are evident in satellite centers 15, 17, and 24. Centers 11 and 28 are old, single-infection centers but because they bear staminate shoots, their lack of spread and intensification is expected.

Another apparent anomally evident from satellite center analysis is that only 2 of 32 centers consisted of single, male infections. Hawksworth (1961) reported an approximate 1:1 ratio of male:female plants for A. vaginatum subsp. cryptopodum. The disproportionate male:female ratio reported here is unexpected and unexplainable.

Occurrence of satellite centers in all topographic categories except "gulches" is expected in light of the relatively erratic means by which birds disseminate dwarf mistletoe seeds. Absence of satellite centers in gulches is apparently not entirely a function of bird activity in those sites. Ponderosa pines in drainage bottoms are frequently mistletoe-free despite their close proximity to heavily infected trees on ridges. The phenomenon is best illustrated in subunit 4. All of the lobes extending west into healthy timber are on ridges, while uninfected portions between them are in drainages. Dwarf mistletoe seeds deposited on trees in drainages apparently do not cause infection due to one or more environmental factors.

CHAPTER VII

CONCLUSIONS AND RECOMMENDATIONS

Results of this investigation suggest that bird dissemination of *A. vaginatum* subsp. *cryptopodum* in Colorado ponderosa pine forests is a rare and haphazard event. Most, if not all, long-distance seed dispersal is effected by way of seeds adhering to birds' feathers with subsequent seed transfer to pine foliage during foraging. Although any bird species may disseminate the parasite, pygmy nuthatches and mountain chickadees are probably most frequent vectors in the area studied.

Pygmy nuthatches and mountain chickadees were never observed in pastures or clearings, except when they flew over them enroute to forested areas or if the clearings contained large, isolated ponderosa pines such as might be the case when seed tree harvesting was implemented. Young pine plantations established following clearcutting would be relatively safe from bird introduction of dwarf mistletoe until trees reached sufficient size to provide adequate cover and harbor an ample supply of insects.

Ponderosa pines in the study area are on poor sites having site indices of 40 to 50 (C. B. Edminster, personal communication). Trees 25 years old are less than 7 m tall (Meyer, 1938). Personal observations suggest that even-aged stands less than 25 years old would not provide suitable habitat for chickadees and nuthatches.

Wherever possible, residual dwarf mistletoe infections should not be left on the perimeter of clearcut areas if it is intended that the areas are to be reforested. A dwarf mistletoe seed was found on a chipping sparrow and that species foraged in both forested and non-forested areas. Chipping sparrows could be significant vectors of the parasite into young pine stands if inoculum is left adjacent to those stands.

Because mountain chickadees and pygmy nuthatches were observed to venture into cleared areas if scattered, large trees were present, reforestation by the seed tree method must include the removal of seed trees within 5 years after harvest cutting. Should seed trees not be removed and become infected, they would literally "shower" the next generation with dwarf mistletoe seeds.

One method of controlling or impeding dwarf mistletoe spread, which was suggested but never tried, is to plant strips of non-host trees at regular intervals to serve as inoculum screens. Birds would probably bridge such screens easily. To be effective in ponderosa pines in the Rocky Mountains, non-host screens would need to be at least 100 m wide, and even then their usefulness would be questionable.

The removal of cavity trees to control or alleviate bird transmission of _A. vaginatum_ subsp. _cryptopodum_ may be feasible in certain instances but probably not desirable in terms of total forest ecology. In one instance, mountain chickadees preyed on the lodgepole pine needle miner (*Coleotechnites milleri* Busck), an important insect pest (Telford and Herman, 1963), and both chickadees and nuthatches probably play an important role in suppressing endemic populations of other potentially harmful insects. In addition, cavity trees in Colorado ponderosa pine forests are nesting sites for a number of other insectivorous birds including white-breasted nuthatches, common flickers (*Colaptes auratus cafer* Gmelin), yellow-bellied (*Sphyrapicus varius* L.) and Williamson's sapsuckers, violet-green swallows, and a variety of woodpeckers.

This study was time-consuming and expensive, and I do not recommend that similar studies with other dwarf mistletoes be conducted unless preliminary surveys indicate that occurrence of satellite centers is extraordinarily high and poses an acute threat to hosts under consideration. However, several other questions with respect to dwarf mistletoe biology were raised and should be investigated:

1. Why do some satellite centers intensify and spread while others remain static?
2. What environmental factors are responsible for severe dwarf mistletoe infection on ridges and little or none in drainages?

3. By what means are pistillate flowers 200 m or more from the nearest staminate flowers pollinated?
4. Why was a disproportionate number of satellite centers started by seeds yielding female flowers?

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