

AN ABSTRACT OF THE THESIS OF

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(Name) (Degree) (Major)

Date thesis is presented May 15, 1965

Title AN ANALYSIS OF A POPULATION OF SNOWSHOE HARES,  
LEPUS AMERICANUS WASHINGTONII BAIRD, IN WESTERN OREGON

Abstract approved   
(Major Professor)

The ecology of a population of snowshoe hares, Lepus americanus washingtonii, was studied in western Oregon from 1960 to 1962. Objectives were to obtain information to control hares, which frequently cause damage to coniferous reproduction in the region, and to compare the life history of this little-studied subspecies with others.

The study area was located on cut-over forest land at 2900-foot elevation in the western Cascades. The climate is characterized by heavy precipitation in winter and summer drought. Snowfall is slight.

Sixty-four live-traps were located in a square grid of 8 rows of 8 traps each, at spacings of approximately 100 and 200 feet. Half the traps were located on a recently clear-cut area and half in young-growth western hemlock and Douglas-fir. Traps usually were set

for three successive days at monthly intervals. Trapped hares were marked and released on the main study area, and hares from nearby areas were removed for necropsy.

In all, 207 hares were caught 889 times on the trapping grid during the 18-month study. One-third of hares tagged and released were not recaptured, but the remainder were recaptured one or more times. Trapping success varied from 3.6 to 44.4 percent. Principle factors influencing movements of hares, trapping success, and distribution of catches were vegetative structure, weather, and differing behavior of adults.

Estimates of numbers of hares were computed from live-trapping data by the recapture, and the calendar-graph methods. Both methods indicated comparable trends in the population. Estimates of hares on the area trapped ranged from 41 in March to 136 in August. Estimated density of hares was 1.6 per acre at start of trapping in October. Density was nearly doubled to about 3.0 hares per acre in late summer.

Most adult females on the area studied had two or three litters a year, averaging three young per litter. First litters were born in May and last litters in August.

Most juveniles approached maximum size by four months. Mean total length of adults of both sexes was greater than that of subadults. Foot and total length of adult females were greater than in

adult males. Mean weight of adult males in winter was 40.6 ounces and of females, 43.4 ounces. Subadults and adults weighed slightly less in early winter than in late fall.

Sex ratio of 205 adult and juvenile hares was 80 females to 100 males; ratio of 84 young juveniles tagged during the summer was 87 females to 100 males. Juveniles tagged (154) exceeded adults tagged (51) by a ratio of 3:1.

Weighted mean range-size of adult hares caught three or more times as computed by the inclusive-boundary-strip, and circular-bivariant-distribution methods was 5.76 and 10.15 acres for males; 3.30 and 7.80 acres for females. Mean home range of juveniles was comparable to the range of adult females. Distribution of catches of hares repeatedly caught and tracking of toe-clipped hares showed that trap-revealed ranges are related to true ranges and that ranges of most adults are fairly stable. A tendency towards farther ranging and linearity of movements was shown by some hares in winter. Location and use of forms are described. Signs of feeding showed that hares fed on conifers and shrubs in winter and herbaceous vegetation in summer.

Young juvenile hares "disappeared" from the population at a high rate. Probability of their survival from birth to the first breeding season was less than 0.18. Crude survival rate of all hares was 0.73.

Neither disease nor parasitism constituted serious decimating

factors, and pathology of 74 hares necropsied was normal. Predation was the most important source of mortality among hares of all ages. Symptoms of "trap sickness" were shown, mainly in winter, by 29 of 207 hares.

The following parasites were found in 50 necropsied hares, and 207 hares examined for ticks and fleas: Protozoa, Eimeria stiedae; Cestoda, Mosgovoyia pectinata americana, and Taenia pisiformis; Nematoda, Trichostrongylus affinis, and Nematodirus triangularis; Acarina, Haemphysalis leporis-palustris; and Siphonaptera, Cediopsyllus simplex and Hoplopsyllus affinis.

AN ANALYSIS OF A POPULATION OF  
SNOWSHOE HARES, LEPUS AMERICANUS  
WASHINGTONII BAIRD, IN WESTERN OREGON

by

HUGH CLARK BLACK

A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of  
the requirements for the  
degree of

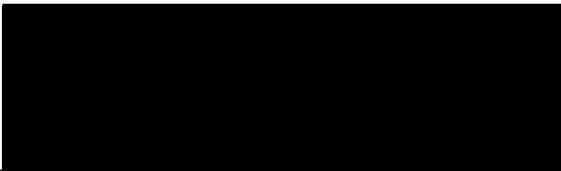
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## ACKNOWLEDGEMENTS

This study was made possible by a research fellowship provided by the Bureau of Land Management, of the U. S. Department of the Interior, and by the assistance of the Forest Research Laboratory, at Oregon State University.

The cooperation of the Willamette Valley Lumber Company in permitting use of the study area is acknowledged, and the help of their timberlands manager, Mr. Morris H. Bergman, was appreciated.

Dr. George Barnes, assistant director of the Forest Research Division of the School of Forestry, helped obtain support for the work. I also wish to thank him for his continued encouragement.

Assistance was given by many persons at the Forest Research Laboratory, and I particularly wish to acknowledge help given by the following:

Mr. Edward F. Hooven, assistant professor of forest wildlife ecology, for the opportunity to do the study, for advising on methods of procedure, and for help with much of the field work.

Mr. Ivan Cutsforth, forest research technician, and Mr. Albert Mozejko, graduate research assistant, for helping with work in the field.

Mr. Ralph Carmichael, assistant in forest management, for assistance with statistical analyses.

Mr. James Overholser, editor and assistant professor of forest products, for suggesting ways of presenting data in tables and figures.

I also wish to acknowledge the help given by the following persons in the Department of Veterinary Medicine, at O. S. U. :

Dr. Dean H. Smith, associate professor of veterinary medicine, for pathological examination of snowshoe hares and for the use of laboratory facilities.

Dr. Stuart E. Knapp, associate professor of veterinary medicine, for identification of parasites, for the use of his laboratory, and for suggesting certain procedures used in the study.

I especially wish to acknowledge sincere appreciation to my major professor, Dr. Robert M. Storm, for his continued interest and encouragement during preparation of the manuscript, and for devoting so much time to its review.

I also wish to thank my wife, Donna, for helping provide the opportunity to complete my graduate program and for her patient support during preparation of this dissertation.



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AN ANALYSIS OF A POPULATION OF  
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INTRODUCTION

The periodic fluctuations in numbers of the snowshoe hare, Lepus americanus, have long been a subject of interest and study. Early naturalists such as Preble (1908), Nelson (1909), and Seton (1909, 1929) reported the alternating periods of scarcity and abundance of varying hares, or "white rabbits," and noted the apparent cyclic nature of these fluctuations. Seton reported that these periods of increase had been remarked on by every observer in the Northwest.

An example of the widespread interest in the periodic fluctuations in numbers of animals was the "Snowshoe Rabbit Enquiry," principally summarized by Chitty (1948, 1950), that gathered and analyzed data on these phenomena in Canada for nearly two decades. Two of the most comprehensive, recent studies of the snowshoe hare (Adams, 1956, 1959; Dodds, 1960b) both sought as their foremost objective, the causes of these fluctuations. While explanations for these changes in abundance have been rife, definitive answers are elusive, and Cole (1954) noted that regularity approaching periodicity is apparent throughout biological phenomena. Nevertheless, these investigations have produced some of the most comprehensive data on

the life history of the snowshoe hare--notably the outstanding ecological studies of Adams, and Dodds.

Audubon and Bachman (1849) described in considerable detail the habits of the "northern hare" in their treatise, "The Quadrupeds of North America". Seton (1909) wrote a comprehensive life history of the snowshoe hare that has been referred to widely. Additional notes on habits of the snowshoe rabbit were included in other early accounts by naturalists such as Soper (1921) and Klugh (1926). More recently, studies of the life history of the hare have been made by many investigators, including Aldous (1937), Criddle (1938), Grange (1932), Severaid (1941, 1942), and Bider (1961). Severaid's study of the snowshoe hare in Maine was the fullest account of the life history of the snowshoe hare to that time. Bider's recent work represents an important ecological study of the snowshoe hare in Quebec.

The snowshoe hare had not been studied extensively in the Pacific Northwest, prior to the present study. For example, Dalquest (1942) described the geographic variation in more than 300 specimens of snowshoe hares from the region and noted that since Nelson's "Revision of the Rabbits of North America" in 1909, little had been published about the snowshoe hares of the region. Notes on the life history have been contributed by Dice (1926), Bailey (1936), Scheffer (1933), and Dalquest. Orr (1934) also made a few observations of the habits of snowshoe hares in Oregon during this time. But with Moore's

(1940) review of the problems caused to reforestation by the feeding activities of wildlife, attention increasingly was given to this role of the snowshoe hare.

Nelson (1909) reported the destructiveness of snowshoe hares to forest seedlings, and Baker, Korstian, and Feterolf (1921) gave a good account of the damage caused by snowshoe hares in natural and planted coniferous plantations in Utah. These authors also noted the seasonal nature of this damage and its relationship to the hare's feeding habits. In the same period, Corson and Cheyney (1928), Cox (1938), and Wilson (1942) reported on the kind, amount, seasonal nature, and significance of the damage to coniferous reproduction in the Lake States caused by the feeding activities of the snowshoe hare. Cox, however, considered the snowshoe hare an important "silvicultural agent" in thinning thickets of conifers. Grange (1949) called the hares "natural thinning agents" and observed that a large number of trees escaped damage, and that snowshoe rabbits did not effectively prevent regeneration of jack pine in the Lake States. Aldous and Aldous (1944), and Krefting and Stoeckler (1953) later reviewed the serious damage done by snowshoe hares to coniferous plantations in the Lake States. Both Aldous and Aldous, and Cook (1945) noted that the feeding activities of snowshoe hares on conifers had not been given serious attention until large-scale planting was begun.

In the Pacific Northwest, Moore (1940) analyzed the sources

and nature of wildlife-caused damage to coniferous reproduction in the Douglas-fir region of western Oregon and Washington. He found that rabbits and hares retarded growth of seedlings more than any other animals in the region. Since Moore's review, reforestation problems caused by wildlife feeding on coniferous reproduction have been given increased recognition (Mitchell, 1950; Staebler, Lauterbach, and Moore, 1954; Lawrence, 1958; Lawrence, Kverno, and Hartwell, 1961; Heacox and Lawrence 1962; and Radwan, 1963).

The present study was undertaken because of the need for additional knowledge of the snowshoe hare in the face of an expanded planting program and increased emphasis on the rapid and complete regeneration of Douglas-fir in the Pacific Northwest (Payne, 1964). The ecology of the snowshoe hare needs to be better understood to effectively control damage by snowshoe hares to coniferous reproduction in the region. This information is needed to guide and coordinate control measures. For example, knowledge of critical periods in the annual cycle of a snowshoe hare population and of the susceptibility of hares to trapping may guide the timing and means of direct measures of control. The potential for "ecological control" also is recognized; that is, that damage to regeneration of conifers may be alleviated by environmental manipulations that are practicable through changes in forest-management practices, and other measures.

The foremost objective of this study was to investigate as

many aspects as possible of the ecology of a normal population of the snowshoe hare, Lepus americanus washingtonii Baird, in western Oregon, as revealed by mark-and-recapture-methods. Specific attention was given to those parameters of the hares' ecology, such as habitat preferences, feeding habits, and home range and movements, that may be affected by changes in silvicultural methods.

Live-trapping was to be accomplished periodically at monthly intervals on a cutover area populated with snowshoe hares in western Oregon. Welded-wire traps of a standard size would be used mainly, but two other sizes of traps were to be included. Trapping for three successive nights each month was planned to continue throughout an annual cycle of the snowshoe-hare population; others were to continue the investigation for several years. Hares caught were to be examined, measured, and tagged, and the trapped samples of the populations were to be analyzed. Hares on the main trapping grid were to be marked, released, and recaptured, but hares trapped on comparable habitats nearby were to be sacrificed and necropsied.

This report presents an analysis of the life history of a normal population of snowshoe hares in western Oregon and is based primarily on data collected by live-trapping, field observations, and necropsy of hares in the laboratory. The main topics covered in this thesis are: The habitat, and environmental factors that affected distribution of hares; an analysis of trapping results and factors

influencing catches; population estimates and comparison of two census methods; home range and comparison of two methods used to determine home range; and other data on the hares' life history, particularly, the diseases and parasites of hares studied.



Figure 1. The study area as seen from the vicinity of Station D-3, in July 1962. The more recently logged and burned open area joins the older cutover and restocked area, or second growth, in the background of this photograph. The abundance of slash left on the ground in the open area is evident.

## STUDY AREA

The main study area was located in Linn County in the western Cascades of northwestern Oregon, in the southwest corner of the Willamette Valley Lumber Company's McLeod Tree Farm (Figure 1). It is situated on Sections 19 and 30 (T12S, R2E); about half of the study area lies in the southwest quarter of Section 19 and the remainder lies in the northwest quarter of Section 30. The area is 45 miles east of Corvallis, by road.

It is located in the transition zone (Bailey, 1936), on an irregular plateau that lies between the McDowell Creek and Crabtree Creek drainages; both of which flow into the South Santiam River. Drainage is provided, to the west, by Scott Creek, tributary to McDowell Creek. The main study area, as defined by both trapping grids, is gently sloping and has a varied, but generally west exposure. Mean elevation is between 2800 and 2900 feet. The area is further identified by its proximity to Green Peter mountain, situated two miles to the southeast.

Some live-trapping of hares was carried out on nearby areas, which were located on the east border of Section 19; the southwest quarters of Sections 17 and 20; and the southeast quarter of Section 18 (all in T12S, R2E). These areas had been cutover in 1943 and were medium to well stocked with a mixture of second growth western



hemlock, Tsuga heterophylla, and Douglas-fir, Pseudotsuga menziesii.

Ground vegetation was comparable to that found within the second growth on the main study area. Topographically, these secondary trapping areas also were comparable to the main-study area. However, locations trapped on Sections 17 and 18 were on moderate to steep slopes with a generally north exposure and at elevations between 2600 and 2800 feet.

### History<sup>1</sup>

The entire area had supported a virgin stand of Douglas-fir and western hemlock, one or the other predominating on different sites. That portion of the trap-grid located within the second growth had been logged in 1943. That portion in the open, poorly stocked area had been cutover in 1949. In November 1952, a hot slash fire burned over the entire 1949-cutover of approximately 2200 acres and continued burning uncontrolled for two weeks. The fire extended about two miles north and west of the main study area, which was situated on the southeast edge of the burned-over area.

A stocking survey made by the Willamette Valley Lumber Company in February 1955 listed the open burned-over area as

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<sup>1</sup>Information obtained in an interview (December 22, 1961) with Mr. Morris Bergman, timberlands manager of the Willamette Valley Lumber Company, Dallas, Oregon.

unstocked and that part now referred to as the second growth was recorded as moderately stocked with predominantly western hemlock that averaged five years old.

Most of the area deforested in 1949 was planted with Douglas-fir seedlings in the winter of 1957-1958, and the area was re-examined in July 1958 by Tree Farm Management Service of Sweet Home, Oregon. Medium stocking (40-69%) was found on the planted area and stocking within the second growth was good (average 80%). The second growth, which had escaped the fire in 1952, primarily was stocked with hemlock that was 10-years old on the average. A few natural seedlings of western hemlock were scattered throughout the open area. Planted seedlings on the east half of Section 19 were poorly spaced and heavily damaged by wildlife; stocking averaged less than 150 live seedlings to an acre. A marked sample of seedlings in the southeast quarter of the section also had been severely damaged by wildlife.

By 1960, the area cutover in 1949 and burned in 1952 was poorly stocked, particularly around the perimeter adjoining the second growth. Damage caused by wildlife, primarily by snowshoe hares, was adversely affecting survival of planted and wild seedlings.

### Climate

The mild and moist climate of the western Cascades is strongly influenced by its nearness to the Pacific Ocean (Decker, 1960; Sternes, 1960). Temperatures are moderate and there is a prolonged growing season throughout the region. The long western slope of the western

Cascades causes a heavy precipitation by the interception of moisture brought from the Pacific by the prevailing westerly and southerly winds. Snowfall along the western border of the range is comparatively slight.

The range of precipitation in the vicinity of the study area is illustrated by comparison of precipitation at the study area (Table 1) with the average annual precipitation recorded at nearby weather stations (Table 2). For example, nearly twice as much precipitation was recorded at Snow Peak Camp, at an elevation of 1200 ft, as at Lacombe, at an elevation of 665 ft. Snow Peak Camp is on the western slope of the western Cascades and both stations lie north and west of the study area.

Snowfall occurred only once at elevations below 1000 ft in the vicinity of the study area from October 1960 to March 1962. Above 2000 ft, snowfall was markedly greater and the depth of the average snowfall increased rapidly to the plateau area, at about 2900 ft elevation; a similar transition was effected descending McDowell Creek drainage to the southwest.

### Geology

The Cascades are largely volcanic in character and of comparatively recent geologic origin (Baldwin, 1964). The Range is divided into two physiographic divisions, the western Cascades and

Table 1. Temperature and precipitation at the study area from November 1960 to March 1962.

Date	Max. Daily Temp. (Deg.F. )	Min. Daily Temp. (Deg.F. )	Mean Monthly Temp. (Deg.F. )	No. of Days ≤ 32°F	Precip- itation (Inches)
Nov. 1960 <sup>1</sup>	63	16.	36.1	>16	13.51
Dec.	68	19	38.8	>19	6.03
Jan. 1961	69	15	40.0	>18	6.30
Feb.	58	26	35.5	21	20.41
Mar.	63	23	36.0	25	13.30
Apr.	68	24	40.8	22	5.54
May	83	25	45.8	10	5.71
June	97	30	57.5	3	1.80
July	94	34	58.0	0	0.75
Aug.	89	32	59.9	1	2.17
Sept.	81	26	48.9	9	4.38
Oct.	82	24	44.0	16	9.30
Nov.	68	15	35.4	>24	11.40
Dec.	63	9	32.7	25	14.23
Jan. 1962	70	-1	32.2	27	3.96
Feb.	72	1	34.2	21	6.69
Mar.	54	13	33.1	>12	7.21
Annual (1961)	97	9	44.5	14.5	95.29

<sup>1</sup> Observations were begun November 5, 1960.

Table 2. Annual precipitation at weather stations in the vicinity of the study area in 1960 to 1962, and at the study area in 1961

Station	Location (Distance in Miles and Direction From Study Area)		Elevation ( Feet)	Annual Precipitation (Inches)		
				1960	1961	1962
Snow Peak Camp	6	N	1,200	91.15	99.34	-- <sup>2</sup>
Lacomb <sup>1</sup>	8	NW	665	52.55	52.61	43.41
Waterloo <sup>1</sup>	10	W	420	49.32	51.32	38.62
Foster	7	SW	600	58.66	60.25	44.80
Cascadia <sup>1</sup>	9	SE	796	67.51	69.64	52.44
Quartzville <sup>1</sup>	14	NE	823	92.63	94.80	-- <sup>2</sup>
Study area	--		2,900	-- <sup>2</sup>	95.29	-- <sup>2</sup>

<sup>1</sup> Official U. S. Weather Bureau Station

<sup>2</sup> Data unavailable

the high Cascades; the study area is located on the western edge of the western Cascades.

The Cascade mountains of Oregon are a broad upwarp composed of a basal portion of early Tertiary tuffs, breccias, lavas and mudflows, exposed in the Columbia River Gorge and other deep valleys. A thick middle section of mid-Tertiary basalts and andesites forms the deeply eroded western Cascades. Valleys have been carved deeply into the western part of the range owing to heavy precipitation. The formation of the mantle of soil has also been accelerated by the heavy precipitation on this region. Topography is highly variable.

The explosive phase of volcanism in the Cascade Range was succeeded by a period of quieter extrusions during which time the Cascade andesites and basalts were extruded along the crests and margins of the Cascade Range. These flows have been called the Cascade andesites or the Cascan formation and were formed during the Pliocene. Andesite is the principal component of the soil-parent materials in the region of the study area.

Pliocene-Pleistocene arching of the Cascade Range was accompanied by the incision of the Columbia River Gorge and other streams draining the western slopes of the range. For example, both the North and South Santiam Rivers, which bound the study area, are west-flowing and formed incisions during this period. Glaciers also formed during the Pleistocene in the upper parts of the valleys

of west-flowing rivers. Local glacial action may be seen in the vicinity of the study area, especially along the North fork of Crabtree Creek.

## Soils<sup>2</sup>

The fairly uniform soils within the study area have been classified in the Keel series. These soils occur at elevations of 2500 to 4000 feet, on slopes to 30 percent. On the main study area, the Keel soil consists of a moderately fine textured, well drained yellowish-brown Lateritic soil developed from residuum or colluvium in rhyolitic porphyry rocks on hilly or mountainous topography. It has a moderately well developed textural and structural profile, and an A-B-C-D-horizon sequence. The A-horizons are dark brown and medium textured, the B-horizons are dark yellowish-brown, sub-angular blocky clay or light silty clay loams. The keel soil on the area has a modal depth of 36 to 60 inches (average 48 inches) and is stony.

Plant competition (for moisture) is rated as slight on this soil and it ordinarily does not support plant competition restrictive

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<sup>2</sup>Data from an unpublished survey of soils that included the study area on 46,000 acres of lands in Linn County owned by the Willamette Valley Lumber Co. The survey was accomplished in 1961 by the U. S. Soil Conservation Service, Albany, Oregon.

to survival and growth of seedlings. Average site index for Douglas-fir is low Site III.

#### Weather Data

Temperature and precipitation were recorded throughout the study. This was done to provide a description of the weather at the study area, and to facilitate comparison of trapping success and other behavior of hares with local weather conditions.

Operation of a continuous recording Taylor-thermometer and a rain gauge were begun in November 1960 and continued through March 1962. Temperatures at six inches and five feet above the ground were recorded. The element near the ground was shaded, but otherwise was unprotected. (The recording thermometer was placed within a standard instrument shelter in July 1961.) Temperatures at the two levels were compared, but mean data are based on the values from the five-ft level. Temperature charts were changed and precipitation was measured at weekly intervals. Data were tabulated as follows: The maximum and minimum temperature recorded each 24-hour period were averaged to find the mean daily temperature; the mean of the daily means each month equalled the average monthly temperature. The amount of precipitation was recorded monthly. Since it was not always possible to know on which days precipitation may have occurred, or when the collection represented a period overlapping two months, the average daily precipitation was calculated and multiplied by the number of



days of record in each of the months.

Notes on wind direction and velocity, as estimated by the Beaufort wind scale, cloud cover, depth of snow, and surface-moisture conditions were also recorded during each trip to the area.

Data were correlated with records from local weather stations (Table 2). Stations of the U. S. Weather Bureau recording temperature and precipitation were located 8 to 14 miles from the study area, at Lacombe and Waterloo to the west, and at Cascadia and Quartzville to the east. These stations were all at elevations below 1000 feet. Two unofficial weather stations also were maintained in the vicinity; a station at low elevation, at Foster, seven miles southwest of the area, operated by the Linn County Fire Patrol Association, and a station at Snow Peak Camp, six miles to the north, operated by the Willamette Valley Lumber Company. The latter station was situated in the Crabtree Creek drainage at an elevation of about 1200 feet.

#### Synopsis of weather data (Study area and western Cascades).

The heavy precipitation in November 1960 was the first effective precipitation occurring in the fall and was only the second time since May that substantial precipitation was recorded (U. S. Weather Bureau, 1959). Heavy snows fell on higher elevations of the Cascades during November and six inches of snow fell on the study area in mid-November, but melted by the end of the month. Very heavy precipitation was recorded throughout the region at this

time and an average of 1.5 inches of rain fell on the study area each day from November 15-18. No snow fell on the study area during December 1960 and January 1961. Weather during this period was abnormally dry, warm, and windy. January is usually the heaviest snow-fall month of the year, but snowfall was extremely light in the region (U. S. Weather Bureau, 1960). February was one of the windiest, wettest, and warmest of record in Oregon (U. S. Weather Bureau, 1960). More than 20 inches of precipitation was recorded at the study area during February 1961, but less than 7 inches fell on the area in February 1962 (Table 1). Snow covered the ground to a depth of 12 inches during the last part of February and most of March 1961. The entire month of March was marked by wet and stormy weather, which continued into April. Snow-cover was absent during the first part of April, but 12 inches of snow fell during the trapping period, on April 21-22. Temperatures were abnormally high during June, July, and August (U. S. Weather Bureau, 1960). The first snow of the winter occurred in late December 1961, but was not persistent and did not exceed three inches. Very heavy rains occurred during the trapping period in mid-December and an average of nearly two inches of precipitation was recorded on each of the three days. During January 1962, snow averaged 8 to 12 inches deep on the area, with drifts to 30 inches. But most of the snow in the open area was melted by February, although patches remained

within the second growth. Precipitation during February was below long-term monthly averages in the region (U. S. Weather Bureau, 1961). However, more than 18 inches of snow fell on the study area in February and ten or more inches of snow, with drifts to 30 inches, remained throughout most of March.

Weather data recorded on the study area are summarized in Table 1, and mean monthly temperature and monthly precipitation are shown in Figure 2. The characteristic weather pattern is clearly evident in the graphs. That is, heavy precipitation in winter and summer drought; conversely, the maximum mean monthly temperatures closely coincide with minimum monthly precipitation.

Precipitation recorded at weather stations in the vicinity of the study area is summarized in Table 2. These data show a close correlation with stations at Snow Peak Camp and at Quartzville for 1961.

In 1961, the average annual temperature at Lacombe and Cascadia was about 52° F, compared to 44.5° F at the much higher elevation of the study area. The difference between the mean monthly temperatures at these stations and at the study area was comparable throughout the year. (Temperature-data were not available for stations at Snow Peak Camp, Waterloo, Foster, and Quartzville.)

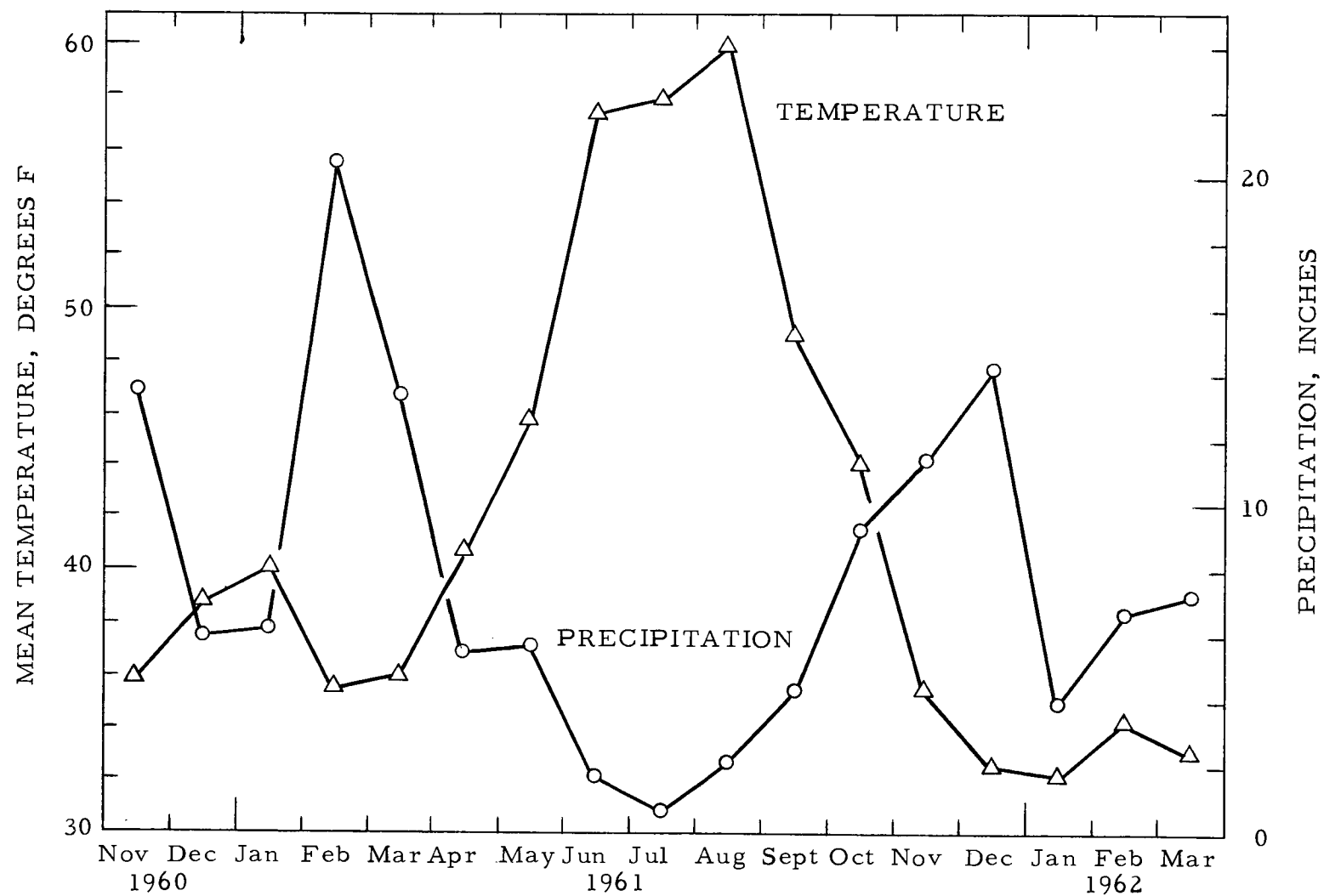


Figure 2. Mean monthly temperature and monthly precipitation at study area from November 1960 to March 1962.

## Vegetation

The vegetation on the main study area represented two successional stages that followed clearcutting of an old growth stand of western hemlock and Douglas-fir. That portion of the main study area covered with a stand of predominantly advanced hemlock reproduction was cutover in 1943. The unstocked area was cutover in 1949 and slash was burned in November 1952. The result was two very different types of cover.

The older cutover area, referred to as the "second growth" was well stocked with advanced reproduction of western hemlock and Douglas-fir, and had an understory of shrubs and dense herbaceous vegetation in openings. The more recently clearcut part of the study area, identified as the "open area", was in an earlier stage of succession. Vegetation in this area was comprised of perennial forbs, sedges, scattered shrubs, and clumps of coniferous saplings. Species making-up the understory vegetation occurred for the most part in both successional stages and differed only in their relative abundance.

Ground and shrub layers were given most attention in the analysis of vegetative cover. The extent of canopy closure within the second growth was recorded, but no distinction was made between conifers comprising the overstory. Their abundance was measured in stems present on sampling plots by size-classes, e. g., seedlings,

saplings, and pole stage.

One-hundred and forty-four circular, milacre sampling plots (radius of 3 ft 8 1/2 in.) were located systematically one chain (66 ft) apart in a square grid. The grid was superimposed on the smaller trapping grid--stations were spaced one and one-half chains equidistant--so that 12 rows of 12 plots each were located on the main study area, beginning at Station A-1. Plots sampled were located along trap-lines A, C, E, and G, and on either side of trap-lines B, D, F, and H. This procedure was used to permit following the existent trap-lines, which were marked, and cleared in the second growth. Plots that fell at intersections of the trapping grid were located about five feet from the trap-stations. Plots were marked with wire pins and plastic flag.

On each plot, the presence of one or more plants of a species was recorded and the frequency of each species' occurrence on a plot was expressed as the percentage of plots where that species was found--following the procedure used by Yerkes (1960). Abundance of the more common species were also recorded as a percentage of each plot occupied by that species. Uncommon species found on the area were also collected and identified.

No attempt was made to sample vegetation quantitatively on that portion of the larger trap-grid that was not included in this sample. It was assumed that observations made on the smaller grid

were representative of vegetation on the larger area, because there were no important changes in the relative proportions of the two types of cover or in composition of the vegetation encompassed by the larger grid.

A comparatively small number of species made up the majority of the plant cover in both parts of the area. Ground cover in the open area mainly consisted of herbaceous plants of which false dandelion, Hypochaeris radicata, and short sedge, Carex brevipes, were the most abundant and widely distributed species. Only a few coniferous saplings occurred and the density of shrubs was low.

In the second growth, western hemlock occurred most frequently in all size-classes. Douglas-fir seedlings and saplings were nearly absent, but pole-size Douglas-fir was a more important component of the second growth than indicated by sampling. Bear grass, Xerophyllum tenax, mostly absent from the open area, was an important ground cover, particularly in the openings or thinly stocked parts of the second growth. Both species of huckleberry were more common in the second growth than in the open area. Bracken fern, Pteridium aquilinum, was dense in openings in the second growth; some of which were completely occupied by this fern.

### Stocking of Conifers

Only one Douglas-fir seedling was present on each of 10 of the plots sampled in the open area and these had been heavily damaged by hares. A few scattered Douglas-fir saplings were present in the open area, but none occurred on plots sampled. Sampling plots within the second growth also were nearly devoid of fir seedlings and saplings, and no saplings or pole-size firs occurred on plots sampled. But this area was moderately stocked with Douglas-fir.

Western hemlock was scarce in the open area, but it was the most common tree within the second growth; its succession apparently being favored by its silvical characteristics and by its being clipped by hares to a much lesser extent than Douglas-fir. (deVos [1964] observed that snowshoe hares may affect the availability of food, and plant composition by preferentially feeding on certain species resulting in a differential survival of plants utilized.) Western hemlock seedlings occurred on about one-third of plots within the second growth, and an average of 2.2 seedlings were found on each stocked plot. Most of these seedlings were moderately or heavily damaged by wildlife. Sapling-and-pole-stage hemlocks were found on 38.7 percent of plots and discounting two thickets of hemlock (34 and 13 stems occurred on each of two plots respectively) an average of 2.4 stems occurred on each occupied plot. The canopy over 11 other



plots in the second growth was also comprised of hemlock.

### Occurrence, Distribution, and Abundance of Plants

Sixty-one species of plants were identified on the main study area. These are listed by vegetative classes in Table 36, in the Appendix. The frequency of occurrence of 24 of the most abundant species is listed in Table 3 and relative density of the 8 most abundant herbaceous plants and shrubs are summarized in Table 4. Most of the remaining species were represented by a small number of individuals and were not found on sampling plots.

These tables provide a comparison of the relative abundance of understory vegetation composing the two types of cover. Forbs were more common in the open area and shrubs were more abundant in the second growth, with exception of willow.

Red sorrel, Rumex acetosella, Thyme-leaved speedwell, Veronica serpyllifolia, small fire-weed, Epilobium adenocaulon, pearly everlasting, Anaphalis margaritacea, and white-flowered hawkweed, Hieracium albiflorum, occurred on both parts of the grid, but were more common and characteristic of the earlier stage of vegetative succession represented in the open area. Bracken fern, bear grass, and both species of huckleberry, Vaccinium sp., were comparatively denser and characterized the understory vegetation within the second growth. Salal, Gaultheria shallon, and long-leaved

Table 3. Occurrence of the more abundant herbaceous plants and shrubs on 144 mil-acre plots on the main study area in August 1961.

Species	Occurrence on Plots (Percent) <sup>1</sup>	
	Open Area (69 plots)	Second Growth (75 plots)
Western sword-fern, <u>Polystichum munitum</u>	15.9	21.3
Western brake-fern, <u>Pteridium aquilinum</u>	18.8	69.3
Red fescue, <u>Festuca rubra</u>	1.4	1.3
Short sedge, <u>Carex brevipes</u>	89.9	48.0
Bear-grass, <u>Xerophyllum tenax</u>	8.7	62.7
Red sorrel, <u>Rumex acetosella</u>	50.7	8.0
Sticky mouse-ear (Chickweed), <u>Cerastium glomeratum</u>	2.9	0
Broad-leaved lupine, <u>Lupinus latifolius</u>	15.9	9.3
Evergreen violet, <u>Viola sempervirens</u>	0	28.0
Fire-weed, <u>Epilobium angustifolium</u>	2.9	0
Common western willow-herb, <u>Epilobium adenocaulon</u>	55.1	4.0
Dwarf dogwood, <u>Cornus canadensis</u>	1.4	2.7
Thyme-leaved speedwell, <u>Veronica serpyllifolia</u>	5.8	1.3
Pearly everlasting, <u>Anaphalis margaritacea</u>	95.6	56.0
Canada thistle, <u>Cirsium vulgare</u>	11.6	0
Hairy cat's-ears (False dandelion), <u>Hypochaeris radicata</u>	100.0	65.3
White-flowered hawkweed, <u>Hieracium albiflorum</u>	49.3	17.3
Coulter's willow, <u>Salix coulteri</u>	29.0	5.3
Long-leaved Oregon grape, <u>Berberis nervosa</u>	1.4	6.7
Salal, <u>Gaultheria shallon</u>	0	21.3
Oval-leaved huckleberry, <u>Vaccinium ovalifolium</u>	42.0	66.7
Red huckleberry, <u>Vaccinium parvifolium</u>	14.5	34.7
Western dewberry, <u>Rubus vitifolius</u>	31.9	34.7
Evergreen blackberry, <u>Rubus laciniatus</u>	7.2	0

<sup>1</sup>For example, western sword-fern occurred on 15.9 percent of the 69 plots sampled in the open area and on 21.3 percent of the 75 plots within the second growth.

Table 4. Density and frequency of occurrence of the eight most abundant herbaceous plants and shrubs on 144 mil-acre plots on the main study area in August 1961.<sup>1</sup>

Species	Open Area (69 Plots)						Second Growth (75 Plots)					
	Cover Class <sup>2</sup>					Occurrence on Plots (Percent)	Cover Class <sup>2</sup>					Occurrence on Plots (Percent)
	1	2	3	4	5		1	2	3	4	5	
Western brake-fern, <u>Pteridium aquilinum</u>	6	1	1	3	2	18.8	5	24	8	9	6	69.3
Short sedge, <u>Carex brevipes</u>	51	10	1	0	0	89.9	35	1	0	0	0	48.0
Bear grass, <u>Xerophyllum tenax</u>	6	0	0	0	0	8.7	21	12	11	3	0	62.7
False dandelion, <u>Hypochaeris radicata</u>	24	19	18	8	0	100.0	31	9	5	4	0	65.3
Coulter's willow, <u>Salix coulteri</u>	17	3	0	0	0	29.0	4	0	0	0	0	5.3
Oval-leaved huckleberry, <u>Vaccinium ovalifolium</u>	23	4	2	0	0	42.0	22	15	12	1	0	66.7
Red huckleberry, <u>Vaccinium parvifolium</u>	8	1	1	0	0	14.5	12	10	4	0	0	34.7
Salal, <u>Gaultheria shallon</u>	0	0	0	0	0	0	14	0	0	2	0	21.3

<sup>1</sup> Based on plots in the open area, western brake-fern occurred on 18.8 percent of the 69 plots. Density of this species on each of the occupied plots is indicated under cover class. e.g., six of the plots were in cover class 1, etc.

<sup>2</sup> Cover class was based on the percentage of each plot occupied by the vertical projection of the normal growth form of a species, as follows: cover class 1 (1-4%), 2 (5-24%), 3 (25-49%), 4 (50-74%), and 5 (75% or more).

Oregon grape, Berberis nervosa, occurred in low density within the second growth, but were absent in the open area.

Western rhododendron, Rhododendron macrophyllum, occurred in medium density on cutovers in the vicinity of the study area, but was uncommon on the study area. Slender thermopsis or yellow lupine, Thermopsis gracilis, was not recorded on sampling plots, but patches were present in the open area and in the second growth. While evergreen violet, Viola sempervirens, frequently was found on sampling plots within the second growth, it was not abundant and was an insignificant component of the understory. American twin-flower, Linnea borealis, was also present in the second growth in low density, but was not recorded on sampling plots. Eight species of grasses were identified on the grid, but none were common and most only occurred in the open area. Red fescue, Festuca rubra, was the most abundant and widely distributed of the grasses. The rusty sedge, Carex subfusca, was present in low density, mainly in the open area, and the common wood-rush, Luzula multiflora, was also present in low density in the open area and occasionally present within the second growth.

### Mammals<sup>3</sup>

Populations of small mammals on the study area were sampled by trapping. Additional information was obtained by direct observations, particularly of California ground squirrels, Citellus beecheyi, and by capture of small mammals in traps set for hares. Records of ground squirrels, bushy-tailed wood rats, Neotoma cinerea, spotted skunks, Spilogale gracilis, and Douglas' or pine squirrels, Tamiasciurus douglasii, were obtained as a result of the trapping activity to take hares. The presence of other mammals was revealed by their sign. For example, long-tailed weasels, Mustela frenata, and spotted skunks were identified by their tracks; the presence of a few moles, presumably Townsend's moles, Scapanus townsendii, were indicated by their runways and molehills. Observations of larger mammals were also based mainly on their sign, e. g. , tracks, droppings, and the remains of mammals consumed by predators.

Small mammal populations. Populations of small mammals were sampled on the main study area in May and September 1961. It was felt that a knowledge of their density and relative species

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<sup>3</sup>Nomenclature follows that of Hall and Kelson (1959), excepting that the generic name Dama is replaced by Odocoileus, and the generic name Spermophilus is replaced by Citellus (American Society of Mammalogists, 1960).

composition would provide a more complete description of the environment, and might help identify favorable habitat of snowshoe hares. Also, the numbers and kinds of mammalian and avian predators may be influenced by the abundance of small mammals.

Sherman live-traps were located at each station on the grid established for trapping hares. That is, 64 small mammal traps, spaced one and one-half chains apart, were located in a grid of eight rows of eight traps to a row. Traps were baited with whole oat groats and set for two nights on May 20-21, and for three nights on September 6-8, 1961. (Weather records that include the two trapping periods are summarized in Table 37.) All mammals caught were removed from the area. Sex and age determinations were not recorded.

Results of the two samplings of small mammals are summarized in Table 5. Deer mice, Peromyscus maniculatus, Townsend's chipmunks, Eutamias townsendii, and vagrant shrews, Sorex vagrans, were the species most frequently taken and represented the most abundant small mammals present, with exception of the California ground squirrel. Ground squirrels frequently were taken in the larger traps, in the open areas, from April through September (Table 10). No shrews were taken during the two trap-nights in May. Also, a single creeping or Oregon vole, Microtus oregoni, and two western jumping mice, Zapus trinotatus, were taken in

Table 5. Small mammals caught in Sherman live-traps and removed from the main study area in 1961.

Species and Number Caught <sup>1</sup>						Small Mammals Caught Each Trap-night
Date	<u>Sorex</u> <u>vagrans</u>	<u>Eutamias</u> <u>townsendii</u>	<u>Peromyscus</u> <u>maniculatus</u>	<u>Microtus</u> <u>oregoni</u>	<u>Zapus</u> <u>trinotatus</u>	
<u>First Sampling Period</u>						
May 20	0	5	7(2)	0	0	12(2)
May 21	0	7(1)	9(4)	0	0	16(5)
Subtotal	0	12(1)	16(6)	0	0	28(7)
<u>Second Sampling Period</u>						
Sept. 6	1	4	24(8)	1	1(1)	31(9)
Sept. 7	4	9(1)	8(4)	1(1)	9	22(6)
Sept. 8	3(1)	3	15(6)	0	0	21(7)
Subtotal	8(1)	16(1)	47(18)	2(1)	1(1)	74(22)

<sup>1</sup>Small mammals caught in the open area are indicated in parentheses.

September, but these species had not been trapped in May. Deer mice were more abundant in September, but the number of chipmunks apparently was comparable in both trapping periods.

Half of all small mammals taken in Sherman live-traps in May and September were deer mice, about two-thirds of which were caught at stations on the edge or within the second growth, although the stations were divided about equally between the two types of cover. The remainder of the small mammals caught, with few exceptions, were taken at stations within the second growth.

During the three trapping nights in September, one small mammal was caught for each 2.4 effective trap-nights.

Other mammals. Coyotes, Canis latrans, and bobcats, Lynx rufus, were the principal mammalian predators that frequented the area. Tracks of one or more coyotes were seen on or in the vicinity of the grid in most months each winter. Scats of coyotes containing hair and bone fragments of snowshoe hares were found on the study area in August 1961 and February 1962. Coyote footprints were seen in the dust near the area in August 1961; scats occasionally were seen on roads in the vicinity of the study area, and coyotes were heard calling within a mile or two of the area in August 1961 and February 1962. Also, a young coyote was seen on the access road north of the study area in August 1961.

Signs of bobcat seldom were encountered. Tracks of a bobcat



were seen in the snow two miles north of the study area in March 1961; scat of a bobcat was found on the grid in August 1961; and bobcat tracks were seen on the area four times, in December 1961 and March 1962.

Coyotes and bobcats probably visited the area regularly and signs of their activity on or in the vicinity of the grid were common. In addition to those noted, evidence of their having fed on hares in summer and winter also were recorded. Neither predator was present in large numbers, but likely coyotes were more numerous than bobcats.

A short-tailed weasel, Mustela erminea, was caught on the grid in a small mammal trap in October 1961, and long-tailed weasels were seen in the vicinity of the study area twice. Tracks of long-tailed weasels were seen repeatedly on the grid, in the open area and within the second growth, during the trapping period in January 1962. A few spotted skunks also were present on the area, but were not considered a threat to hares.

Another potential mammalian predator of hares on the study area was the black bear, Ursus americanus. A fresh bear scat that contained only vegetable matter was found on the grid in July.

No evidence was found that any of these mammals preyed heavily on hares; however, weasels may be a potential predator on young hares. But Dodds (1960b) reported that weasels were not

serious predators on hares in Newfoundland, and Morse (1939) also had found them unimportant predators on hares in Minnesota.

The study area and environs constituted good summer deer range, since the cutover areas were in a stage of plant succession that provided an abundant supply of food for deer. Black-tailed deer, Odocoileus hemionus columbiana, were seen commonly in the vicinity and were observed on the study area in most months of the year, but cold weather and snow caused deer to move to lower elevations. Usage of the area by deer in winter was negligible, although some interspecific competition for available browse occurred.

An abundance of fresh sign of deer--tracks, beds, plants browsed, and droppings--was present on the main study area in June, and a doe and her twin fawns were flushed from within the second growth in mid-June. Groups of deer fecal pellets also were found on half of the plots (on which pellets of hares were counted) in the open area and on one-third of the plots sampled within the second growth.

#### Avian Predators<sup>4</sup>

Great horned owls, Bubo virginianus, were present in the vicinity, but may not have preyed heavily on snowshoe hares; no

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<sup>4</sup>Nomenclature follows that of Peterson (1961).

pellets of owls or castings of other raptors were found. A large owl sighted on the study area at dusk in October 1960, tentatively was identified as a great horned owl. Two great horned owls were heard calling near the study area in December 1960, and in November 1961 a great horned owl was seen three miles north of the study area. Also, in the same month and on the grid, a patch of fur and imprints in the snow, possibly made by the wingtips of a great horned owl, marked an unsuccessful attack on a hare.

Red-tailed hawks, Buteo jamaicensis, were the only large raptors seen frequently in the vicinity of the study area. Individuals usually were solitary and were recorded throughout the year, but were seen more commonly in late summer. The following observations were made in 1961: On the evening of August 8, a western red-tail was observed on a perch at the edge of the second growth. The hawk, which apparently was watching the open area, flew onto the perch at 8:00 p.m. (PDST) and remained until dusk. This was in good habitat of snowshoe hares, about one mile north of the study area. On August 9 at 6:10 a.m. a western red-tail was seen perched on a snag in the northeast corner of the grid. Five minutes later the hawk flew across the area and alighted in a tall fir at the southwest corner of the area, where it remained for several minutes. Both hawks presumably were hunting and their selection of perches along the boundary between the second growth and open areas would

have placed them in a favorable position to watch for hares. However, other prey, including numerous ground squirrels, was available to them.

A pair of ferruginous hawks, Buteo regalis, also were seen over the study area in August 1961.

A goshawk, Accipiter gentilis, was sighted three miles north of the main study area twice, in April 1961. Cooper's hawks, Accipiter cooperii, may also have occurred on the area, but none was recorded. The ability of these accipiters to hunt in the second growth may have enabled them to take an occasional juvenile hare.

Common ravens, Corvus corax, frequently were observed flying over the area throughout the year. There was no indication that they may have attempted to take hares, although the diurnal activity of immature hares exposed them to attack by these corvids.

Dodds (1960b) reported that horned owls sometimes feed upon hares in Newfoundland, and that common ravens and the common crow, Corvus brachyrhynchos, also may take a few young hares.

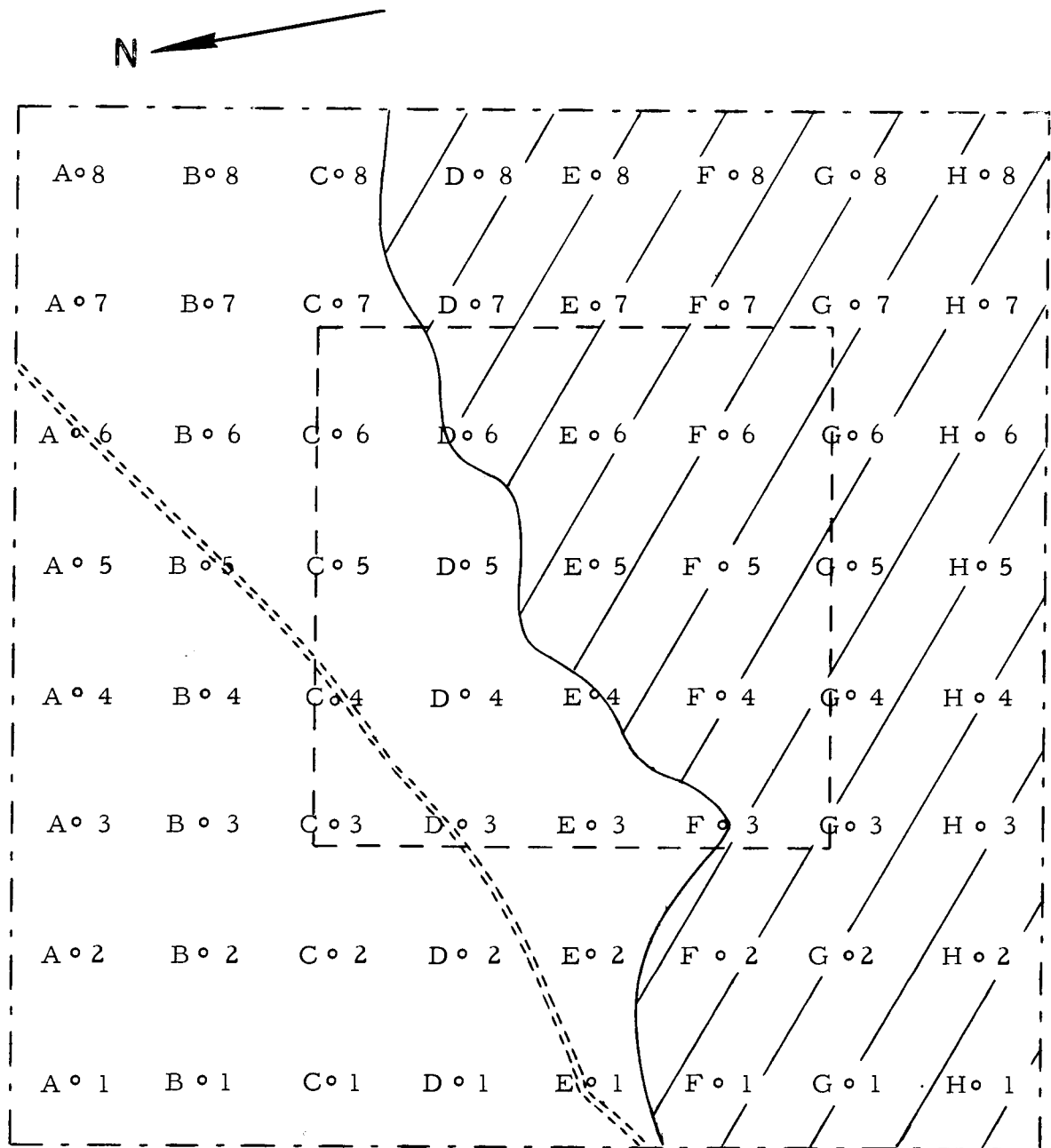


Figure 3. The location and designation of each station on the live-trap grid from October 1961 to March 1962; stations were spaced three chains apart. The smaller area outlined in the center of the diagram indicates the area trapped from October 1960 to September 1961, when trapping stations were spaced one and one-half chains apart. The "second growth", or that part of the area occupied by advanced coniferous reproduction is represented by shading; the "open area" is unshaded.

## METHODS OF PROCEDURE

Live-trapping was the principal technique. Direct observations were made in the field, and hares were necropsied in the laboratory. The abundance of fecal pellets of hares was sampled, and ground obstructions and canopy closure were estimated.

### Trapping

Thirty-six trapping stations were located on the study area in June 1960, by Hooven, in a grid consisting of six rows of six traps each, spaced one and one-half chains apart (99 ft). (Traps had been placed on the grid before trapping was begun to permit hares to become accustomed to them.) The grid was laid out by hand compass and pacing. Trap-lines were oriented in an east-west direction and the grid was positioned so that it included about equal parts of both cover types (Figure 3). Trap-lines were designated by letters and the stations along each line were numbered, for example, A-1, A-2, etc. Each intersection of the grid was marked with a stake and metal tag. Within the second growth, the trap-lines were partially cleared to facilitate checking traps. A trap was located near each grid-intersection and in no cases were traps located more than 10 feet from a station.

During the second trapping period (October 22-24, 1960), 28 additional traps were located around the perimeter of the grid, at the

same spacing between stations. In all, 64 traps were arranged in a square grid consisting of 8 rows of 8 traps each, and covering about 15 acres.

The welded-wire traps used in the study were manufactured by the National Live Trap Company, Tomahawk, Wisconsin (Figure 4). They were 9 x 9 by 26 inches long. Access was provided by a single entrance at one end of the trap. The 28 traps added in October 1960 were of similar construction, but 25 were slightly larger (9 1/2 by 9 1/2 by 32 inches long) double-door traps. This larger-sized trap afforded access from either end and was tripped by a centrally located treadle. Since an animal could see directly through the trap, trap-shyness presumably may have been reduced by this design. But two hares were caught at the same time in this type of trap on two occasions and in each instance one or both hares had been severely injured by the other; one fatally. Only a single door was set on these traps following the third trapping period, in November. Traps of this type were mostly replaced by single-door traps in December and the change-over was completed in August 1961.

Ten smaller traps of the single-door model were used during the three trapping periods in August and September 1961. These traps were located at stations on Lines D, E, F, and G within the second growth. Their dimensions were 6 1/2 by 6 1/2 by 21 inches long. These additional traps were used in an attempt to increase the catch of

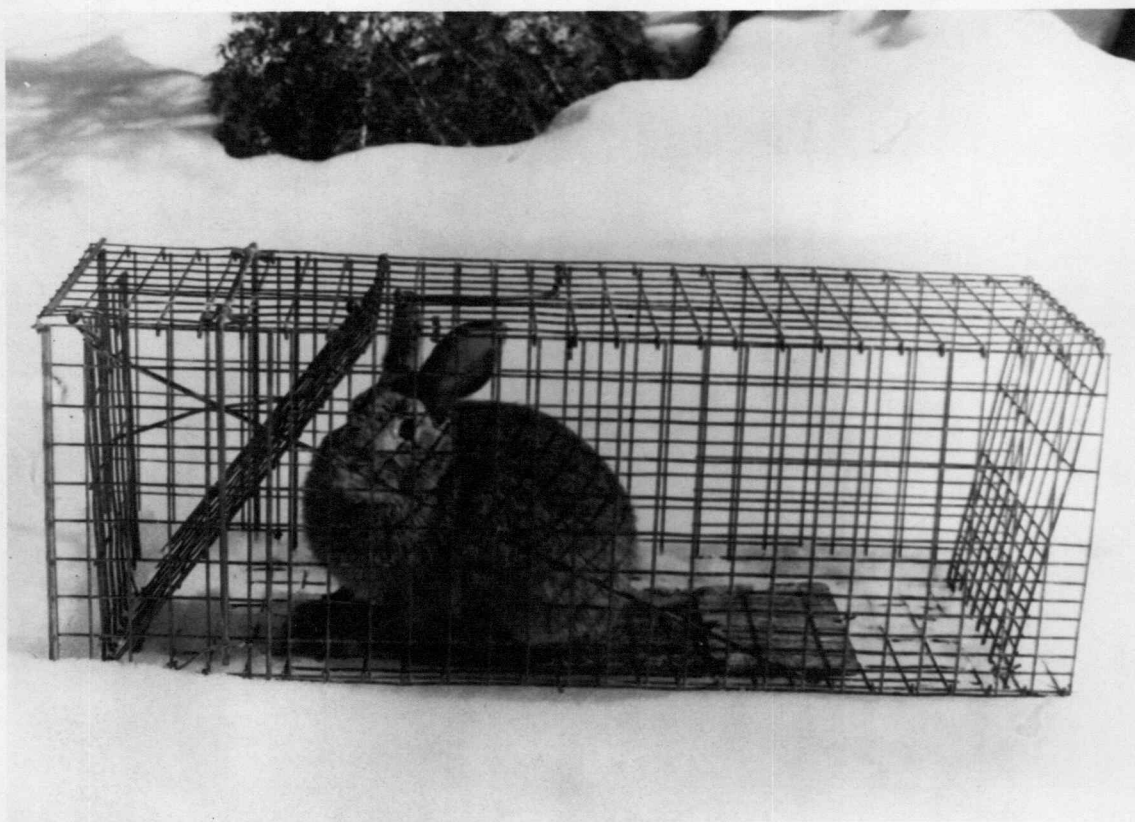


Figure 4. A welded wire live-trap manufactured by the National Live Trap Company of the type used to trap snowshoe hares in this study--an adult hare is in the trap.



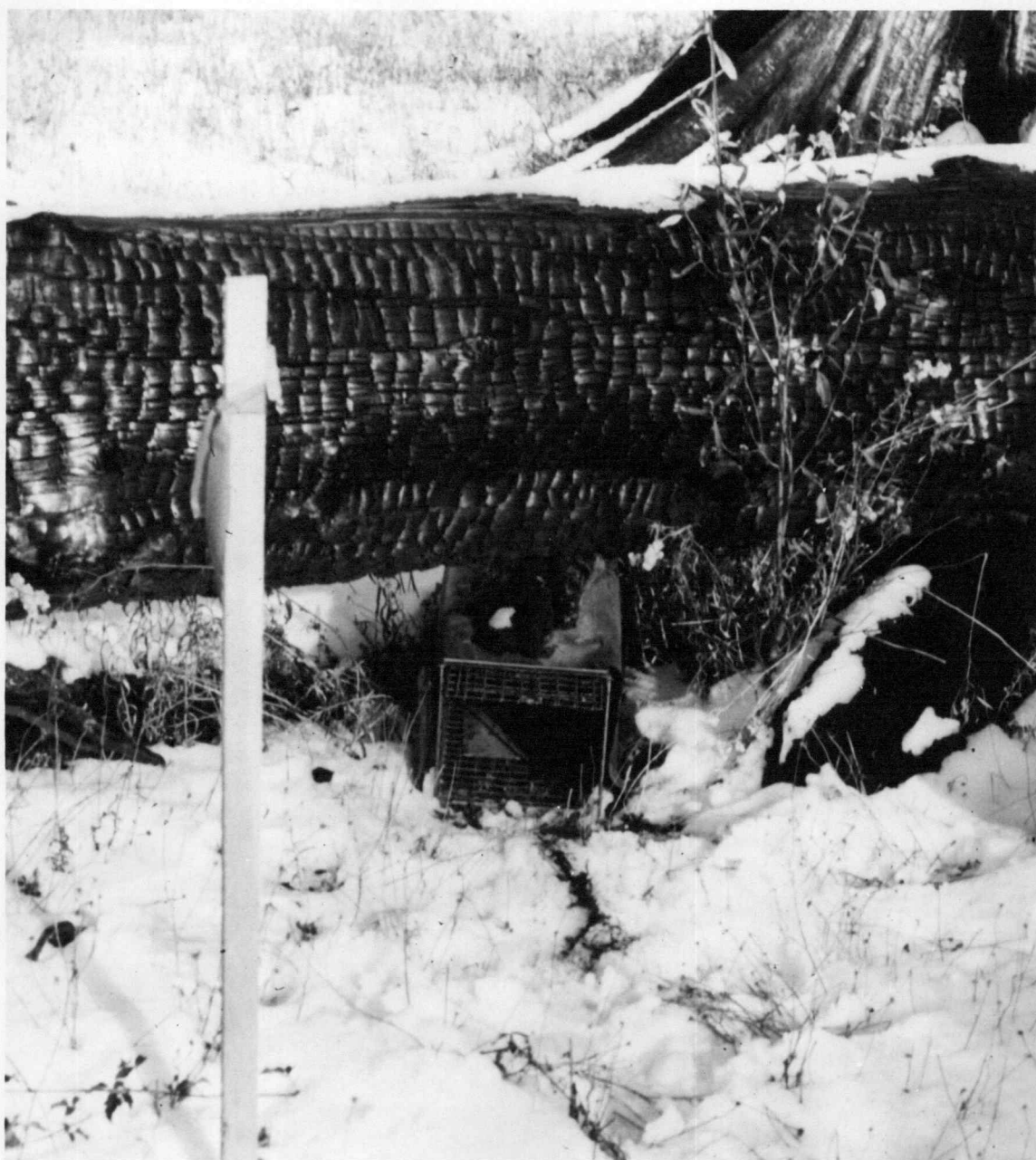


Figure 5. Station A-7, in the open area, in January 1962. The trap is covered with tar paper and sheltered by a log; the stake and tag marking the station is in the foreground.



Figure 6. The appearance of a trap at Station B-2, located in the open area, following a six-inch snowfall during the trapping period in January 1962.

juvenile hares.

Traps were covered with tar paper to provide protection to captive hares (Figures 5 and 6). Protection was needed to shield trapped hares from exposure, particularly from rain and snow in winter and direct exposure to the sun in summer. A covering also was needed to keep snow from becoming packed under the treadles, preventing their operation. Dodds (1960) covered traps (set for hares) with fir or spruce boughs in Newfoundland, to prevent icing and snow-clogging.

Traps were located in the most likely looking, protected spots; they were placed near shelter of logs, shrubs, or trees, to avoid direct exposure to the summer's sun and to prevent snow from blocking entrances. Each trap was placed on smoothed ground and covered with a piece of bark or wood to hold it steady when a hare entered.

An increase in the spacing between traps, from one and one-half chains to three chains (198 ft) was accomplished in October 1961, after a year's trapping on the smaller grid, to facilitate measurement of movements and determination of home range. Results obtained during the first 12-months of trapping had indicated that the area covered by the smaller trapping grid was probably too small to adequately measure movements of most older juvenile and adult hares. Furthermore, it seemed probable that many of the hares that had not been recovered after tagging occupied ranges mainly lying outside of the smaller grid.

Selection of the longer spacing between traps was in part arbitrary, since it was desired to retain some of the original stations and to follow the existent lines of traps where possible. Accordingly, the new grid was laid-out by pacing and hand compass, to form a larger trapping grid centered around the initial grid. The new grid extended proportionately farther into the open area, but the number of stations in both cover types was the same. Station A-1, in the new alignment of traps, was located six chains north and west of the station previously designated A-1 (at the northwest corner of the grid). (Designation of stations on the larger grid is distinguished by underlining.) Correspondingly, stations on the east and south sides were located no farther than four and one-half chains from stations on the former grid. Sixteen of the original stations were retained within the new, expanded grid, i. e., the odd-numbered stations on Lines A, C, E, and G. All new stations were marked with a stake and tagged (Figure 5) and the lines of traps were marked with flag (plastic tape) and partially cleared.

Survey, clearing and marking of the new grid was completed in September, and transfer of traps to the new stations was accomplished in mid-October 1961.

Traps usually were set for three successive days at intervals of four weeks. But trapping was conducted within two weeks of the first trapping period in October 1960 and in December 1960, an extremely poor catch prompted a second trapping period within an interval

of only one week. Also, in September 1961, two trapping periods were carried out within an interval of three weeks. On two occasions, in April and May 1961, each period of trapping was reduced to two trap-nights to avoid additional losses of hares.

The doors of the traps were hooked-open between the first five trapping periods, allowing hares to move freely in and out of traps. It was thought that this procedure might accustom hares to entering traps, but since it might also induce trap-proneness, the practice was discontinued in January 1961 and thereafter the traps were sprung between trapping periods. There was also a chance that a hare might release the wire hook, while in a trap, and become caught.

### Baits

Baled alfalfa hay of good quality was used to bait traps for each of the first four trapping periods. A half-apple was added to the hay used to bait each trap set in the fifth trapping period, during December 28-30, 1960, and hay or apple-baits were used separately in alternate traps set during the sixth trapping period, in January 1961. Thereafter apples of different varieties were the only baits used; the apple-bait was suspended at the back of a trap by means of an S-shaped wire hook about four inches long.

One-half of an apple was used initially to bait each trap, but later a whole apple was used. (Apples invariably were wholly or

partially eaten by trapped hares, except by the younger juveniles.)

Whole apples were bothered less readily by ants in summer and there was little likelihood of an entire apple being consumed by small rodents during the three nights the traps were set. A fresh apple was used to rebait a trap after each capture.

### Handling Procedures

When a hare was caught, the trap was turned on end and the wire securing the door was depressed, while the door was held open with the left hand. Then the ears of the hare were grasped and the animal was withdrawn partially from the trap. At this point, the hindlegs were grasped securely with the left hand and the hare was removed from the trap. The right hand was then shifted from the ears to a grip on the body, back of the head. A number of alternative means of handling a hare were found satisfactory, including a one-hand grip that immobilized the hare and permitted one man to accomplish tagging. Methods of handling were comparable to those described by Lord (1963) for handling cottontail rabbits.

The tar paper covers were kept on traps while hares were removed, since it was noted that the animals became more excited during handling if the traps were uncovered. Dodds (1960) also reported that covering traps with a dark material will reduce attempts to escape.

While held securely, hares could be examined, measured (Figure 7), and tagged with a minimum of struggling and with little possibility of injury to the hare. (Standard measurements are described in the Appendix.) This handling procedure minimized disturbance of the animals and reduced chances of a hare's escaping during removal from a trap, and during handling.

The sequence of measurements and observations began with tagging, or recording of tag numbers of hares previously tagged; ears were examined carefully for old tag-puncture marks before tagging. Hares were then measured, sexed, aged, and any injuries or other anomalies were recorded. They were examined for ectoparasites by parting fur about the head, particularly around the eyes and the base of the ears. The kind and number of ectoparasites were recorded and samples were collected, and preserved for identification. During the breeding season, the position of testes in males was recorded, according to whether the testes were retracted or had descended into scrotal sacs. Adult females were examined for signs of lactation and the abdomen of each was palpated to determine pregnancy. An attempt was made to count the number of fetuses in pregnant does. (This examination was facilitated by placing the hare on the ground and covering its head with a sack, while holding it securely by the hind legs.) Weighing was the last step in the handling procedure; hares were held in a cloth sack and weighed to the nearest half-ounce on a



Figure 7. Measuring the head-length of an adult snowshoe hare, March 1962; standard measurements taken on all hares included length of the head, ear, tail, left hindfoot, and total length and weight.



spring scale. Following release the behavior of each hare was observed and unusual responses noted.

### Marking

Hares trapped on the main study area and at nearby locations were ear-tagged. A small number of tagged hares on the main study area also were marked by toe-clipping.

Ear-tagging. Each hare was ear-tagged when first captured with a pair of numbered, monel metal tags. The tags were size 0, "fingerling tags", manufactured by the National Band and Tag Co. They were affixed to the medial edges of the ears at first; a method successfully employed on brush rabbits, Sylvilagus bachmani, by Hooven. But on the larger ears of the snowshoe hares it was found that tissue tended to grow over the tag, or the tag turned and became partly obscured; both effects made it difficult to read the tag numbers. It also was noted that where tags were attached to the lower, medial edge of the ear there was a tendency for the tissue to become necrotic. However, no tags were lost by any of the hares tagged in this manner, nor by a more frequently used procedure in which the tags were attached to the distal edge of the ear about midway between base and tip.

The ears of all untagged hares were checked carefully for old-tag scars, but none was noted. It was common for hares to have the tips of their ears torn or split and for this reason tags were not

fastened to the tips of the ears. An occasional puncture wound, probably caused by fighting, also was noted.

Individual hares were identified by the number stamped on only one tag. For example, number 999 designated the hare with tag-number 999 in the left ear and number 1000 in the right ear.

Toe-clipping. The method devised by Dell (1957) to mark snowshoe hares by toe-clipping was tested and the effects on marked hares were observed.

One or two toe-ends were removed from the hindfeet of 15 tagged hares during February 25-27, 1961, but no more than one toe-end was removed from each foot (Figure 8). Each of the first eight hares marked by toe-clipping had only one toe-end removed. The next seven hares each had one toe-end removed from both hindfeet. Surgical scissors were used to sever the toe-ends at the first metatarsal joint. No anesthetic or post-operative treatment was used.

Toes were numbered from the inside out, following the system of numbering used by Dell (1957). Thus, "1L" designates that the first inside toe on the left hindfoot had been removed. This numbering system permits marking of 24 individuals by removal of not more than one toe-end from each hindfoot, and does not employ toes of the front feet for marking purposes. Identification of hares with two hindtoes removed was provided by the combination of toes excised. For example, "2L, 3R" designates a hare from which the second toe-end on the left



Figure 8. Tracks of a snowshoe hare marked by toe-clipping. These are the tracks of an adult female, Number 855, with toe-ends 1L and 3R missing, as seen on soft powdery snow.

hindfoot and the third toe-end on the right hindfoot had been removed.

It was possible for one person to successfully mark a hare by toe-clipping, while the hare was held securely in a muslin sack that covered all but the hindfeet. However, Dell (1957) found that toe-clipping is best accomplished by two persons, one to hold the hare and the other to remove the toe-ends.

### Pathological and Parasitological Examinations

Procedures varied according to whether or not hares were necropsied at the Diagnostic Laboratory, in the field, or in the laboratory as part of an intensive parasitological examination.

Standardized procedures were used at the Diagnostic Laboratory in making necropsies. In each case, hares were drenched in an antiseptic solution, and their general condition and any superficial lesions were noted. The abdominal cavity was opened with an incision along the costal arch and down the midventral line. The various organs were examined in situ and then removed and examined individually. Samples of intestinal contents were cultured for determination of Salmonella sp. Samples of blood from the heart, and specimens of spleen, liver, and kidney were also cultured for determination of Pasteurella tularensis. The lungs and gastrointestinal tract were examined for parasites, but contents were not washed through sieves.

Hares necropsied in the field, and laboratory in connection with parasitological examinations were examined for gross lesions only. Many of the hares examined died following captivity of one to several weeks and their carcasses were held in cold storage prior to necropsy. Live hares were killed with a 5 cc injection of a sedative (0.2 mg pentobarbital sodium/cc ) and were immediately placed in a plastic bag containing a chloroform-saturated pad of cotton to facilitate collection of fleas. Dissection was accomplished on white trays and contents of the gastrointestinal tract were washed through soil sieves with 20, 42, and 65 meshes to the inch. Contents of the stomach, small intestine, and cecum - large intestine were screened separately. All parasites collected in the laboratory and in the field were preserved in 70 percent alcohol.

Samples of fleas and ticks collected during each trapping period in the spring and summer of 1961 were mounted permanently for identification. Fleas were bleached and cleared, according to procedures outlined by Hubbard (1947), preparatory to mounting in Canada balsam or Hoyer's mounting medium.

Blood smears were made from each of 35 hares handled during the trapping period of September 6-8, and from each of seven hares trapped at sites off the main study area in September and October 1961. The combined samples included six adults and 36 juveniles, and each age-group was divided equally between males and females.

Smears were prepared using blood from an ear-vein. The blood films were stained with Giemsa's stain following the method outlined by Lillie (1954).

Fecal samples of a small number of the hares also were examined for coccidia.

### Fecal-pellet Counts

The accumulated fecal pellets of hares were enumerated on plots used for sampling vegetation. These circular, mil-acre plots were each spaced one chain equidistant in a square grid consisting of 12 rows of 12 plots each. Sixty-nine of the 144 plots were located in the open area and the remaining 75 were situated within the second growth. Most of the plots were cleared of fecal pellets during the summer of 1961. Fecal pellets of hares were counted and the presence or absence of pellet groups of deer on each plot sampled also was noted. No records were kept of the occurrence of droppings of ground squirrels or of wood rats.

### Physical Obstructions and Canopy Closure

The percentage of each plot barred to hares by physical obstructions was estimated. This was done to provide a better description of the habitat, and to determine if usage by hares, as indicated by the abundance of fecal pellets, was influenced by the extent to which

each plot sampled was occupied by logging slash, and trees, shrubs or herbaceous vegetation of such density that hares were barred. In summarizing these data, plots with up to nine percent obstruction were considered "open" and the amount of obstruction present on the remainder was recorded in four categories, as shown in Table 13.

The percentage of canopy closure over each sampling plot within the second growth also was recorded in a similar way.

## ANALYSIS OF TRAPPING RESULTS

There was a marked difference in the total number of hares caught on the first, second, and third trap-nights. In all 247, 286, and 351 catches were recorded on each of the trap-nights (Table 6, and Figure 9). To test the significance of these observed differences, the catches on each trap-night were tabulated for each of the 21 trapping periods; dummy values (Li, 1957) were calculated for the third night of trapping periods in April and May.

The data were analyzed by analysis of variance and were found highly significant for both nights and periods. The differences between nights were then tested by the method of least significant difference. The results of these tests showed that the number of hares caught on the second and third, and the first and third trap-nights were significant at the five percent level; the latter was also significant at the one-percent level. Differences between number of hares caught on the first and second nights were nonsignificant at the five-percent level.

### Recovery of Tagged Hares

Recovery data are summarized in Table 7. A comparatively large number of hares were tagged during the first three months of the study and most of this total (86.7%) were recaptured one or more



Table 6. Snowshoe hares handled on the main study area from October 8, 1960 to March 19, 1962.

Trapping Period	Date	Hares Caught (Including Recaptures)				Hares Caught (Excluding Recaptures)		
		First Trap-night	Second Trap-night	Third Trap-night	Total	Hares Caught One or More Times	Hares Caught Two or Three Times	Hares Caught for the First Time
1	Oct. 8-10, 60	9	8	3	20	13	5	13
2	Oct. 22-24	14	7	24	45	30	11	20
3	Nov. 19-21	11	24	25	60	39	16	17
4	Dec. 20-22	0	3	4	7	7	0	4
5	Dec. 28-30	6	2	14	22	19	3	7
6	Jan. 21-23, 61	11	9	14	34	17	12	4
7	Feb. 25-27	11	5	8	24	16	6	2
8	Mar. 21-23	12	19	18	49	24	17	3
9	Apr. 22-23	13	14	--	27	18	9	3
10	May 19-20	10	14	--	24	15	8	1
11	Jun. 13-15	4	6	15	25	21	4	7
12	Jul. 11-13	12	16	16	44	42	2	26
13	Aug. 8-10	33	25	30	88	62	19	33
14	Sept. 6-8	16	19	18	53	41	10	20
15	Sept. 27-29	9	9	13	31	23	8	8
16	Oct. 24-26	20	19	22	61	40	15	18
17	Nov. 19-22	15	23	11	49	31	13	7
18	Dec. 19-21	7	20	21	48	33	11	2
19	Jan. 13-15, 62	9	8	21	38	26	9 <sup>1</sup>	4 <sup>4</sup>
20	Feb. 10-15	18	20	25	102 <sup>3</sup>	37 <sup>2</sup>	26 <sup>1</sup>	5 <sup>4</sup>
21	Mar. 17-19	7	16	15	38	25	10	3
Total		247	286	317	889	579 <sup>5</sup>	214	207

<sup>1</sup> Twenty-six hares were handled two to six times--20 of which were handled two or three times during the first three trap-nights.

<sup>2</sup> Thirty-seven hares were handled one or more times during the six trap-nights--30 of which were handled one or more times during the first three trap-nights.

<sup>3</sup> In all, 102 catches were recorded during the six trap-nights; 63 catches during the first three trap-nights, and 39 catches during the last three trap-nights.

<sup>4</sup> Five hares were tagged during the six trap-nights--two of which were tagged during the first three trap-nights.

<sup>5</sup> Total includes three tagged hares that escaped during handling; one each in January and May, and an unidentified tagged hare that escaped in September 1961, and one hare that was released untagged in January 1962.

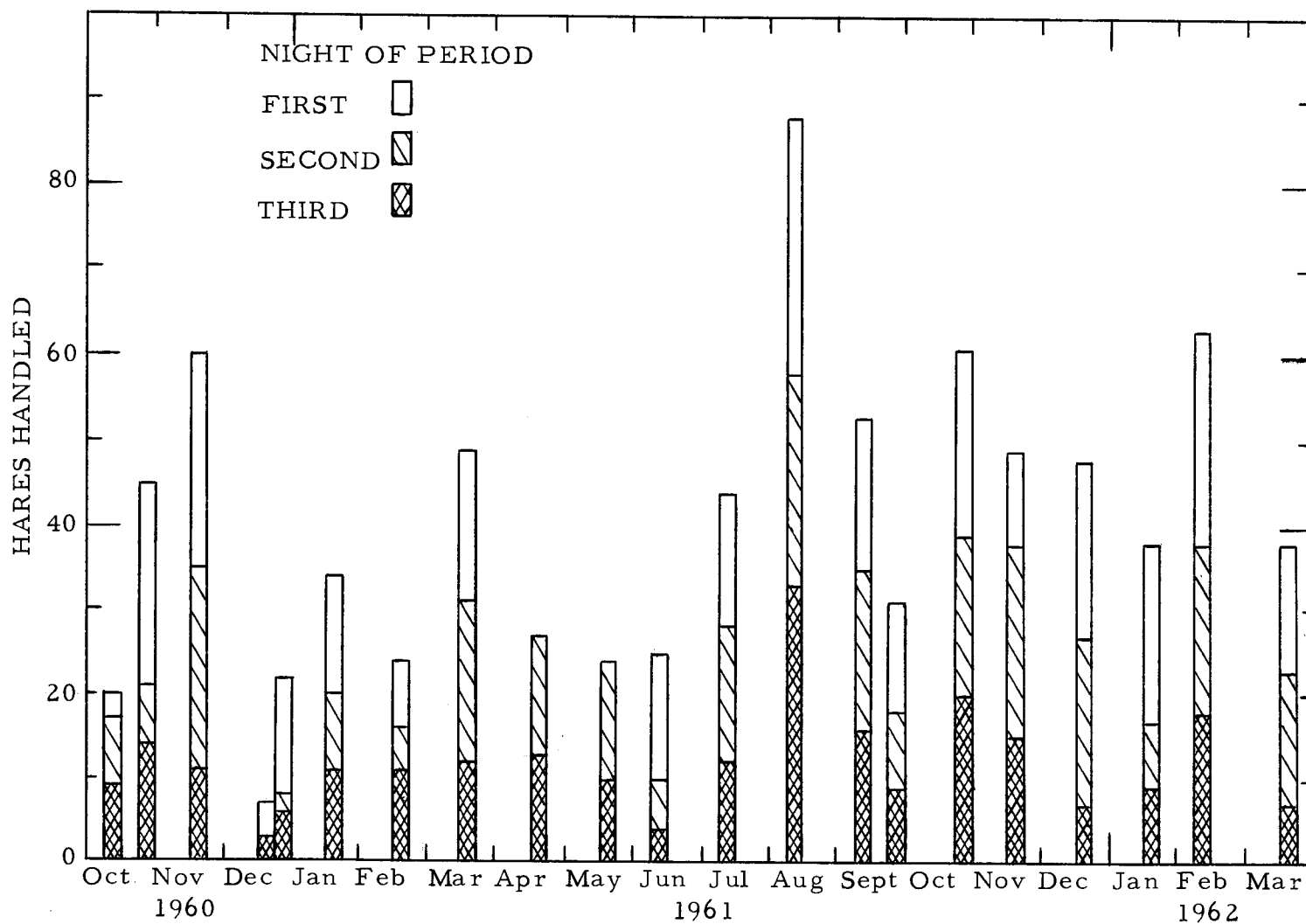


Figure 9. Hares handled in each trapping period, by trap-nights. Since some hares were caught two or three times during a trapping period, individuals handled in each period were fewer than the number of catches.

times. The continued recapture of a small proportion of these hares is indicated in Figure 10. Returns also were comparable for hares tagged and released from January through June 1961. Two factors account for the high returns from hares tagged during the fall and winter of 1960-61: The hares tagged were adults and older juveniles (Table 24), animals less susceptible to predation and other mortality factors, and these hares were potentially recoverable for the longest time.

The first six months of 1961 were marked by small additions to the numbers of individuals tagged on the study area (Figure 11). Most of the hares tagged during this period were adults or subadults; only five juveniles born in 1961 had been tagged by the end of June. All but three of the 20 hares tagged during the first six months of 1961 were recovered subsequently.

Presumably the adult hares that were tagged included hares which had been present on the study area, but which had not been caught since the beginning of trapping and tagging in October 1960. They may also have included hares which had immigrated to the area, particularly, since 10 tagged hares were known to have died in traps or soon after release from traps, during this period. Both contingencies seem equally probable. For example, Adams (1959) reported adult hares were present on his island-study area in northwestern Montana for up to six and one-half months before being taken.

Table 7. Frequency of recapture of hares tagged and released from October 1960 to March 1962.

Date Tagged	Hares Tagged and Released	Times Recaught							Recaught One of More Times	Trapping Periods Remaining
		0	1-2	3-4	5-9	10-14	15-19	≥ 20		
Oct. -Dec., 60	60	8	14	12	16	5	1	4	52	16
Jan. -Mar., 61	9	1	0	2	1	4	1	0	8	13
Apr. -Jun.	11	2	4	1	3	1	0	0	9	10
Jul. -Sept.	83	42	17	13	8	2	1	0	41	6
Oct. -Dec.	27	12	5	2	5	3	0	0	15	3
Jan. -Mar., 62	12	10	2	0	0	0	0	0	2	0
Total	202	75	42	30	33	15	3	4	127	--

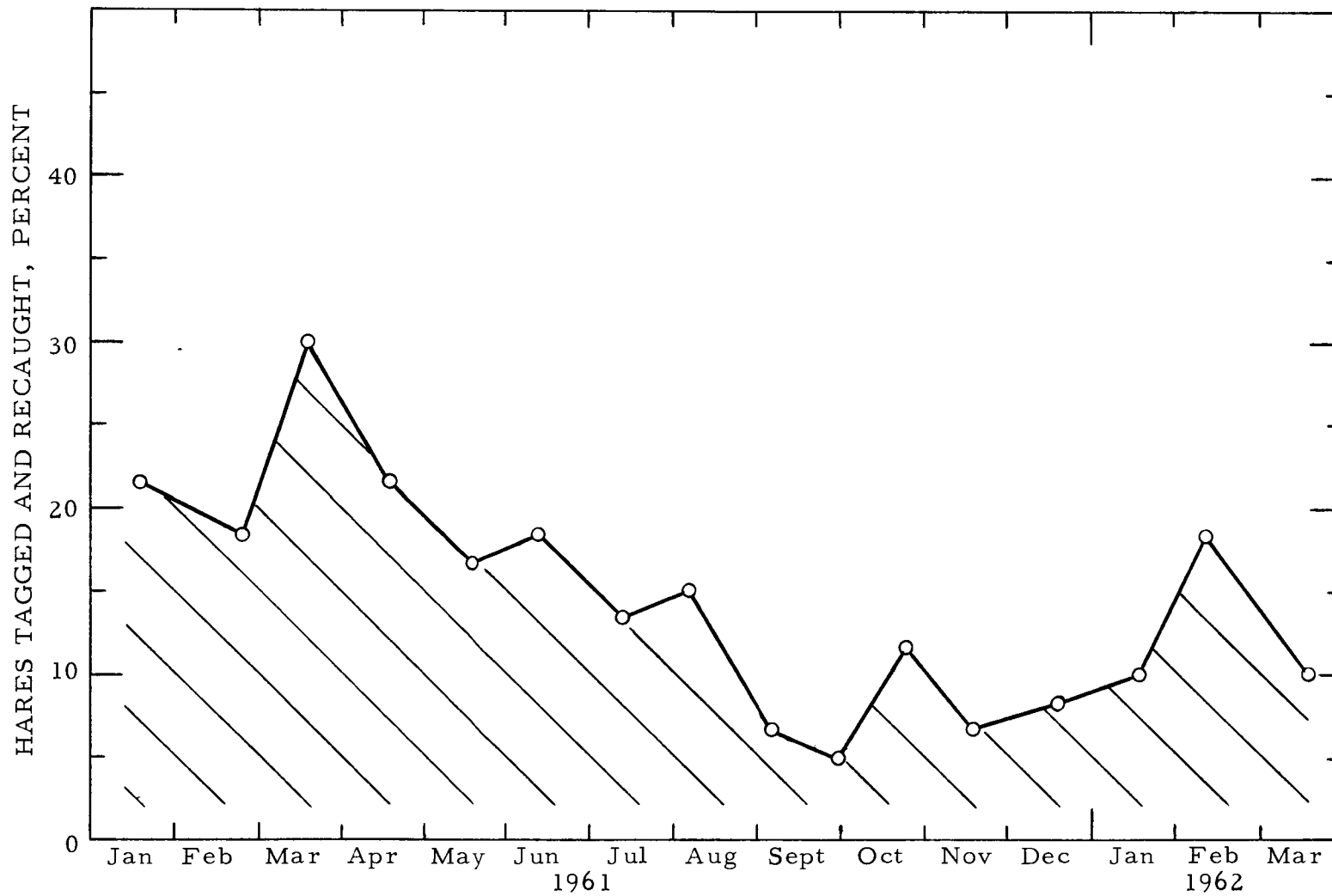


Figure 10. Percentage of hares tagged during October-December 1960 and recaptured in each subsequent trapping period.

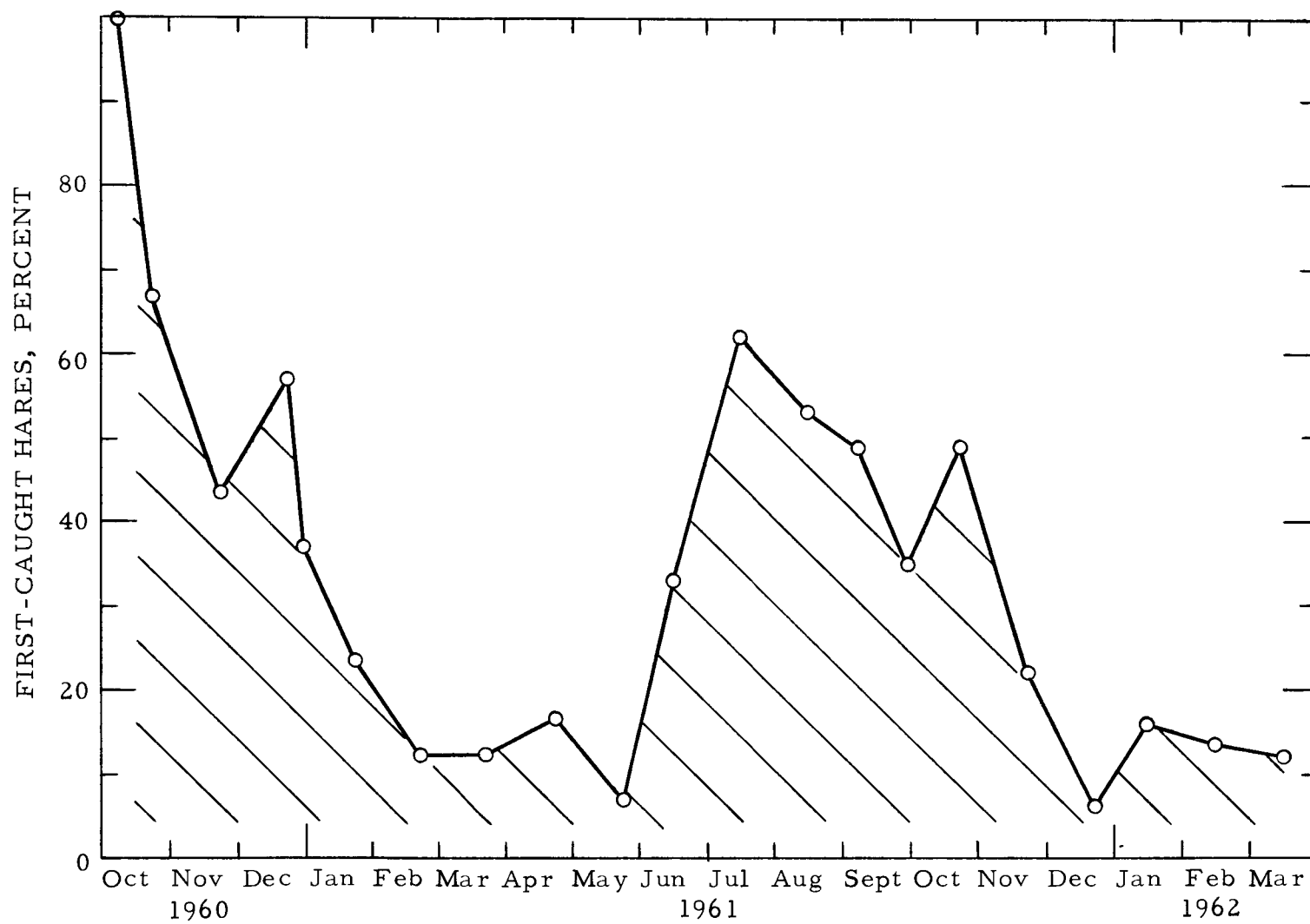


Figure 11. Percentage of hares caught for the first time in each trapping period.

July, August, and September marked the mass influx of juveniles born in the 1961-breeding season. Eighty-seven hares were caught for the first time during this quarter and all but two were juveniles; 83 of these were tagged and released, but half (50.6%) were not recovered (Figures 12, and 31). It is assumed that a high rate of mortality, especially among the immature hares, and dispersal off the study area were the main reasons for the low recovery. However, there was less opportunity for recovery of hares tagged during this quarter as the study was concluded in March 1962.

Use of the larger trapping grid was begun in October 1961 and it is probable that this grid included hares, particularly juveniles, whose range had not extended onto the smaller trapping area. Twenty-two of the 27 hares tagged from October through December 1961 were juveniles. Returns were comparatively low.

Twelve hares were tagged during the final three months of the study, from January through March 1962. But because the study was terminated in March, there was little opportunity for recovery of tagged hares and the incomplete returns are not meaningful.

In summary, more than one-third (37.1%) of all hares tagged and released during the 18 months of the study were unaccounted for; the remainder were recaptured one or more times (Table 7). About half (52.0%) were recaptured from one to nine times. Only 22 (10.9%) were recaptured ten or more times.

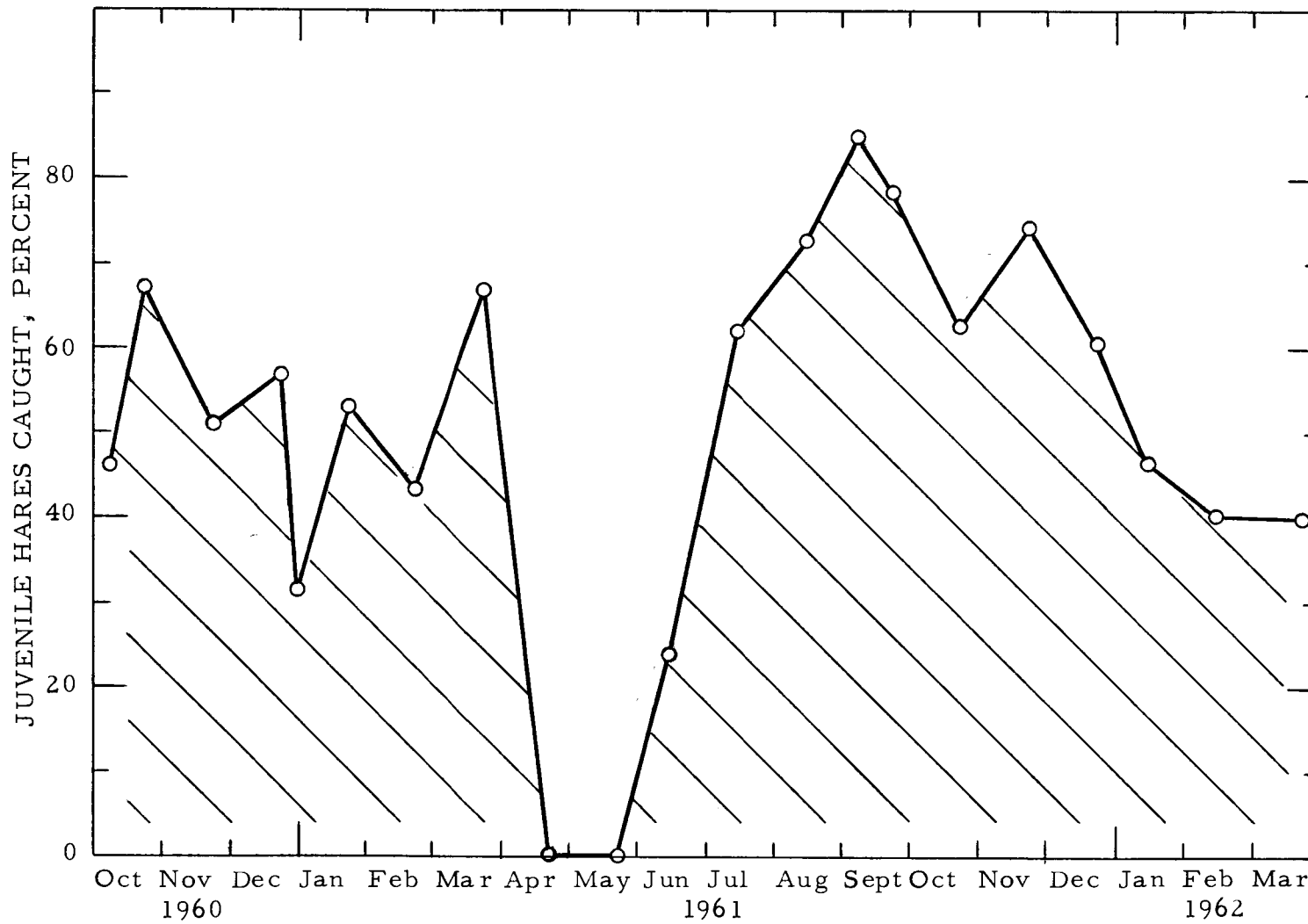


Figure 12. Percentage of juvenile hares caught in each trapping period.



### Trapping Success

Examination of factors that affected the efficiency with which hares were taken, and the behavioral characteristics of hares that influenced trapping success are pertinent, because many of the findings of this study are based on analyses of trapped samples of the population. For example, the trap-revealed range of hares was determined by the relationship of the population of hares to the grid of traps, etc.

Trapping success is influenced by daily and seasonal changes in the weather, seasonal changes in availability of food and bait acceptance (Fitch, 1954), behavioral differences between sexes--particularly, the differing behavior of adults during the reproductive period--and among different aged hares, and the presence of avian or mammalian predators. Moreover, catching of other animals, including other hares, may influence the response of individual hares to such traps. Other factors also may influence the reaction of hares to traps, such as their size, ease of entrance, covering, and location with respect to protective cover. Trapping success is adversely affected if traps are not in good working order, if bait (hay) becomes lodged under the treadle of a trap, or if snow covers the entrance of a trap.

Trapping success, based on catches of hares each trapping

period divided by the effective trapping nights<sup>5</sup> in each period, is illustrated in Figure 13. Trapping success was not correlated closely with the size of the population. Comparison of trapping success with the estimated population each trapping period, as determined by the calendar-graph and mark and recapture methods, shows little correlation. Trapping success was high in August when the population was at its peak, but comparable success was realized in April 1961 and in February 1962, at comparative lows in the annual-population cycle. In the discussion of age composition and sex ratios, it was noted that adult males were not present in expected proportions in the trapped samples during the summer. This is an indication that behavioral differences between males and females influenced their susceptibility to capture.

There were no unusual conditions existent during the trapping period in December 1960 that might explain the failure to catch a single hare during the first night that traps were set and to catch only seven hares in the remaining trapping nights. The weather was fair and clear, with moderate temperatures for the period (Table 37, Appendix). Trapping success improved a week later during a

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<sup>5</sup>Effective trap-nights are defined as the net trap-nights for taking hares. That is, the number of traps times days set, corrected by deducting traps sprung, malfunctioned, closed by snow, or occupied by other animals.

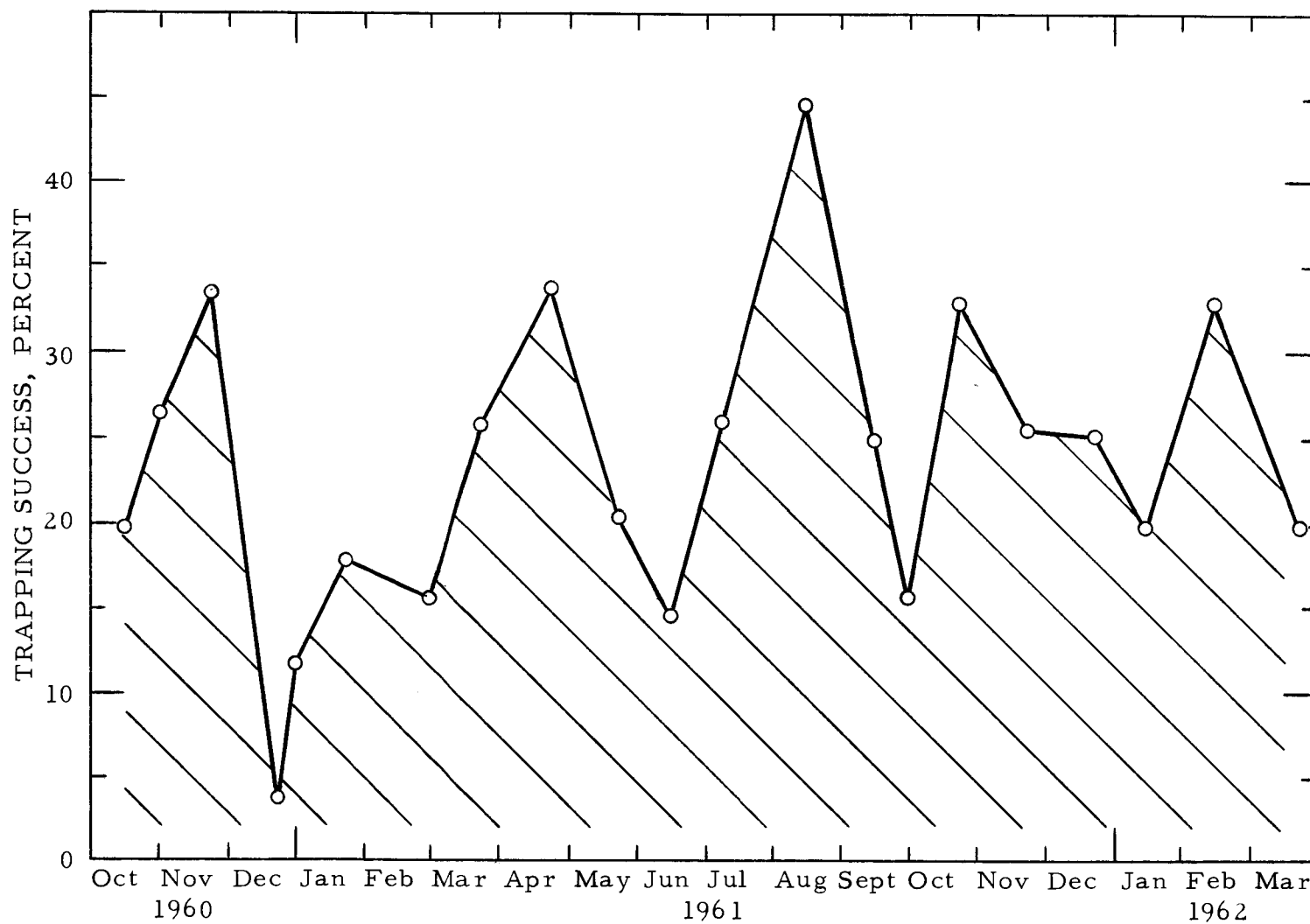


Figure 13. Trapping success, based on the catches of hares each trapping period divided by the number of effective trapping nights in each period.

continuing period of fair weather, but remained below average.

A low point in trapping success was recorded in June, coincident with a low in the population of adult hares. But trapping success increased rapidly with the influx of juveniles of both sexes that were readily taken in traps. The addition of a second trap to each of 10 stations within the second growth, during August and September, also contributed to the trapping success at that season. The decline in success registered during the second trapping period in September may have been caused by the shortened interval between periods of trapping. But the increase in the following month's catch likely resulted from the expansion of the trapping grid to include the range of many hares that had not been previously exposed to traps.

In summary, the live-trapping procedure was comparatively efficient, but trapping success was highly variable. It ranged from 3.6 percent in December 1960 to 44.4 percent in August 1961. Mean success was 22.3 percent, or on the average it required about five trap-nights to take one hare. Deducting trap-nights lost because of malfunctioning of traps, interference by other animals, and closing of traps by snow, trapping success averaged 23.6 percent.

Trapping success in the open area as compared with the second growth (small grid). The number of catches at each trap-station is summarized in Table 8 for the first 15 trapping periods, from October 1960 through September 1961. During this 12-month

period, traps were spaced one and one-half chains apart, and were set 43 nights. Each trapping period was for three days, with exception of April and May 1961, when the traps were set for only two nights each month.

Trapping data were analyzed in this manner to determine whether or not some stations were located better and consequently more effective than others; to permit comparison of the catches of hares in the open area with catches in the second growth; and to gain insight into the distribution and behavior of the population.

Table 8 shows that nearly four times as many catches were made in the second growth as in the open area (433 to 120). But the ratio of catches per station in the two cover types was on the order of 3 to 1, since 36 stations were located within, or on the edge of the second growth and only 28 stations were located in the open area. Also, two traps were set at each of 10 stations within the second growth for the three trapping periods in August and September 1961.

There was a tendency for a hare to be recaught at the same station a second or third time during a trapping period, but a different hare or hares would frequently be taken at the station during the next trapping period. For example, juvenile male No. 907 was caught on seven out of nine trap-nights during the three trapping periods in January, February, and March 1961, at Station C-7, on the edge of the second growth. Of the 120 catches recorded in the open area, 105

individual hares (sum of individuals caught each trapping period) were represented. In the second growth, 280 hares (sum of individuals caught each trapping period) were included in the total of 453 catches, indicating that many hares were captured repeatedly.

Thirteen hares, representing 24 catches, were taken at Station D-8 within the second growth; the highest number of catches at a single station during the 15 trapping periods.

Of the 28 stations located in the open area, 11 had taken none or only one hare from October 1960 through June 1961, and prior to the influx of hares born in 1961. There was an indication that trapping success was lowest on Trap-line A, the trapline farthest from the second growth. Only six catches were made on Line A from October 1960 through May 1961, and no hares were caught at Stations A-1 and A-8 during this period. No comparable differences, with regard to location of stations in the grid, were noted within the second growth.

Within each cover type, variation in the number of individual hares caught at each station was comparatively low (Table 8). Aside from fewer catches at stations in the open area located farthest from the second growth, no important influence was accounted for by the position of stations. Two stations located within the second growth, F-7 and H-7, took no hares from October 1960 through June 1961, apparently as a result of chance. But 10 juvenile hares were caught during the next four months, from July through October, at Station F-7.

Table 8. Trapping success in the open area as compared to the second growth for the 15 trapping periods from October 1960 to September 1961. (Traps were spaced one and one-half chains apart--area of grid was 14.4 acres.)

Location and Number of Stations	Stations and Frequency of Catches						Sum of Catches	Sum of Hares Caught at Each Station By Trapping Periods <sup>1</sup>
	0	1-4	5-9	10-14	15-19	> 20 (Catches)		
Open area (28 stations)	2	18	5	3	0	0	120	105
Second growth (36 stations)	<u>0</u>	<u>1</u>	<u>10</u>	<u>16</u>	<u>6</u>	<u>3</u>	<u>433</u>	<u>280</u>
Total	2	19	15	19	6	3	553	385

<sup>1</sup>

Hares caught more than one time in a period were counted only once.

Table 9. Trapping success in the open area as compared to the second growth for the six trapping periods from October 1961 to March 1962. (Traps were spaced three chains apart--area of grid was 57.6 acres.)

Location and Number of Stations	Stations and Frequency of Catches						Sum of Catches	Sum of Hares Caught at Each Station By Trapping Periods <sup>1</sup>
	0	1-4	5-9	10-14	15-19	> 20 (Catches)		
Open area (32 stations)	7	16	8	1	0	0	86	53
Second growth (32 stations)	<u>0</u>	<u>8</u>	<u>14</u>	<u>8</u>	<u>2</u>	<u>0</u>	<u>250</u>	<u>119</u>
Total	7	24	22	9	2	0	336	172

<sup>1</sup>

Hares caught more than one time in a period were counted only once.

Trapping success in the open area as compared with the second growth (large grid). Data are summarized for the six trapping periods from October 1961 through March 1962, in Table 9. During this six-month period, traps were spaced three chains apart. Each monthly trapping period was for three trap-nights, with one exception. In February, the 32 traps in the open area were set for an additional three nights, or a total of six consecutive nights.

Results were comparable to those obtained on the smaller grid for the first 12 months of the study. That is, nearly three times as many catches were recorded in the second growth as in the open area and the number of individual hares taken in both cover types also were in similar proportion to those observed on the smaller grid.

There appeared to be a direct relationship between the number of catches and the distance from the second growth; Lines A and B, farthest from the second growth, had the lowest number of catches. No hares were taken during the six trapping periods (traps were set 21 nights) at 6 of the 16 stations on these lines. No similar difference was found in trapping success at stations within the second growth, with respect to distance from the edge of the open area.

One to four hares were caught at most stations in the open area, and fewer hares were repeatedly recaptured than in the second growth. Eleven catches were recorded--out of a possible 21-- at only one of the 32 stations located on this area. This exceptional



record was of an adult male, No. 929, that was recaught on each of six successive nights at the same station (D-4), during February 1962.

Within the second growth, there were about twice as many catches as individual hares caught. This reflects the tendency for individuals to be taken repeatedly at the same stations. For example, a juvenile male, No. 349, (tagged in November 1961) was recaught 12 times at the same station, on each trap-night of the remaining trapping periods.

#### Effects of Weather on Movements of Hares and Trapping Success

In analyzing the effects of this important influence, the limitations of the observation need to be considered. For example, the time and amount of activity of hares were not studied, although the comparative amounts of activity in the open area and within the second growth were inferred from tracks in snow. Certainly these signs indicated the distribution of activity between the two areas, but few observations were made relative to the time that this activity occurred. Furthermore, it is not intended to imply that the amount of activity, i. e. , movement, was directly related to trapping success.

Observations of weather conditions were made during the daytime, with the exception of temperature. The weather conditions during the nighttime--the principal period of hare's activity--that

may have influenced movements of hares the most were not observed. (A recent study by Keith [1964] of the daily activity pattern of snowshoe hares in north-central Alberta showed that nearly 60 percent of the recorded movement occurred between 8:30 p. m. and 1:30 a. m. ) Also, the time and duration of precipitation each trap-night were not recorded. These may have been important factors, especially if precipitation were in the form of snow, since a snow in the early hours of darkness might cover traps and interfere with trapping success, particularly in the open area; whereas, snow falling in the early morning hours may not have interfered much with movements of hares or barred their entry into exposed traps.

The weather conditions immediately preceeding a trapping period also may have had an important influence on the activity of hares and trapping success, but daily observations, excepting temperature, were not accomplished prior to most trapping periods.

Effects of weather on trapping success. Pertinent weather data are summarized for each trapping period in Table 37 (Appendix). To facilitate comparison of weather conditions with results of trapping, this table also lists the number of hares caught each trap-night and trapping success for each trapping period.

The average trapping success each period was not influenced much by extreme changes in the weather. Trapping success was generally better during stormy periods than during fair weather. The

two periods of lowest trapping success both occurred during periods of uninterrupted fair weather, in December 1960. However, the average trapping success also was good during the summer when fair weather prevailed and when trap-nights were often clear and warm.

The number of catches each trap-night fluctuated widely and often varied during periods of relatively unchanging weather. Changes in the cloud cover may have accounted for some of the variations in catches among trap-nights within a trapping period.

Trapping success in January and February 1961 were comparable, despite widely different weather conditions. During the trapping period in January the number of catches was about the same each night. The ground was bare, and for the first two trap-nights the weather was fair, but the third trapping night was overcast with a trace of rain. The weather conditions were drastically altered during February, and the trapping period had been preceded by extremely rainy weather. Weather during the trapping period was continually overcast, cold and stormy, and the ground was covered with 10-12 inches of snow. Nevertheless, trapping success was comparable to January, although the number of catches was smaller. Stormy weather continued through the trapping period in March and the ground was covered with snow, but trapping success and the number of hares caught increased over the previous two months.

Trapping success was good on both trap-nights in April,

despite 6-8 inches of new snow on the first night of trapping. The number of catches was similar on both nights. In May, trapping success was comparable on each of the trap-nights; while the ground was bare, and the weather throughout the trapping period was continually overcast with intermittent light rain.

Each trapping period after September 1961 was characterized by comparatively stormy weather. Comparison of trapping success with weather conditions demonstrates that good results were generally achieved during these periods of inclement weather. For example, snow covered the ground when trapping began in November, and nearly four inches of rainfall were recorded in 24 hours on the third trap-night. Catches were good each night, but lowest on the third night--a very wet, cold, windy, and foggy night--during which the activity of the hares seems to have been much reduced. Still heavier total precipitation, mostly of rain with occasional snow, occurred during the following trapping period in December. Almost two inches of precipitation were recorded each day of this period that began with snow-covered ground. The results showed a small catch the first trap-night, but large catches on each of the remaining two nights.

In January 1962, the ground was covered with snow throughout the trapping period and two or more inches of snow fell on both the first and third trap-nights. However, the number of catches was nearly the same on the first and second nights, but more than twice as many

catches were recorded on the third trap-night.

The pattern of catches during the last trapping period, in March 1962--a period of comparatively fair weather--was comparable to that reported in December 1961. That is, a small number of catches on the first night and a much larger catch on both remaining nights.

On the basis of these observations, trapping success apparently was not influenced much by the amount of precipitation, whether of rain or snow, or by the lack of precipitation. Nor was there any evidence that the daily range of temperature influenced trapping success. The presence of various amounts of snow on the ground also did not seem to affect the total catch much.

Effects of weather on the activity of hares in winter. The number and distribution of tracks made by hares in snow gave an indication of their activity, and the relative amounts of activity in the two types of cover. The other indices of activity, i. e., evidence of feeding, amount and distribution of fecal pellets, trapping success, and distribution of catches, all were related indirectly to behavior of the hares. But the failure to enter traps limits the usefulness of trapping data to interpret hares' activity.

Observations were recorded whenever tracking conditions were favorable, but most records of activity were made during trapping periods when the ground was covered with snow.

In mid-November 1960, the ground was covered with six inches

of new snow and tracking conditions were good. No tracks of hares were noted on the grid in the open area, but tracks were seen frequently within the second growth. Thus hares were active during and soon after the snowfall, within the protection afforded by the coniferous reproduction, but apparently did not travel in the open habitat.

Most of the snow had melted before the trapping period a week later, but five inches of snow fell on the third trap-night and provided good tracking conditions. Very few tracks of hares were seen in the open area, but there was an abundance of tracks throughout the reproduction. Most of the tracks seen were made after the snowfall and apparently during the early morning hours. However, nearly all of the hares caught had entered traps before the snowfall or before much snow had accumulated on the ground, and only six had entered traps during the snowfall, as their tracks were nearly filled in with snow.

Poor to good tracking conditions existed on each day after traps were set during the trapping period in February 1961. The ground was covered by snows on both days before trapping began and approximately six inches of snow fell during the first trap-night. Also, a light snowfall occurred during the second trap-night, but no tracks of hares were seen in the open area on the first and second days after traps were set and few tracks were seen within the second growth on the day after traps were set. However, the amount of snowfall the first trap-night would have covered most of the exposed tracks.

The week following the trapping period in February was marked by stormy weather, intermittent snowfall, and 10-12 inches of snow on the ground. Thus, any old tracks in exposed places had been obliterated by the intermittent snows, and there were few fresh tracks in the new snow on March 3. No tracks were seen in the open area on March 10, and tracks were distributed sparsely within the second growth. It also was noted that hares moved in the shelter of conifers, rather than in openings.

Twelve inches of snow fell during the first trap-night in April. Although there was no additional snowfall during the second trap-night, there was no sign of movement of hares in the open area during either night. It is likely that during the second trap-night, when the temperature was below freezing, hares may have moved on the crusted snow without leaving tracks.

Three inches of fresh snow was on the ground, tracking conditions were favorable, and tracks had accumulated for about 24-hours at the start of the trapping period in November 1961. Tracks of several hares were seen along each of the trap lines in the open area, but the activity was much greater within the second growth, as indicated by the abundance of tracks. Overall, there seems to have been much more activity than indicated during snowy nights.

During the trapping period in December 1961, tracks of hares were absent in the open area and presumably there had been little or no

movement in this habitat, or snowfall had covered tracks. Evidence of only a moderate amount of movement was seen within the second growth. There had been eight inches of fresh snow on the ground and light snowfall changing to rain on the day traps were set. The snow evidently had fallen during the night and early morning hours and apparently caused the hares to remain inactive. Hard rains on each of the trapping nights melted snow in the open area, but much activity was noted within the second growth after the first trap-night.

Light snowfall occurred on the first and third trap-nights during the trapping period in January 1962 and tracking conditions were optimal. But practically no activity of hares was indicated in the open area during the first two trap-nights, and no hares were caught in this habitat during the trapping period. After the first trap-night, tracks were noted across Trap-lines A and B. An abundance of tracks were seen within the second growth, presumably indicative of normal activity, which had occurred mainly after the snowfall in the early morning hours. Several hares had traveled across the open area during the third trap-night. The tracks of hares were seen next to or within 20-30 feet of six traps in this cover type. Several instances also were noted of hares having moved in the vicinity of open traps within the second growth.

Tracks of hares were absent in the open area and few tracks were encountered within the second growth during the trapping period in March 1962. The 12-18 inches of granular snow apparently crusted



over each night and there was little movement during daytime when the snow was not frozen; the temperature on each trap-night was below freezing.

Tracking of hares showed that they frequently traveled in the open area without entering traps. But a paucity of tracks also may be misleading, if snow becomes crusted over at night. Thus, while the distribution of catches in both cover types proved a good measure of the influence of weather on the movements of hares, failure to catch hares may not indicate their absence. For example, Fowle and Edwards (1954) observed that an animal may pass a trap without being attracted to it by reason of failure to sense the bait or because other factors are holding its attention at the time.

These observations show that the relative amount of activity in both types of cover was influenced by snowfall and possibly to a lesser extent by the presence of snow on the ground. Hares apparently were inactive during heavy snowfalls and their movements during and immediately after snowstorms were confined to the second growth; travel in the open virtually ceased during and for one or more nights following heavy snowfalls. Failure to enter traps during these periods also was evidenced. It is not known whether this was normal behavior, or atypical behavior elicited by the increased availability of browse following heavy snowfall. It is also uncertain whether or not hares preferred the second growth and avoided the open area, because of the

greater protection afforded by the reproduction.

Severaid (1959) also observed that snow, plus cold temperature, caused hares to be quite inactive and a noticeable reduction in consumption of food followed. Dodds (1960) found that hares were considerably less active during periods of wet weather, and he observed that rain or snow will decrease success of snaring hares at any time of the year. He further noted that the activity of hares is reduced with increased snow cover. Bider (1961) summarized the winter movements of hares in Quebec as follows: "The occurrence of wind, the darkness of the night, the precipitation and the accumulation of snow determine when and how the area is utilized; but where the hares will be is determined specifically by food and cover."

#### Other Factors That Influenced Trapping Success

The welded-wire traps operated well and rarely malfunctioned, although a few traps failed to release because of improperly adjusted trigger mechanisms. But the tripping of traps, mostly by small mammals, was a continual problem (Table 10). Most of the empty traps that had been tripped likely were sprung by chipmunks or pine squirrels, as evidenced by the tooth-marks and fecal pellets left by these rodents on the apple-baits. Both species, however, were in hibernation for much of the winter as were the California ground squirrels. Only two pine squirrels were caught in the larger welded

Table 10. Trapping results summarized for each period of three months from October 1960 to March 1962.

Date	Trap-nights	Traps Sprung or Closed By Snow	Other Animals <sup>2</sup> Caught	Effective Trap-nights	Catches of Hares	Average Trapping Success (Percent)
Oct. -Dec. 60	864	22	8	834	154	18.4
Jan. -Mar. 61	572	33(30)	2	537	107	19.9
Apr. -Jun.	448	61(43)	18(16)	369	76	20.5
Jul. -Sept.	852	37	40(32)	777	216	27.7
Oct. -Dec.	575	7	1	567	158	27.8
Jan. -Mar. 62	672	1	1(1)	670	178	26.5
All	3983	161(73)	70(49)	3754	889	23.6

<sup>1</sup> Traps closed by snow are indicated by parentheses.

<sup>2</sup> Ground squirrels are indicated by parentheses.

wire traps. Although chipmunks were far more abundant, none was taken in this type of trap, since they were able to escape through openings in the traps. The incidence of sprung-traps was correlated closely with the months these two sciurids were active. For example, approximately 10 traps were tripped each trapping period from May through November, mostly at stations within the second growth, but only one or no traps were found sprung in each of the trapped periods from December through April, in both years. A few hares were known to have entered traps that were set improperly and to have escaped capture, because the trap-doors caught against the sides of the traps, or were caught by twigs. In one instance, a hare escaped through the back of a trap that was unfastened.

Small mammals continually visited traps, but apparently this did not cause hares to avoid traps. Ants and other insects attacked apple-baits during the summer, but without noticeable interference to trapping of hares--baits were consumed only partially in most instances during each three-day period of trapping. In all cases, however, baits were replaced after each catch and at the start of each trapping period.

Thirteen wood rats were caught, and all were trapped within the second growth; seven were released and the others were removed from the area. Wood rats might have posed a problem comparable to that of the ground squirrels, had they been abundant, since both entered traps readily. (The traps baited with apple were likely more attractive

to these mammals than traps baited with hay. But Adams [1959] noted that deer and long-tailed voles were attracted to traps baited with hay and occasionally tripped the traps. There was no indication, however, that deer disturbed traps baited with either hay or apple, on the study area in western Oregon.)

A spotted skunk was caught and released, within the second growth, in October 1960. In September 1961, two spotted skunks were caught and released, but two more--presumably the same individuals--were caught on the third night of this trapping period and were removed from the area.

The most unusual catch recorded was that of an immature blue grouse, Dendragapus obscurus, that was caught in a large welded-wire trap, in the open area, in August. (Two other blue grouse were caught in August, in the same type of traps, at a location near the main study area. None of the three birds was injured.)

California ground squirrels were very abundant in the open area and all too readily entered traps from April through September; one was also caught in mid-March. Three of five ground squirrels caught during cold weather, in April, did not survive confinement overnight in the covered traps. Ground squirrels interfered with trapping of hares in the spring and summer by entering traps in the open area during the day--all but three of the 49 ground squirrels that were trapped were caught at stations in the open area. To minimize this nuisance, most

of the trapped ground squirrels were removed from the area. Had they been allowed to remain, the distribution of hares caught in the two cover types would have been affected further. But their having occupied traps apparently did not cause hares to avoid the same traps.

Effects of covering traps. Traps were covered to provide protection to trapped hares, especially in winter (Figure 5). There was no evidence that hares avoided covered traps in preference to traps without covers, based on use of uncovered traps at locations near the main study area. Rather, it is possible that the coverings may have enhanced the attractiveness of the traps, as suggested by the discovery of a hare in a trap that had been hooked-open between trapping periods.

Baits. Traps had been baited with alfalfa hay from the beginning of the trapping activity and this bait seemed to attract hares effectively. However, traps used off the main study area were baited with apples, following the poor trapping success on the main study area during December 20-22, 1960, in an effort to find a better bait. The results of this trial were surprising, since five hares were caught on December 29, with only eight traps, each of which had been baited with a piece of apple. At the same time, only two hares were taken in the 64-traps set on the main study area, all of which were baited with hay. A half-apple was added to the hay with which each trap was baited, on the third night of trapping, and 14 hares were caught; twice the number taken in the previous two days of trapping.

Results obtained in the next trapping period, in January, when traps were baited alternately with apple or hay, clearly indicated a preference for the apple-baits. Only 5 of the 34 catches were in traps baited with hay, and all of the 11 hares trapped on the first night were caught on apple-baits.

Apples were used to bait all traps on the main study area thereafter and provided a very satisfactory bait for both juvenile and adult hares throughout the year. It is interesting to note, however, the differences in responses to baits--whether simply the result of chance or because of changes in seasonal bait-preferences is unknown. For example, in May, 17 traps that were set at a location north of the main study area had been baited alternately with alfalfa hay or apple. Six adult hares were caught in these traps and four of the six were taken in traps baited with hay and only two in apple-baited traps.

There were no problems attendant to the baiting of traps with hay, but it was bulky, inconvenient to carry, and required more time to bait each trap. Hay used in traps as bait occasionally slipped down and became matted under the treadles, preventing release of the trapdoors. Hay had to be removed from the traps at the end of each trapping period, because of frequent molding when left in the traps. Conversely, apples were easy to carry in the field, baiting of traps was accomplished quickly and easily, and it was unnecessary to remove unconsumed apples at the end of each trapping period.

Green and Evans (1940a) noted that the most satisfactory of various baits tested were small bundles of alfalfa, dampened with water and placed frozen in the traps. Adams (1959) tried several kinds of baits, including apples, carrots, parsnips, dandelions, Douglas-fir twigs, and alfalfa hay, and found that most attracted hares successfully. But he regularly used hay as a bait, since he found that it was effective at all seasons of the year, and was fairly selective in attracting only hares. Dodds (1960) described use of fresh birch twigs placed at the entrance of traps to attract hares. He also noted that good results were obtained simply by placing traps on well used paths in deep snow. Bider (1961) found that celery was an effective bait for trapping snowshoe hares in Quebec.

Comparison of single and double-door traps. It was difficult to make a meaningful comparison between the two larger sizes of traps used. The large double-door traps were set immediately after their placement at 25 stations around the perimeter of the grid and prior to the start of the second trapping period in October 1961, whereas the single-door traps had been in place for several weeks. Also, only one door was opened on the larger traps that were used after November. Proportionate numbers of hares were caught in both sizes of traps in October, but in November the number of catches in the smaller traps exceeded those caught in the larger traps by a ratio of 2:1. The larger traps were less rigid and some malfunctions occurred because of



careless setting. Nevertheless, both sizes of traps were effective in catching hares.

Comparison of two sizes of single-door traps. Ten of the small, single-door traps were placed at stations within the second growth for each of the three trapping periods in August and September, to increase the catch of young hares. This anticipated result was only realized in part, but an opportunity was afforded for comparing the efficacy of the two sizes of traps to take hares. Based on a sample of 90 trap-nights for each size of trap, twice as many hares were caught in the larger traps. Fifty-seven hares were caught in the 10 pairs of traps; 33 in the large traps and 14 in the small traps. The sex ratios and age composition of the catch was distributed uniformly between the two sizes of traps, except the sex ratios of juveniles was mostly males, in the small traps, and preponderantly females in the large traps. Two adult hares, a male and a female, were caught in small traps, although they could not turn around in the traps or sit in a normal position. Also, an adult hare injured her foot while struggling in a small trap. For these reasons, this size of trap is not recommended for trapping snow-shoe hares.

Disturbance of traps. Although access onto the area was restricted, a few traps were disturbed by man in both years. The area was opened to the public during the big-game hunting season in October, and for fishing from late April until the beginning of the fire season in

May. During the remainder of the year there was a limited amount of travel in the vicinity by fire-protection personnel, loggers, etc.

In October 1960, one welded-wire trap was stolen and a second moved, apparently by hunters. Two additional traps of the same type also were taken, following the trapping period in June. No other disturbances were noted and there were no indications that any hares had been taken or released from traps.

Effects of snows on trap-operations. Falling snow, or wind-blown snow interfered with the operation of traps that were set and occasionally barred entry of hares. For example, heavy snows during the trapping periods in February and April 1961 covered unprotected traps, and snow was blown into the entrances of traps at exposed stations in the open area and barred entry of hares. Forty-three traps were closed by a snowfall during the first trap-night in April. These estimates of trap-closure were partly arbitrary, since it was not known whether there was some activity by hares before these exposed traps were snowed-shut.

Traps located at stations within the second growth seldom were covered-up by snow, since most were located under conifers. In a few cases, overhanging branches were weighed down by snow and partially blocked the entrances of traps. Traps were cleared of snow each day, however, and usually were affected for only one night during a trapping period.

### Effects of Weather on the Distribution of Catches

The poor trapping success during both trapping periods in December 1960 occurred during a period of mild clear weather, and only one hare was caught in the open area out of a total of 31 catches (Table 37). Whatever the factors that may have influenced trapping success, it is apparent that hares did not enter traps in the open area as readily as within the second growth. Whether this resulted from reduced movement in the open area, because of the clear nights, is not known.

Fair weather also occurred throughout each of the five trapping periods from June through September and trapping success varied, but on each trap-night about the same small proportion of hares was caught at stations in the open area. The weather also was fair and clear on each of the trap-nights during the trapping period in March 1962, when not a single hare was caught at stations in the open area.

The distribution of catches between the two cover types during periods of fair weather with mostly clear nights suggests that the catching of hares in the open cover--and presumably their activity in this habitat--may be diminished on bright nights, especially in winter.

Catches of hares appeared to be greater in the open area on overcast nights and on rainy nights, but not during snowstorms and other very stormy weather. Trapping success in the open area was irregular

during stormy weather and the number of catches fluctuated widely. For example, during the trapping period in October 1960, trapping success was uniformly good each trap-night, but only two hares were caught in the open cover on the first two trap-nights--the first night was marked by heavy precipitation and the second by partial clearing and no precipitation. However, eight hares were caught in the open area on the third trap-night, which was overcast with a trace of precipitation. Also, during the trapping period in February 1961, five hares were taken in the open area on the first trap-night, but none in this habitat on the other two nights; all three nights were overcast, but the weather was milder on the first trap-night. In March, the weather was overcast on each trap-night, but the catch in the open area increased markedly following a warming trend that also melted the snow in this habitat. Thus, 13 of 37 catches on the second and third trap-nights were recorded in the open area, whereas only one of 12 hares caught on the first trap-night was captured in the open habitat. Weather conditions were similar during the trapping period in May and again more catches were made in the open area on the trap-night with milder weather. This same apparent relationship between mild overcast weather, and proportionately higher catches in the open area, is demonstrated by results in December 1961. Seven hares were caught in the open area on each of the second and third trap-nights, while none had been caught in this cover on the first trap-night. This period was

marked by extremely heavy precipitation, with hard rain on each trap-night; the absence of catches in the open on the first trap-night may have been the result of the heavier precipitation on that night and because the ground was covered by snow. The ground was bare in the open area on the second and third trap-nights.

The change in the trapping procedure in February 1962; i. e. , the closing of traps within the second growth following the regular three-day trapping period and the continuation of trapping for an additional three days in the open area, demonstrated the influence that traps set in the second growth had on the number of catches in the open habitat. About one-third of all catches were in the open area during each of the first three trap-nights, but an average of 13 hares were taken daily in the 32 traps set in the open area during each of the three added trapping nights. The weather was overcast and moderate, and intermittent showers occurred throughout the period; heavy precipitation during the fifth trap-night did not affect the catch.

One or more inches of snowfall were recorded on each of three trapping periods: Five inches of snow fell during the third trap-night in November 1960 and the number of catches in the open area dropped, on the second trap-night, from 12, or half of all catches, to 4 of 25 on the night with snowfall. In April 1961, eight inches of snow fell during the first trap-night and precipitation in the form of light rain mixed with snow occurred during the second trap-night; no hares were caught

in the open area during this trapping period. The trapping period in January 1962 was marked by continual heavy overcasts and below freezing temperatures, and two inches of snowfall on each of the first and third trap-nights. No hares were caught in the open area during this period.

In summary, the record of catches showed that during fair weather in winter few hares were caught in the open area, but that a small proportion of the catch each trap-night was taken in the open area during fair weather in summer. The catch in this habitat was irregularly higher when nights were overcast, but diminished during cold rainy nights with heavy precipitation and dropped close to zero during trap-nights of heavy snowfall.

Bider (1961) correlated movements of hares in winter with plant communities, nighttime temperature, wind, and light. He found that vegetative structure and weather play important roles in determining the range of hares, and that high wind, with or without snow, is the most restrictive of these physical factors. He also noted that wind and light are less important in regulation of movements in summer, since both are modified by foliation.

### Weight at First Capture

The age at which young hares were first caught is significant, since it gives an indication of their movements and behavior in response to traps. Presumably very young hares either did not enter traps, or their range was so limited that they seldom came into contact with them.

Of juveniles that were born in 1961 and later caught, half of the females and 55 percent of the juvenile males were caught for the first time during June, July, and August. Their weights at first capture are listed in Table 11. The distribution of these weights, of juveniles born in 1961 and caught in 1961 and 1962, also is shown in Figure 14.

There were no significant differences between the mean weight of juvenile males and females caught from June to August 1961, or between the mean weights of juveniles of each sex caught from September 1961 to March 1962, based on a t-test of the data at the five percent level.

Adams (1959) also found that the mean weights of the two sexes of juvenile hares, at time of first capture, were not significantly different. Their mean weight was 535 grams or 19.5 ounces. This corresponded to an age of 53 days.

The results on the study area in western Oregon were comparable, based on the initial weight of the 62 juveniles of both sexes caught in June, July, and August 1961. Their mean weight at first capture

was 20.6 ounces. This corresponds to an estimated age of about six weeks (Figure 21); the smallest hares caught may have been no more than three weeks of age. However, 56 hares born in 1961, but caught for the first time after August were much heavier and their mean weight at first capture was 32.4 ounces (Figure 14).

Table 11. Weight at first capture of juvenile hares born in 1961 and caught during June, July, and August 1961.

Weight (Ounces)	Females	Males	Total
0-3	0	0	0
4-7	0	0	0
8-11	3	5	8
12-15	8	10	19 <sup>1</sup>
16-19	2	0	2
20-23	2	5	7
24-27	3	10	13
28-31	7	2	9
32-35	1	0	1
36-39	1	2	3
40-43	0	0	0
44-47	0	0	0
Total	<u>27</u>	<u>34</u>	<u>62<sup>1</sup></u>

<sup>1</sup>One juvenile was not sexed in July, 1961.



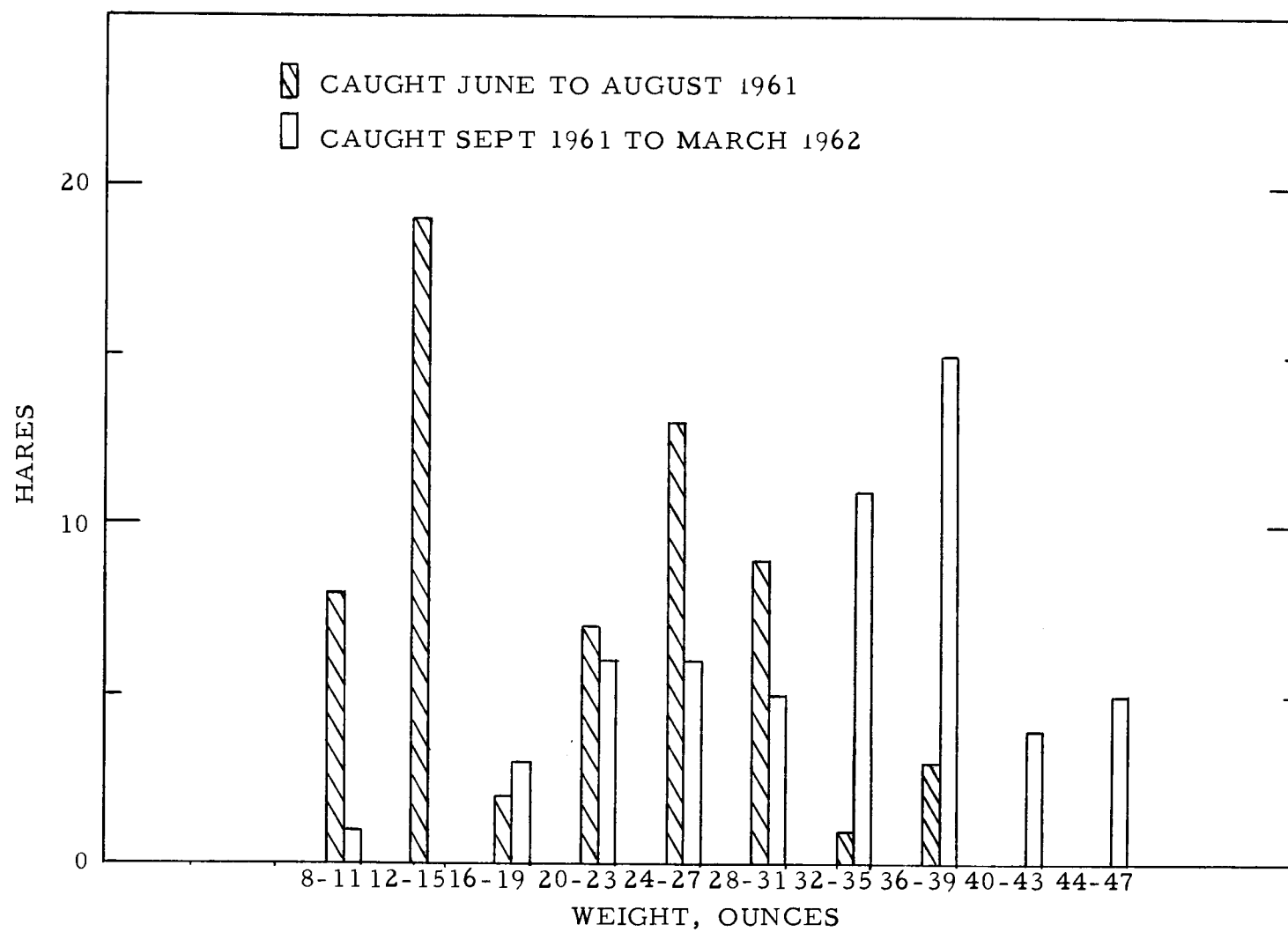


Figure 14. Distribution of weights at first capture of juvenile hares born in 1961 and caught in 1961-1962.

### Failure of Hares to Enter Traps

Tracking of hares in snow afforded observations of their response to traps that were baited and set. Hares were seen to have traveled close to traps without showing any apparent response to them; others moved around traps and to the entrances, but failed to enter. Whether this passive behavior, in the first instance, would be considered "trap avoidance", or simply failure to smell or to be attracted by the bait, or to see the traps, is uncertain. However, in the case of hares that moved to the entrances of traps, but did not enter, their behavior probably represents an active aversion to entering traps, i. e., trap shyness.

During the trapping period in November 1960, the hares that were caught had entered traps before much of the five-inch snowfall occurred on the third trap-night. However, there was not a single instance of a hare having passed near a trap or actually having visited a trap, without entering--although this behavior was hard to detect within the second growth.

Two examples of hares avoiding traps while traveling in the daytime were seen during the trapping period in February 1961. A hare had moved within a few feet of each of two widely separated traps within the second growth. However, both traps were nearly barred by snow and overhanging branches that were weighed down by snow.

After the snowfall on the first trap-night in April, tracks of hares made during the early morning hours were seen near three traps within the second growth, although one of the traps was snowed-shut. No response to the baited and set-traps was indicated.

Hares that had been released often passed close to open traps and hares frequently were disturbed from forms close to traps that were set, but undisturbed hares rarely were seen sitting or moving near traps. However, an unusual observation made on May 13, at a trapping location about one mile north of the main study area, revealed the failure of some hares to enter traps readily in the daytime. Two adult hares were seen sitting on a trail 8-10 feet apart and the same distance from an open trap baited with apple. Minutes later, a third hare crossed the trail within a few feet of the trap. This observation simply evidenced the presence of hares close to traps, their lack of attraction to the bait, and their failure to enter traps during the spring.

During the trapping period in November 1961, and despite a considerable amount of activity by hares in the open area, only one hare was caught in that habitat on the first trap-night. Nevertheless, evidence was seen repeatedly of hares having traveled close to most of the traps within the open area, without having been attracted to any of the them.

Many observations of failure of hares to enter traps were recorded during the trapping period in January 1962. No hares had

been caught in the open area and there was scant activity there, but hares were very active within the second growth and trapping success was fair. However, dense tracking was observed immediately in front of and around 10-open traps within the reproduction during the first trap-night, as is illustrated in Figure 15. The tracks of one hare led alongside a baited trap and past the open entrance, and tracks of a second hare approached directly to the entrance of the same trap. Tracks of hares were seen nearby four other open traps during the first trap-night. There was no additional snowfall during the second trap-night, but evidence was seen repeatedly of hares having passed close to traps that were set, without entering. For example, tracks of hares were seen at the entrances to four traps and nearby 14 others, all within the second growth. Trap shyness was also noted on the third trap-night, but the behavior of the hares was not so readily interpreted because of the intermixing of old and new tracks.

These observations reveal that hares frequently reacted passively to baited and set-traps and often actively avoided entering traps. This confirms the behavior indicated by the results of trapping, and by the large number of hares that were disturbed from forms near open traps.

Evans (1949) found that a wide range of behavior existed in the reaction of house mice, Mus musculus, to traps, and made the following comment pertinent to this study: "The factors making for trap acceptance are not understood, and extensive investigation of this problem is desirable before trapping can be considered a thoroughly satisfactory technique for population studies."



Figure 15. An example of "trap avoidance" as indicated by the fresh tracks of a snowshoe hare (or hares) about the entrance of a trap located at Station D-8, in the second growth, January 1962.

## ENVIRONMENTAL FACTORS THAT AFFECTED DISTRIBUTION AND ABUNDANCE OF HARES

The distribution of the accumulated fecal pellets of hares on plots in the open area and within the second growth is summarized in Table 12. It was apparent, on the basis of these data, that the hares spent a greater amount of time within the second growth than in the open area. (Weathering conditions that may influence the rate of decomposition of fecal entities were assumed comparable within the two types of cover.) Although there was a wide variation in the number of fecal pellets among plots sampled in both cover types, nearly four times as many pellets were present on each plot within the second growth as in the open area. The number of fecal pellets of hares on each plot sampled in the open area ranged from 0 to 1889 (mean 161), and from 31 to 2443 in the second growth (mean 602). The difference between the means is significant at the five percent level.

These observations do not reveal the extent of seasonal variation in the use of the two types of habitat, nor permit meaningful estimation of the numbers of hares. But the distribution of fecal pellets showed that the entire area was utilized by hares. Some gradation in the intensity of usage of the open area was indicated, being lower farthest from the second growth and higher adjacent to the boundary between the second growth and the open area. Trapping data and

observations in the field also indicated greater usage of the second growth. For example, immature hares apparently remained in that part of the area for several weeks.

Adams (1959) also found a significant correlation between the mean numbers of fecal pellets of hares and the density of cover. Pellets occurred in greatest concentration where trees and shrubs were thickest. Conversely, where trees were distributed sparsely and ground cover consisted of low herbs, pellets were scarce or absent. Adams concluded that the hares' preference for dense cover has an optimum density stage beyond which increasing the density may not improve the habitat.

### Physical Obstructions

Table 13 indicates the distribution of fecal pellets in relation to the physical obstructions on the ground. An abundance of logging debris, illustrated in Figure 1, left following clear-cutting of the mature stand of timber, and later snag-falling operations, constituted the principal obstructions on the surface. There were additional obstructions within the second growth that included dense clumps of bear grass, thickets of shrubs, and advanced reproduction of western hemlock and Douglas-fir. While the heavy concentrations of slash may have occupied useable habitat, it provided protective cover from the weather and from predators. The effects of these obstructions also

were diminished during periods of deep snow that facilitated movements of hares, and browse that had been out-of-reach previously became available.

There was a tendency, on both areas, to have fewer fecal pellets on those plots with most physical obstructions. But the differences between the means within each type of cover were nonsignificant at the five percent level. The net effect of the various obstructions seemingly was to concentrate usage and hence accumulation of fecal pellets on the unobstructed portions of each plot.

Adams (1959) had anticipated that the distribution of hares was influenced by physical obstructions, but quantitative observations failed to show significant relationships between the numbers of pellets and the percentage of obstructions. He concluded that physical obstructions do not appreciably influence the abundance and distribution of hares. Rather, the presence of the trunks and stems supporting vegetative cover may enhance the habitat.

#### Canopy Within the Second Growth

Advanced reproduction of western hemlock and Douglas-fir constituted the principal canopy within the second growth. Approximately half of the plots examined in this part of the area were open or only covered partially overhead by the coniferous reproduction. However, the degree of closure of the canopy apparently did not influence



Table 12. Distribution of hare-fecal pellets accumulated on plots sampled on the study area, in 1961, in percent.<sup>1</sup>

Location of Plots	Fecal Pellets on Each Mil-acre Plot					
	0-9	10-99	100-299	300-599	600-999	≥ 1000 (pellets)
Open area (69 plots)	16.6	53.7	12.9	11.1	3.7	1.8
Second growth (75 plots)	0	8.3	23.6	27.8	26.4	13.9

<sup>1</sup> For example, 11 of the 66 plots sampled on the open area had 0-9 fecal pellets to a plot.

Table 13. Mean number of hare-fecal pellets per plot under various conditions of physical obstruction in both cover types.

Number of Plots and Mean Number of Pellets per Plot	Percentage of Plot Barred by Physical Obstructions					
	0-9	10-24	25-49	50-74	≥ 75	All
<u>Open Area</u>						
Number of plots	29	12	19	9	0	69
Mean number of pellets per plot	156	225	143	107	--	161
<u>Second Growth</u>						
Number of plots	15	14	19	19	8	75
Mean number of pellets per plot	680	489	858	469	357	602

Table 14. Mean number of hare-fecal pellets per plot under various conditions of canopy closure within the second growth.

Number of Plots and Mean Number of Pellets per Plot	Percentage of Closure of the Canopy					
	0-9	10-24	25-49	50-74	≥ 75	All
Number of plots	30	15	11	8	11	75
Mean number of pellets per plot	581	561	582	614	715	602

usage of the area by hares, since there were no significant differences, at the five percent level, between mean numbers of fecal pellets per plot (Table 14).

### Significance of Successional Changes

There are many important interrelationships involved in what Adams (1959) termed the "food-cover-predator complex." He noted that in general the abundance of food for hares varies inversely with the density of the cover. Correspondingly, when a hare moves out into the open habitats its vulnerability to predators increases.

Within the second growth, for example, food was available at all seasons of the year, nesting cover was afforded, and the coniferous reproduction provided protection from the weather and presumably enabled hares to move with comparative security from avian predators. It seems probable that as the second growth develops into a pole-size stand, the area will provide much less favorable habitat for hares. On the other hand, the normal successional pattern may be expected to render the "open area" more favorable habitat. This trend was indicated clearly by the occurrence of clumps of sapling-size western hemlock and Douglas-fir that furnish good cover for hares and an increasing amount of shrubs. Herbaceous plants and shrubs eaten by hares also were more abundant and accessible in this part of the area.

The importance of vegetative cover as shelter from avian

predators is not clear. Slash on the ground and the scattered coniferous reproduction within the open area allowed considerably movement by hares, without exposure to hawks or owls. But the continued growth and increasing density of the vegetative cover presumably would provide better protection from such predators.

These habitat-preferences shown by the hares have implications to forest management, particularly with regard to reforestation, since seedlings planted on clear-cut areas may be exposed to considerable clipping by snowshoe hares. This is especially true around the periphery of reforested areas next to cover occupied by hares. The influence of precommercial thinning of young-growth stands of western hemlock and Douglas-fir on the habitat of snowshoe hares also should be recognized, since thinning of these stands may be expected to improve the habitat for hares.

## ESTIMATION OF NUMBERS

Estimates of numbers of hares were computed from live-trapping data by the recapture method, and the calendar-graph method of Adams (1959).

Calendar-graph Method

Adams devised the calendar-graph method as a census technique, which he applied to data obtained by live-trapping and tagging snowshoe hares on an island in Montana. Possibly the unique opportunities afforded by that study, specifically, the fact that movement of hares to or from the island was unlikely, may have suggested this procedure.

In the calendar-graph method, each hare caught is recorded on a horizontal line across a graph, the abscissa of which is marked off by the dates of the trapping periods. Each line starts at the date of first capture and terminates at the date of last capture. The number of hares estimated to be present on or within the vicinity of the trapping grid at any given time is determined by counting the number of hares recorded in the column under that date.

Date for the calendar-graphs are presented in tabular form: Table 15 lists older juvenile and adult male hares tagged and released from October 1960 to March 1961, and adult males tagged and released from April 1961 to March 1962. Table 16 contains similar data for

females. Data for male and female hares born in 1961 (juveniles) are presented in Tables 17 and 18. The dates when each hare were caught are indicated by X's in the columns corresponding to the trapping periods shown at the top of the tables. The data were condensed by omitting individual entry of hares caught and not released and of hares tagged and released, but not recaptured in a later trapping period. Data presented in Figures 16 and 17 is further augmented by addition of records for which data on sex or age were incomplete.

In Tables 15 and 16, all of the lines to March 1961 are extrapolated to the left to the first trapping period. This procedure also was employed by Adams (1959) and is justified by the fact that although some hares were caught and tagged later than others, it was assumed that an equivalent number of hares were present from the beginning of trapping in October 1960. In Tables 17 and 18 (juvenile hares born in 1961) data also were extrapolated prior to the date each hare first was caught, to the trapping period closest to the estimated date of birth. This procedure is based on the use of a growth curve that was constructed as follows: The weight of each juvenile hare when first caught is used as the point of entry on the ordinate of the graph. The age of the hare is then read opposite the point of intersection of the age-growth-curve. As Adams pointed out, these estimates of birth dates are only approximate. The actual growth curve for the population is not known and since the curve represents an estimated average weight-

Table 15. Data for the calendar-graph of juvenile and adult male snowshoe hares tagged and released from October 1960 to March 1961 and of adult snowshoe hares tagged and released from April 1961 to March 1962. The X's indicate those periods when the hares were caught. The entries on each line terminate at the period when hares were last caught. (Hares tagged and released, but not recaptured in a later trapping period are not listed individually.)

	1960					1961								1962							
Tag	Oct.	Oct.	Nov.	Dec.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
No.	8-10	22-24	19-21	20-22	28-30	21-23	25-27	21-23	22-23	19-20	13-15	11-13	8-10	6-8	27-29	24-26	20-22	19-21	13-15	10-15	17-19
999	x	-	-	-	-	-	-	-	x	x	x	-	x								
985	x	x	x	-	x	-	-	x	x												
980 <sup>1</sup>	x	x	x																		
978	x	-	-	-	x																
972 <sup>1</sup>	x	x	x																		
968 <sup>1</sup>	x	x	x	x	-	x															
958	-	x	x	-	-	x	x	x													
953 <sup>1</sup>	-	x	-	-	-	-	-	x	x												
951 <sup>1</sup>	-	x	x																		
943	-	x	x	-	x	x	x	x	x												
941	-	x	-	-	x																
937	-	x	x																		
935	-	x	x																		
933 <sup>1</sup>	-	x	x																		
929 <sup>1</sup>	-	x	x	-	-	x	x	x	x	x	x	-	x	x	x	x	-	x	x	x	x
927 <sup>1</sup>	-	x	x																		
912 <sup>1</sup>	-	-	x	-	x	x	x	x	x												
907 <sup>1</sup>	-	-	x	x	-	x	x	x													
901 <sup>1</sup>	-	-	x	-	x	x	x														
898	-	-	x	-	x	x	-	x	x	-	-	x	-	-	-	x	x	x	x	x	x
896	-	-	x	-	-	-	-	-	x	-	-	-	-	x	-	x	-	-	-	x	x
894	-	-	x	-	x	-	-	-	-	-	x										
878	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	
876	-	-	-	-	x	-	x	-	-	-	-	-	-	-	-	x	-	-	-	x	
859 <sup>1</sup>	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	x	x	-	x	x	x
853	-	-	-	-	-	x	x	x													

Table 15. Continued

	1960										1961						1962				
Tag.	Oct.	Oct.	Nov.	Dec.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
No.	8-10	22-24	19-21	20-22	28-30	21-23	25-27	21-23	22-23	19-20	13-15	11-13	8-10	6-8	27-29	24-26	20-22	19-21	13-15	10-15	17-19
851 <sup>1</sup>	-	-	-	-	-	x	x	x	x	-	-	-	x	-	-	x	-	-	x	x	x
818									x	x	-	x	x	x	x	-	x	-	-	x	
595											x	-	-	-	-	-	-	-	-	-	x
652												x	-	-	-	-	-	-	-	x	
644												x	-	-	-	-	x	x	x		
325																x	x	x	x	x	x
--2	0	4	1	1	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	1	3
--3	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
--4	18	18	14	9	9	9	7	7													
--5	19	19	19	15	14	11	11	9													
--6	37	37	33	24	23	20	18	16	15	10	12	12	12	11	11	13	12	12	12	12	10

<sup>1</sup>Assigned age as juvenile when caught and designated an adult from April 1961.

<sup>2</sup>Hares tagged and released, but not recaptured in a later trapping period.

<sup>3</sup>Hares caught and not released.

<sup>4</sup>Juvenile males born in 1960 as estimated by the calendar-graph method.

<sup>5</sup>Adult males as estimated by the calendar-graph method.

<sup>6</sup>Juvenile and adult males from October 1960 to March 1961 and adults from April 1961 to March 1962, as estimated by the calendar-graph method.

Table 16. Data for the calendar-graph of juvenile and adult female snowshoe hares tagged and released from October 1960 to March 1961 and of adult snowshoe hares tagged and released from April 1961 to March 1962. The X's indicate those periods when the hares were caught. The entries on each line terminate at the period when hares were last caught. (Hares tagged and released, but not recaptured in a later trapping period are not listed individually.)

Tag No.	1960										1961						1962					
	Oct. 8-10	Oct. 22-24	Nov. 19-21	Dec. 20-22	Dec. 28-30	Jan. 21-23	Feb. 25-27	Mar. 21-23	Apr. 22-23	May 19-20	June 13-15	July 11-13	Aug. 8-10	Sept. 6-8	Sept. 27-29	Oct. 24-26	Nov. 20-22	Dec. 19-21	Jan. 13-15	Feb. 10-15	Mar. 17-19	
996 <sup>1</sup>	x	x	x	x	x	x	-	x	-	x	x	x	x									
994 <sup>1</sup>	x	x	x	-	-	x	x															
991 <sup>1</sup>	x	x	x																			
989 <sup>1</sup>	x	x	x	-	-	-	-	-	x													
982 <sup>1</sup>	x	x	x	-	-	-	-	-	-	x	x	x	x	x	-	-	-	-	-	x		
964 <sup>1</sup>	x	x	x	-	-	-	-	x														
962 <sup>1</sup>	-	x	x	-	-	-	-	-	-	x	-	-	x	-	-	x						
960 <sup>1</sup>	-	x	x	-	-	-	-	-	-	-	x											
947 <sup>1</sup>	-	x	-	-	x	x	-	x	x	-	x	x	-	-	-	-	-	x	x	x		
946 <sup>1</sup>	-	x	x	-	-	-	-	x														
939 <sup>1</sup>	-	x	x																			
916 <sup>1</sup>	-	-	x	-	-	-	x	x														
914 <sup>1</sup>	-	-	x	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	x	x	
905 <sup>1</sup>	-	-	x	-	-	-	-	-	-	-	x	x	x									
903 <sup>1</sup>	-	-	x	-	-	-	-	-	-	x	x	x	x	x	x							
892 <sup>1</sup>	-	-	x	-	-	-	-	x														
890 <sup>1</sup>	-	-	x	-	x	x	-	-	-	-	-	-	x									
888 <sup>1</sup>	-	-	x	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	-	x		
884 <sup>1</sup>	-	-	-	x	x	-	x	x	x	x	x											
874 <sup>1</sup>	-	-	-	-	x	-	-	x	x													
872 <sup>1</sup>	-	-	-	-	x	x	-	-	-	x	-	-	-	-	-	-	x	x	x	x	x	
863 <sup>1</sup>	-	-	-	-	x	-	-	x														
861 <sup>1</sup>	-	-	-	-	x	-	-	-	-	-	-	x										
855 <sup>1</sup>	-	-	-	-	-	x	x															
843 <sup>1</sup>	-	-	-	-	-	-	x	-	-	-	-	x	x	-	-	-	-	x	-	x		
841 <sup>1</sup>	-	-	-	-	-	-	x	x	x	x	-	x	x									
838 <sup>1</sup>	-	-	-	-	-	-	-	x	-	-	x	x	x	-	x	x	-	x				



Table 16. Continued

Tag No.	1960								1961								1962				
	Oct. 8-10	Oct. 22-24	Nov. 19-21	Dec. 20-22	Dec. 28-30	Jan. 21-23	Feb. 25-27	Mar. 21-23	Apr. 22-23	May 19-20	June 13-15	July 11-13	Aug. 8-10	Sept. 6-8	Sept. 27-29	Oct. 24-26	Nov. 20-22	Dec. 19-21	Jan. 13-15	Feb. 10-15	Mar. 17-19
835 <sup>1</sup>	-	-	-	-	-	-	-	x	-	x	-	-	-	-	-	x	-	x	x	x	x
833	-	-	-	-	-	-	-	x	-	-	x	x	x	-	-	-	-	x	x	x	x
820									x	x	x	-	x								
805										x	-	x	x	-	-	x					
311																x	-	x	x	x	x
347																	x	x	x	x	
--2	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0
--3	16	16	15	13	12	12	12	12													
--4	17	16	16	15	15	15	15	13													
--5	33	32	31	28	27	27	27	25	21	20	20	18	17	12	12	13	11	11	11	11	5

<sup>1</sup> Assigned age as a juvenile when caught and designated an adult from April 1961.

<sup>2</sup> Hares tagged and released, but not recaught in a later trapping period.

<sup>3</sup> Juvenile females born in 1960 as estimated by the calendar-graph method. Hares born in 1960 and remaining in the population after March 1961 were classed as adults.

<sup>4</sup> Adult females as estimated by the calendar-graph method.

<sup>5</sup> Juvenile and adult females from October 1960 to March 1961 and adults from April 1961 to March 1962, as estimated by the calendar-graph method. (A hare caught in November 1960 was not sexed or aged, but was included in population-estimates.)

Table 17. Data for the calendar-graph of male snowshoe hares born in 1961. The dashed lines start at the estimated time of birth. The X's indicate those periods when the hares were caught. The entries on each line terminate at the period when hares were last caught. (Hares tagged and released, but not recaptured in a later trapping period are not listed individually.)

Tag No.	1961										1962		
	Apr. 22-23	May 19-20	June 13-15	July 11-13	Aug. 8-10	Sept. 6-8	Sept. 27-29	Oct. 24-26	Nov. 20-22	Dec. 19-21	Jan. 13-15	Feb. 10-15	Mar. 17-19
593		-	x	x	x	x	x	-	-	x			
682			-	x	x	x	x	x	x	-	x	x	x
680			-	x	-	-	-	x	x	x			
662			-	x	x								
512			-	-	x	x	-	x	x	x	x	x	x
514				-	x	-	x						
518			-	-	x	x	-	-	-	x	-	x	
526	-	-	-	-	x	x	x						
528			-	-	x	x	x						
536			-	-	x	x							
623			-	-	x	-	-	-	x				
36			-	-	x	x	x						
42			-	-	x	-	-	-	x	x			
44		-	-	-	x	x							
577			-	-	x	-	-	-	x				
542			-	-	x	-	-	-	-	-	-	-	x
409				-	-	x	-	-	x				
449				-	-	-	x	-	-	x	-	-	x
303				-	-	-	-	x	x	-	-	x	x
307			-	-	-	-	-	x	-	x			
313			-	-	-	-	-	x	x				
317			-	-	-	-	-	x	-	x			
332		-	-	-	-	-	-	x	x	x			
338			-	-	-	-	-	-	x	-	x		
349					-	-	-	-	x	x		x	
374					-	-	-	-	-	-	x	x	x
--1	0	0	0	9	8	4	5	3	2	0	2	1	0
--2	0	0	0	1	0	1	0	0	0	0	0	0	0
--3	4	12	38	54	52	43	35	27	24	18	12	9	7

<sup>1</sup> Juvenile males tagged and released, but not recaptured in a later trapping period. <sup>2</sup> Juvenile males caught and not released. <sup>3</sup> Juvenile males born in 1961 as estimated by the calendar-graph method.

Table 18. Data for the calendar-graph of female snowshoe hares born in 1961. The dashed lines start at the estimated time of birth. The X's indicate those periods when the hares were caught. The entries on each line terminate at the period when hares were last caught. (Hares tagged and released, but not recaptured in a later trapping period are not listed individually.)

Tag No.	1961										1962		
	Apr. 22-23	May 19-20	June 13-15	July 11-13	Aug. 8-10	Sept. 6-8	Sept. 27-29	Oct. 24-26	Nov. 20-22	Dec. 19-21	Jan. 13-15	Feb. 10-15	March 17-19
598	-	-	x	x	x								
590	-	-	x	-	x								
587	-	-	x	-	-	-	-	-	x				
583	-	-	x	-	-	-	-	x					
670			-	x	x								
668			-	x	x	x							
664			-	x	x	x							
656	-	-	-	x	x	-	-	x	-	x	-	x	x
646	-	-	-	x	x	x							
642			-	x	x								
637		-	-	x	x								
530		-	-	-	x	x	x						
534			-	-	x	-	-	-	-	x	-	x	
538	-	-	-	-	x	x	x	x	-	x			
547	-	-	-	-	x	x	-	x					
403				-	-	x	x						
425		-	-	-	-	x	-	-	x	-	x	x	
427				-	-	x	-	x	x	x	-	x	x
431				-	-	x	x						
435	-	-	-	-	-	x	-	-	-	-	x	x	x
447		-	-	-	-	x	-	x	x				
454				-	-	-	x	x	x	x			
462			-	-	-	-	x	x	-	x	x	x	
319			-	-	-	-	-	x	x				
324		-	-	-	-	-	-	x	x	x	x	x	
345				-	-	-	-	-	x	x			
--1	0	0	0	2	8	8	0	4	1	2	1	0	0
--2	0	0	0	1	1	0	0	0	0	0	0	0	0
--3	9	22	35	51	51	37	26	23	16	13	8	7	3

<sup>1</sup>Juvenile males tagged and released, but not recaptured in a later trapping period. <sup>2</sup>Juvenile males caught and not released. <sup>3</sup>Juvenile males born in 1961 as estimated by the calendar-graph method.

at-age relationship, each extrapolated value is subject to sampling errors.

In the present study, since hares were unrestricted by natural barriers to movements, the assumption was made that dispersal of hares off the study area was equivalent to immigration onto the area. This assumption was not applied to adults after March 1961, since trapping and handling activities were an important cause of mortality, but it was used in computing numbers of juveniles born in 1961. It is supported by Brant's findings (1962), that grid live-trapping did not appear to disturb the patterns of movements, distribution, or abundance of small mammals.

Adams (1959) compared estimates of numbers of hares, as determined by the calendar-graph method, with results obtained by the recapture method, and a procedure based on sampling of fecal pellets that was calibrated to hare-numbers. He demonstrated that results obtained by the three methods show similar trends.

The calendar-graph method tends to underestimate the true size of the population because of two biases which are unavoidably introduced into the method, according to Adams. First, it may be assumed that the population is continually incurring losses as a result of natural mortalities and predation, and that some animals die before they are caught. The calendar-graph method does not account for such individuals. A second bias is caused by terminating entries at the

period when hares were last caught. It is apparent that released hares lived, on the average, for some indeterminate time following the date of their last capture. Also, adult hares that may have immigrated to the area presumably were present for some time prior to capture. Since a good method was not found to extend the periods on the calendar-graph that hares in both categories may have been on the area, the estimates of numbers tend to be conservative.

The curves representing numbers of hares, as determined by the calendar-graph method, all have a downward bias towards the close of trapping; this trend is particularly evident for the trapping periods in February and March 1962. This result may be explained by the fact that when trapping is terminated there is no further opportunity for recovery of marked animals. Therefore, records of hares which would have been extended are dropped, beginning at some indefinite time prior to the termination of trapping.

Use of the calendar-graph method in this study was necessarily qualified by the assumption of compensating movement off and onto the study area, except as this movement may have been biased by unusual losses on the study area caused by trapping and handling activities. However, the method permits meaningful estimates of numbers, shows trends in size of the population, and is more useful than the recapture method for estimating numbers present each trapping period.

The annual changes in the size of the population as estimated

by the calendar-graph method are shown in Figures 16 and 17. Estimated numbers of subadults and adults caught from October 1960 to March 1961 and of adults caught from April 1961 to March 1962, and of juveniles born in 1961, are shown in Figure 16. Figure 17, represents the estimated numbers of hares of all ages as determined by the calendar-graph method; it is simply a summing of the data presented in the first pair of curves.

### Recapture Method

For the recapture method the marked hares in one trapping period were used as the premarked animals to be sampled in the next trapping period. That is, all marked hares that were released in one period, including previously tagged and newly tagged hares, represented the premarked animals to be sampled in the next period. An estimate of the size of the original population may then be obtained by the proportion of marked individuals trapped in the next period times the number marked and released in the preceding period.

The ratios are:

$$\frac{\text{Size of population sampled (N)}}{\text{Marked hares released in one trapping period (M)}} = \frac{\text{Hares caught in next period (n)}}{\text{Marked hares recaptured from preceding sample (m)}}$$

The method was intended for application where the marking and releasing was all done at one time (a day) and the recaptures also at one time (another day). Since so few animals were recaptured from one

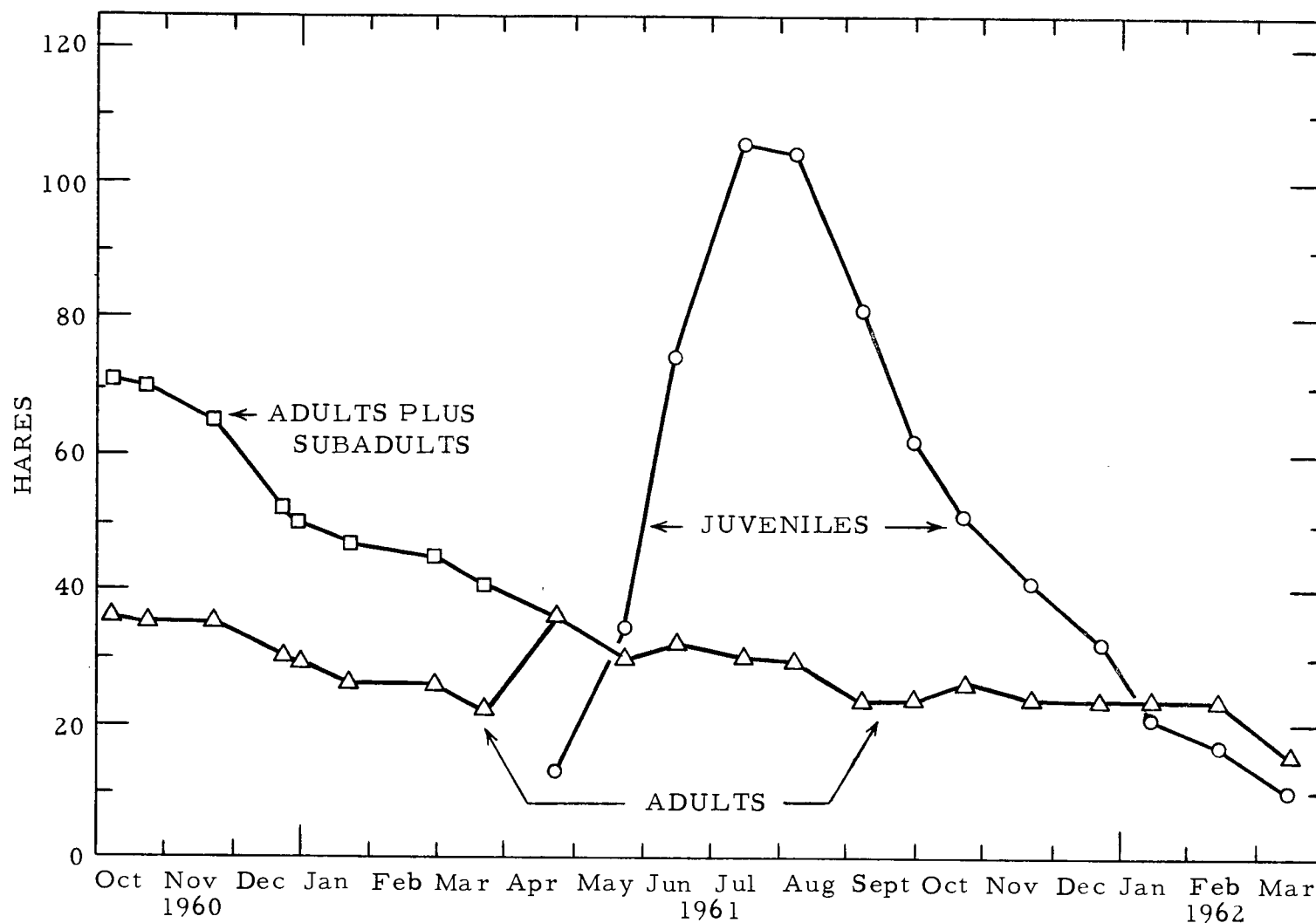


Figure 16. Subadult and adult hares as determined by the calendar-graph method. The upper curve from October 1960 to March 1961 represents the estimate of all subadults and adults and the lower curve represents only the adult portion of the estimated population.

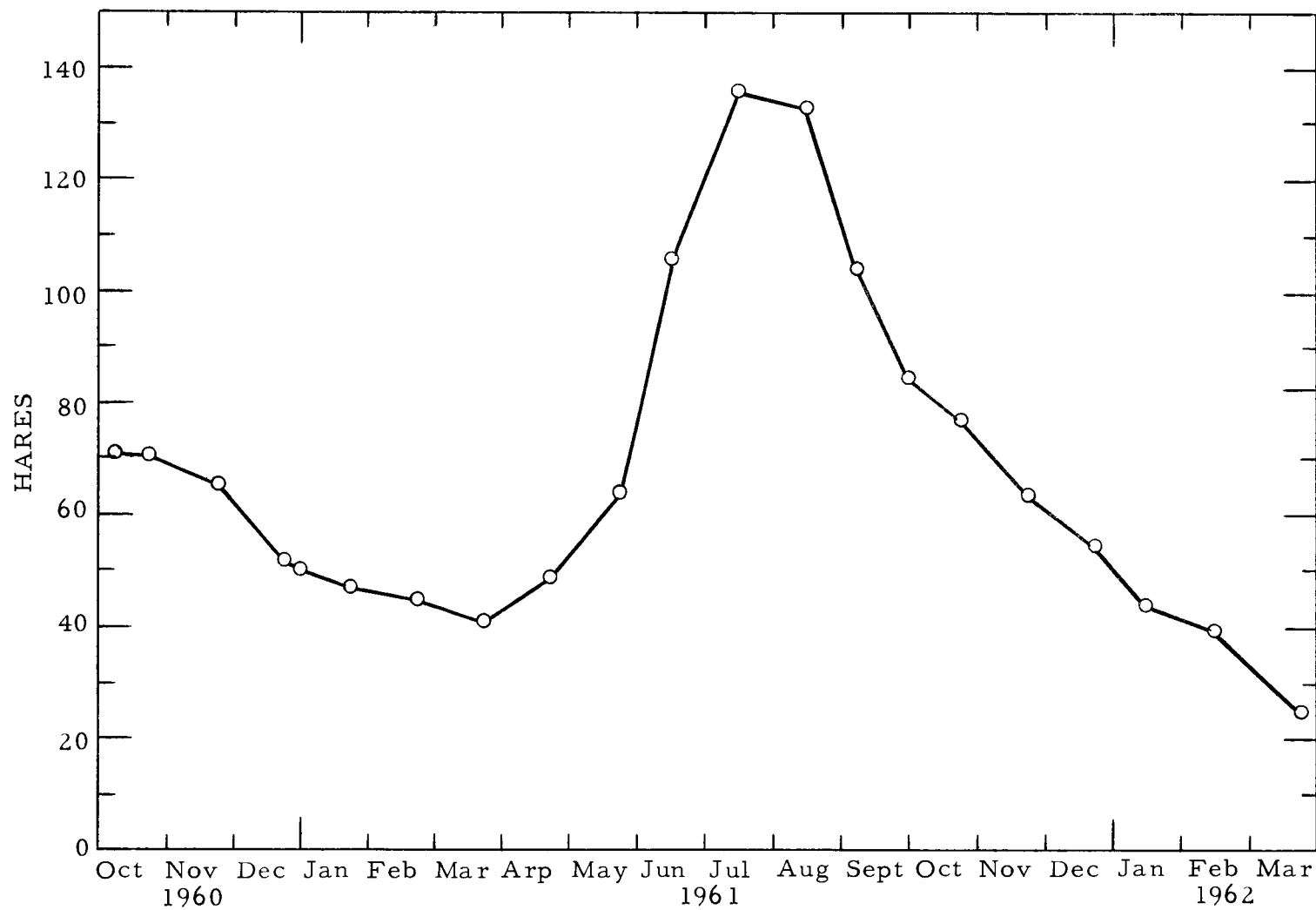


Figure 17. Estimated numbers of hares of all ages as determined by the calendar-graph method.



trap-night to the next and because of the apparent interference of trapping and handling activities with recapture of hares during a trapping period, the captures in each period were grouped together and treated as a single sample, following a procedure used by Adams (1959). Davis also outlined a similar procedure for accumulating the animals caught in a period of time (1960). Nonetheless, because of the small average number of recaptures, the standard error of the monthly estimates were large.

For this procedure, it was assumed that a marked animal has the same chance of capture as an unmarked animal and that no individuals are present at the second trapping period that were not available to be caught at the first trapping period. (Davis [1960] analyzed the method and showed that neither of these assumptions is entirely true. Hayne [1949] also has analyzed the assumptions underlying the method and noted causes of over estimation of population size.) The second assumption is qualified, because of the changes in the population that may have occurred in the interval between trapping periods. But it was assumed that emigration and immigration were negligible, that mortality of marked and unmarked animals was the same, and that the arrival of new individuals by births may have been partly compensated for by the high mortalities among immature hares. The similarity of estimates of the population as made by the two methods is an indication of the applicability of these assumptions.

There were fluctuations in the estimated size of the population as determined by this method, as is illustrated in Figures 18, 19, and 20. These variations apparently resulted from changes in trapping success that caused the number of hares recaptured from a previous period to be very small. For example, the estimated population in November 1961 was 88.7, but the standard error of this estimate, as calculated by Bailey's (1951) method, was 38.7 and the confidence limits at the 95 percent level were 11.3 to 166.1. The wide variance of the estimate resulted from the extremely poor trapping success during the first trapping period in December. Wide shifts in monthly estimates also occurred during the two trapping periods in September. Both were the result of poor trapping success during the second trapping period of the month. The excessive estimate for the second trapping period likely was caused by substantial recruitment to the population that resulted from enlarging the trapping grid.

A comparison of the estimated size of the population, as determined by both methods, indicates that the calendar-graph method is less influenced by seasonal changes in trapping success, while the recapture method is directly influenced by trapping success. The recapture method also is more responsive to changes in the status of the population that may take place between sampling periods, but because the number of marked hares recaptured is often small in comparison to the number caught and released, large standard errors

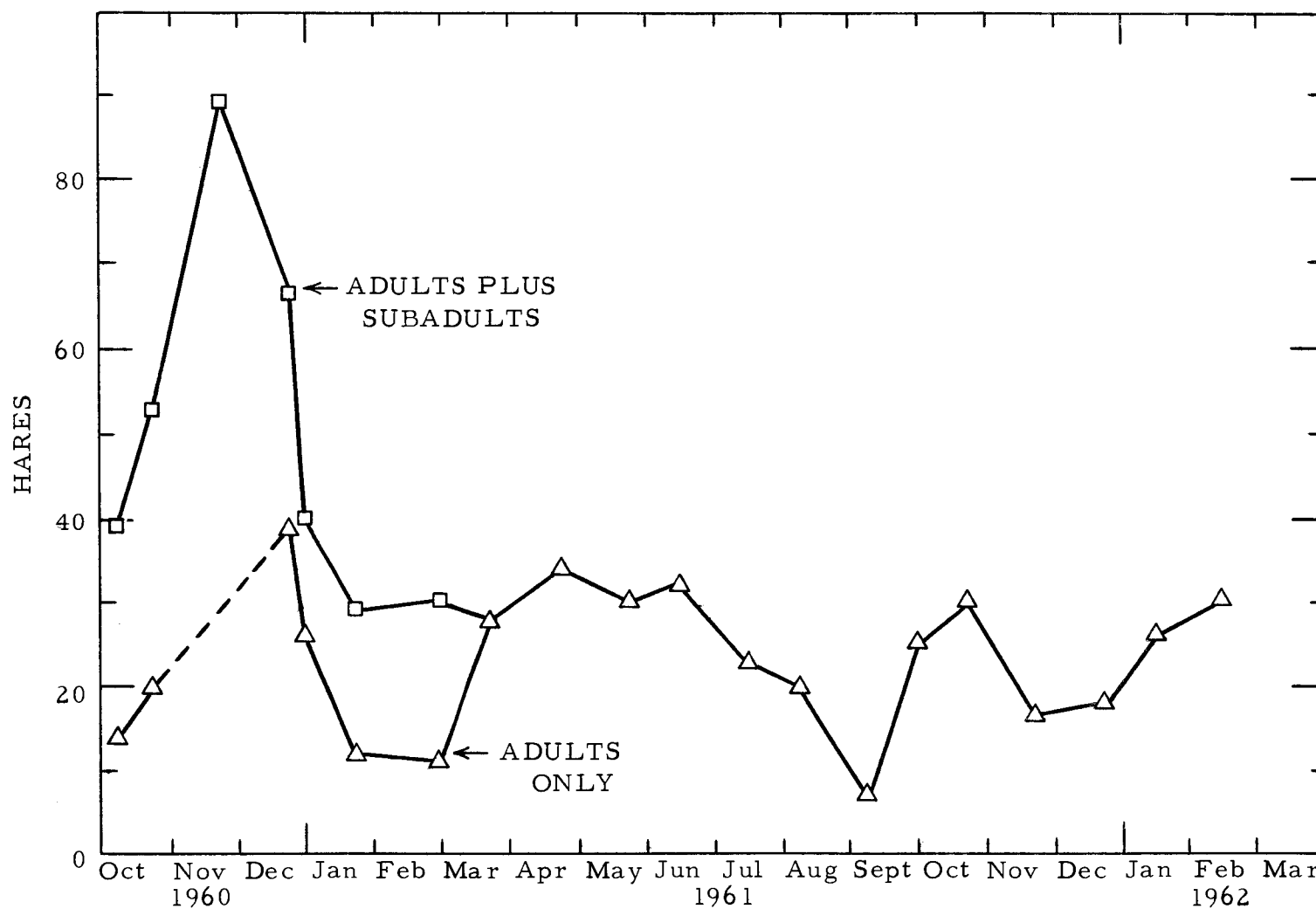


Figure 18. Subadult and adult hares as determined by the recapture method. The upper curve from October 1960 to March 1961 represents the estimate of all subadults and adults, and the lower curve represents only the adult portion of the estimated population for that period.

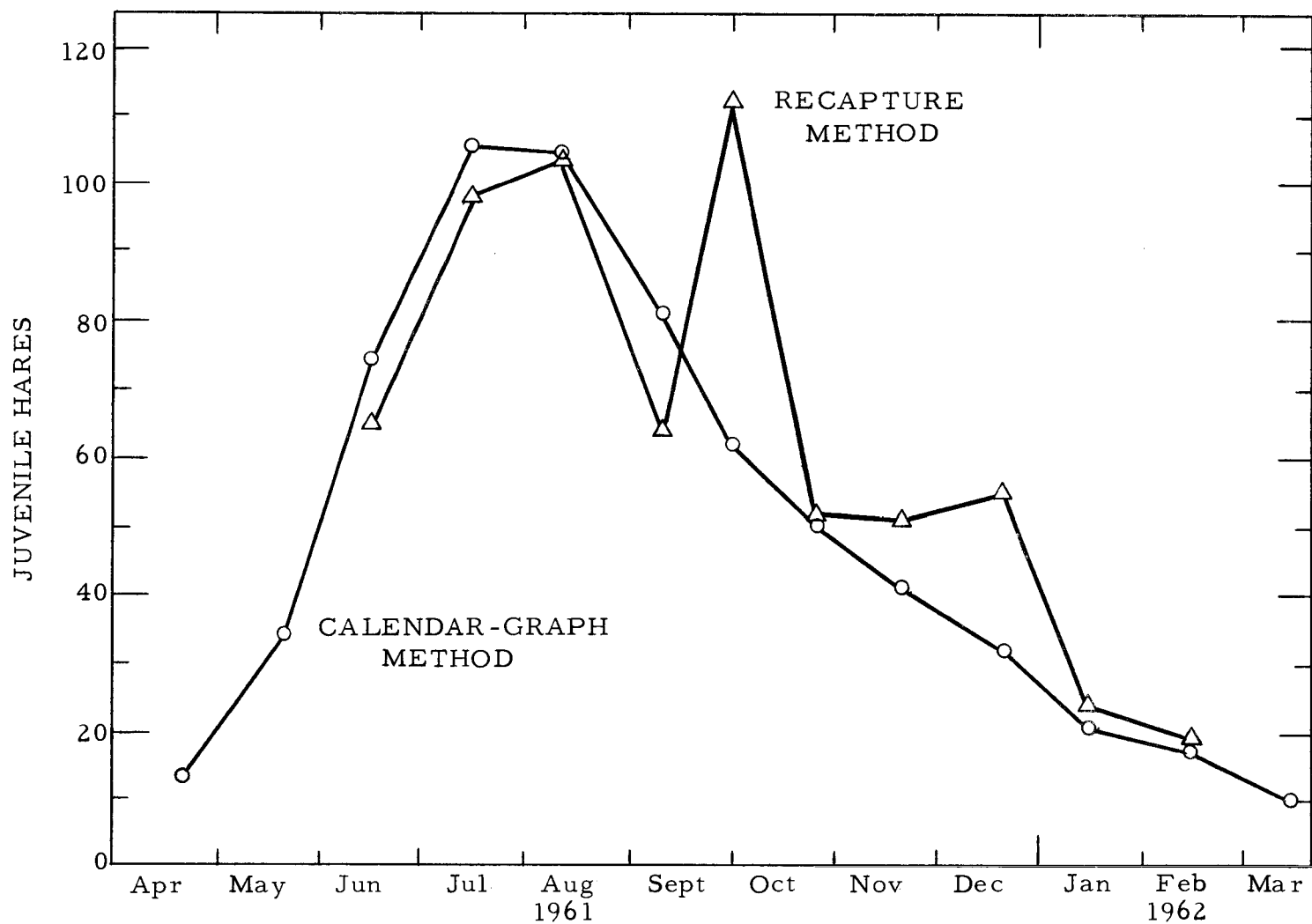


Figure 19. Juvenile hares born in 1961, as determined by the recapture method and the calendar-graph method. This comparison indicates the wide fluctuation in results, as obtained by the recapture method, which are based upon trapping success each trapping period.

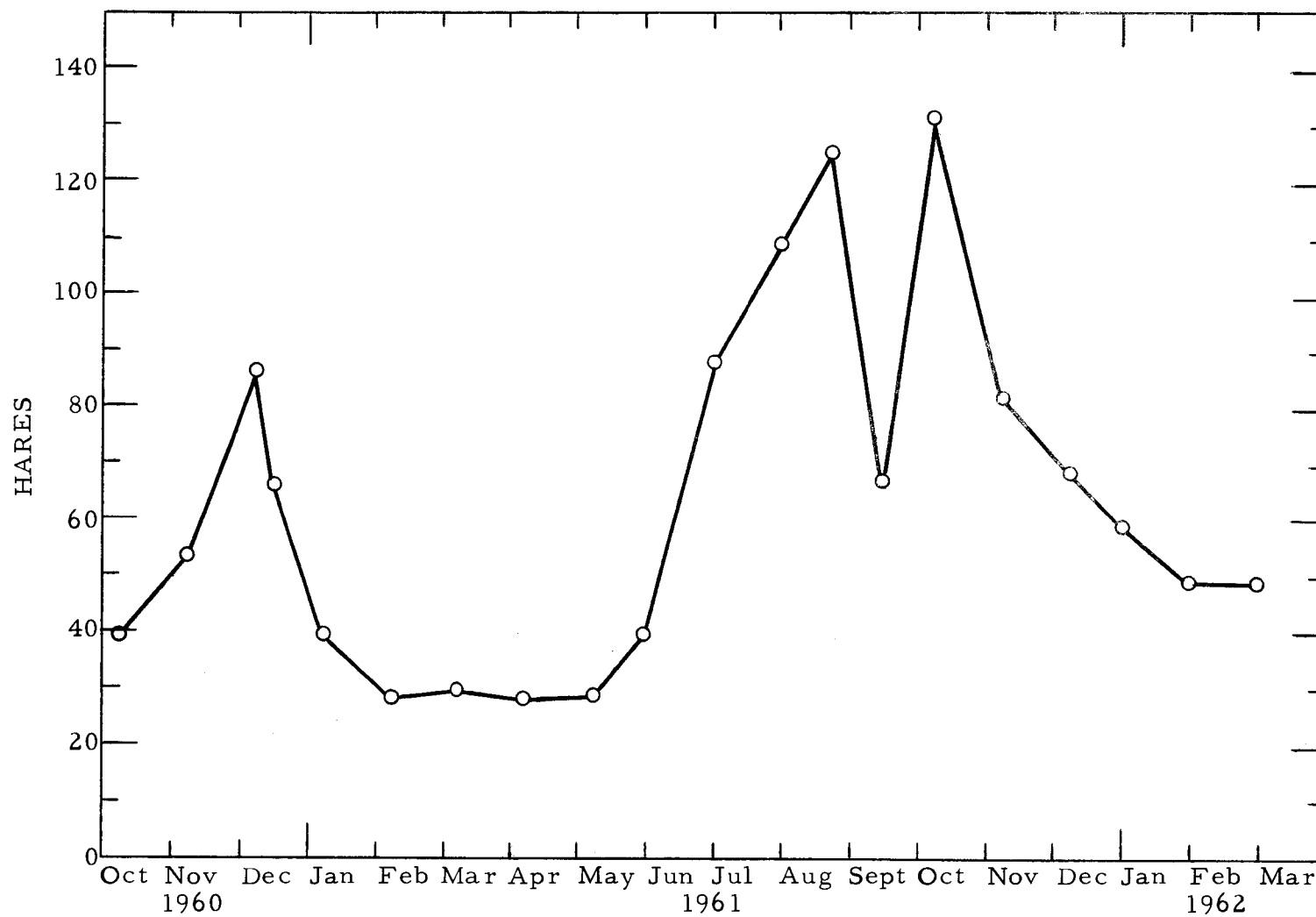


Figure 20. Estimated numbers of hares of all ages as determined by the recapture method.

result. Adams (1959) also noted that the recapture method may underestimate the population because of "trap habit" in some individuals--in violation of the assumption that animals move freely and at random, and respond similarly to traps.

Two significant trends in the population, as indicated by both methods, were the rapid increase in juvenile hares and the almost equally abrupt decline in their numbers, and the comparatively stable numbers of adults. Numbers of juvenile and adult hares reached a peak of 136 in July as indicated by the calendar-graph method. The low point in the population as estimated by this method occurred in March, 1961, when a total of 41 hares were estimated on the area. Both estimates were for numbers present on the area trapped by the small grid. Comparable results were obtained by the recapture method: The largest estimate with an acceptable standard error was in August; the population was estimated as 125.0 juvenile and adult hares, with a standard error of 20.0.

### Estimates of Density

Estimates of population density in terms of animals-per-acre requires that the area from which the animals are trapped be known. Brant (1962) also emphasized that wherever the habitat is continuous, estimates of density must take into account the distances that animals have come to traps.

For this analysis, it was assumed that the animals were trapped, on the average, from an area beyond the stations on the perimeter of the trapping grids by a distance equal to their "average" radius of movements.

Dice (1938) described how densities might be determined by adding a strip equal to one-half the average width of the home range to the border of the live-trapped area, to account for the actual area occupied by the sampled population. Stickel (1946, 1948) suggested a similar procedure in which a buffer strip, equal to one-half the maximum range, is set up around a central part of the larger trapping area. The population was considered to be the total of individuals caught only in the central area, plus one-half of those caught in the buffer area and the central area. Stickel also suggested that males and females, and juveniles and adults be treated separately, since the maximum ranges may vary by sex and age-classes. MacLulich (1951) proposed a technique for estimating populations that employed an estimation of the range of the animal beyond the trapping area, similar to the "buffer area" of Stickel. But Brant (1962) showed that it was unlikely that "one-half the mean width of individual home ranges", as proposed by Dice, was an adequate measure of the width of the area beyond a grid that is occupied by the population sampled. He compared the average distance of movement between capture (av. D.) with the results of intensive removal-trapping on small grids surrounded by marked populations.

Brant found that the movements of the animals to traps were approximately equal to av. D. , that live-trapping did not induce unusually large movements toward or away from the area being trapped, and concluded that av. D. should be a suitable parameter in estimating the size of the area sampled by grid live-trapping. He interpreted these results to indicate that live-trapping did not disturb the movements of rodents in adjacent areas.

The "mean" radius of home range for adult hares as estimated by the circular-bivariant method was 5.68 and 4.85 chains for males and females, respectively. Therefore, the approximate area from which the population of adult hares were trapped, using the weighted "average" radius of movement of adults (5.26 ch), was 44 acres for the small grid and 99 acres for the large grid. The density of hares at the beginning of trapping, based on estimate of numbers by the calendar-graph method, was 1.6 hares on each acre. Near the close of the breeding season, the density of hares was nearly two times larger. In fact, considering the smaller home range of immature hares and that their movements were confined mainly within the second growth, a much higher density in this habitat was indicated.

Enlarging the trapping grid, i. e. , increasing the distance between traps from one and one-half to three chains, and the area occupied by the grid from 14.4 to 57.6 acres, did not cause a corresponding increase in estimated numbers of hares. Actually, the size



of the area trapped--within the "average" radius of adults--was increased slightly more than two times, but the number of hares in February of each year, as determined by the recapture method, increased only from 30 to 49. Estimates made by the recapture method were used in this analysis, since estimates made by the calendar-graph method have a downward bias in the later trapping periods. The estimates of the two populations ( $N_1$  and  $N_2$ ) were compared by determining the standard error of each ( $S.E._1$  and  $S.E._2$ ) and calculating the following ratio, as outlined by Bailey (1951):

$$\frac{N_1 - N_2}{\sqrt{(S.E._1)^2 + (S.E._2)^2}} \quad \text{or} \quad \frac{48.7 - 30.5}{\sqrt{(6.78)^2 + (5.47)^2}} = 2.09$$

Since the ratio is more than two, the populations are significantly different at the five percent level.

A factor that may have reduced the estimated density on the larger grid was the smaller proportion of habitat within the second growth occupied by that grid. The amount of each type of cover included within both grids is important, since the centers of activities of most hares were within the second growth (Figure 25). (The population also may have been smaller in 1962 than in 1961.)

Adams (1959) estimated total populations of hares--adults and young--by recapture, calendar-graph, and pellet-census methods and concluded that the trends in the population as determined by each of the methods were related closely to each other and to the actual population.

Since hares occupied 81 acres on the island, and the estimated number of adults at the beginning of the study in February 1953 was 58 (as obtained by the calendar-graph technique), the density may have been approximately 0.72 hares per acre. This result is slightly higher than the estimated densities recorded in western Oregon, in February 1961 and 1962 (as calculated by the recapture method). However, the maximum population of hares recorded by Adams occurred in August, as in Oregon, but was not greatly higher than the estimated population in February 1953. In the present study, the estimated population in August was four times as large as in February of the same year.

## PRODUCTION OF YOUNG

The position and size of the testes in males and the signs of pregnancy in females were noted for all hares handled in each trapping period. In addition, testes of necropsied males, and the ovaries and uteri of necropsied females were examined grossly in the laboratory. This procedure also enabled determination of the number and age of fetuses in pregnant females.

Aldous (1937) described the changes in position and size of testes of male snowshoe hares as follows: The testes, having enlarged in size, descend from the abdominal cavity into the scrotum in late February. They remain enlarged and in the scrotum through June, but in July rapidly decrease in size and are withdrawn into the body cavity by September. Severaid (1942, 1945), Adams (1959), and Dodds (1960b) also reported that the onset of the breeding season is indicated by these readily observable changes in the testes.

In this study, the enlarged testes of hares were first noted to have descended into the scrota during the trapping period in March 1961.

Testes of each of the 11 adult males handled during the trapping period in April 21-23 were enlarged, in the scrota, and were readily palpable. (Only two to five adult males were handled in each of the six trapping periods from May through September.)

Testes of adult males were found in the scrota in May, but from June to September the location of the testes of adult males was variable. For example, testes of one adult male handled in June were not palpable and apparently were retracted. An adult male handled in July had one testis retracted and one in the scrotum; and testes of an adult male handled in September were partially retracted on September 6-8 and wholly retracted by September 27-29. Observations of the comparative size of testes throughout the breeding season were so few as to preclude conclusions, but it was noted that testes became flaccid as they regressed in size. This condition was seen in four of five adult males examined in August.

Testes of males born in 1961 were not palpable before March of the following year. Also, there was no indication of juvenile females breeding in the year of birth--ovaries of older juvenile females examined in August, September, and October were small and uteri were nonvascularized.

Testes of adult males necropsied in November 1960, and in January 1961 were much reduced in size in comparison to those of adult males in March and April, but were larger than testes of juvenile males examined in September and October. But on the basis of the first pregnancies in females, it appears probable that the enlargement and descent of testes into the scrota of males may precede the breeding season, and diminution in size and withdrawal of the gonads evidently

follows the breeding season.

The earliest date that enlarged testes were observed by Adams (1959) in hares studied in Montana was February 18, and nearly all males were found to have fully enlarged and descended testes by early March. Similar observations were reported by Aldous (1937) for hares in Minnesota, by Severaid (1942, 1945) for captive hares studied in Maine, and by Dodds (1960b) for hares observed in Newfoundland.

The enlargement and migration of the testes from an intra-abdominal position to the scrotum and their subsequent decrease in size, and return at the close of the breeding season also occurs in the cottontail, Sylvilagus floridanus. However, Schwartz (1942) found that the position of the testes--in relation to the scrotum--may be an unreliable indicator of sexual activity. He noted that during the breeding season the testes may be withdrawn from the scrotum as a result of handling, etc. Schwartz also found testes in the scrotum during winter when they are small and when sexual activity is nil. Dodds (1960b) also reported that the position and general appearance of the male gonads is an unreliable indicator of a snowshoe hare's breeding condition.

The condition of the mammary glands and hair around the teats were examined for signs of lactation, e. g. , teats swollen and easily visible. Also, the thickening of the mammary tissue was palpable and milk frequently could be expressed, but this was variable and milk

could not be extracted readily from some adult females that showed other evidence of recent suckling such as hair matted about teats.

Examination and palpation of all female hares handled each trapping period failed to reveal evidence of pregnancy, with one exception, prior to the trapping period in May 1961. Moreover, gross examination of the uteri of a subadult and three adult females necropsied in late February and March showed no signs of pregnancy. The earliest pregnancy detected was that of an adult female, No. 874, found dead in a trap on April 23, 1961 and necropsied. The three fetuses were aged by comparison with growth curves of prenatal snowshoe hares determined by Bookout (1964). Their mean crown-rump length was 28 mm corresponding to an age of 18 1/2 days. Comparing the specimens with Bookout's description of the morphological characters of unborn young indicated an age of 19 days. Back-dating of pregnancy indicates that conception probably occurred April 5 and parturition would normally have been expected after completion of the gestation period of approximately 37 days--as reported by Severaid (1942, 1945), Dodds (1960b), and Grange (1932)--or on May 11. This represents the earliest record of pregnancy obtained during the study.

Palpation of this female on April 22 tentatively indicated pregnancy, but the diagnosis was inconclusive. No pregnancies were detected via palpation of six other adult females handled during this trapping period.

The earliest record of breeding as determined by back-dating of juveniles tagged in 1961 to estimated date of birth was that of a juvenile female, No. 590, that weighed 16 ounces when tagged on June 15. This juvenile was estimated to have been about 5-6 weeks old, indicating parturition probably occurred during the first or second week of May.

MacLulich (1937) observed that pregnancies of hares in northern Canada do not occur before late April. Criddle (1938) reported first pregnancies in southern Manitoba in late March and early April on the average. Aldous (1937), and Green and Evans (1940c) reported that first pregnancies occurred in late March. Severaid (1942, 1945) listed March 20 as the earliest record of pregnancy, but he also observed a birth on April 17--indicating conception occurred approximately March 11. Rowan and Keith (1956) reported the earliest embryos were found April 22. The first palpable pregnancy reported by Adams (1959) was March 19 and he concluded that pregnancies began about March 13. Dodds (1960b) reported earliest breeding of hares in captivity occurred March 26-27, and in the wild on April 4-5. These findings indicate that breeding activity begins at about the same time over much of the range of the snowshoe hare, including western Oregon, but may be later farther north.

During the trapping period from May 21-23, 12 adult hares were handled, including four of those trapped in April. (Records of

all adult females that were retrapped in one or more trapping periods are indicated in Table 16.) All were lactating. Palpation of these hares mostly was inconclusive, although three were not considered palpably pregnant, while four others tentatively were assumed pregnant--and each of the four may have contained two embryos. If, as seems likely, conception was fairly synchronous, parturition may have taken place among this group of females in mid-May and shortly before the trapping period. An additional item of evidence was the capture by hand of an immature juvenile on May 19, estimated as less than a week old, indicating birth had occurred about mid-May.

An adult female trapped from off the main study area on May 21 and held in captivity, gave birth to a litter of three on June 21. Evidently conception must have taken place approximately May 15.

Conaway and Wight (1962) analyzed conception dates in populations of wild cottontails, and demonstrated close synchrony in the onset of breeding. Marsden and Conaway (1963) also found that breeding of wild cottontails is highly synchronized and that reproductive behavior of an entire population may be influenced by inclement weather. While few observations of this nature were obtained for snowshoe hares in Oregon, it seems likely that the findings concerning reproductive behavior of cottontails also may be relevant to this species.

In all, 22 adult females were handled repeatedly during the seven trapping periods, from April through September, that



encompassed the period of reproductive activity in 1961. Most of these females were caught one or more times in each of three or more trapping periods--six were caught in only one trapping period and one hare, No. 888, was handled repeatedly in each of the seven periods. None was found lactating in April and only one of the seven handled was pregnant. Likewise, in September, none of the hares examined during either of the trapping periods was found lactating or pregnant.

All of the 12 adult females handled during the trapping period in May were lactating, but only four were considered pregnant. In June, half of the adult females examined were lactating, and 7 of the 11 were found pregnant. During the trapping period in July, pregnancies were detected in 11 of the 12 adult females examined and apparently most were near term. Autopsy of an adult female, No. 861, that had died in a trap during this period, revealed three unborn young that were estimated to be 24-days old--indicating conception occurred approximately June 18. None of the 11 adult females examined in August was found pregnant (data on two others were unrecorded) and only 4 of the 12 were lactating.

Adams (1959) palpated females to determine whether or not they were pregnant and used the same technique to estimate the number of unborn young in each pregnant female by counting embryos. He had not tested the method against the results of internal examinations, but palpation-counts made during a single pregnancy in each of 11 individual

pregnancies showed that observations were highly variable.

This procedure also was attempted in this study, but results were inconclusive. The reliability of determination of pregnancy by palpation is uncertain and it is doubtful that pregnancies may be accurately determined as early as six days after beginning of pregnancy as assumed by Adams. Since the length of the palpable gestation period is needed to determine average number of litters born to a female by the method of Green and Evans (1940c) and since it is unknown, use of this procedure to estimate the average number of pregnancies is limited.

#### Number of Litters

On the basis of repeated examinations of the 22 adult females handled during the breeding season, it is likely that most adult females on the area studied may normally have from two to three litters each year. No evidence was obtained of an individual female producing four litters during the breeding season in 1961.

Other investigators have reported a range of two to five litters a year, but the average is less than three. Aldous (1937) believed that two litters a year for each adult female was more likely than three. MacLulich (1937) reported that hares in Ontario had an average of three litters a year. Criddle (1938) estimated the number of litters as from three to five each year. Green and Evans (1940c) found an average of 2.3 litters a year for each adult female examined over a period of

seven years in Minnesota. Among captive hares studied by Severaid (1942) in Maine, average number of litters for 16 and 17 females was 3.00 and 2.75 in each of two years, respectively. Rowan and Keith (1956) found that hares in Alberta averaged 2.75 litters a season. Adams (1959) used the method of Green and Evans (1940c) to estimate the average number of litters born to each adult female on his study area in northwestern Montana and found the incidence of pregnancy was 2.9 pregnancies to a female for the breeding season in 1953 and 2.8 in 1954. Dodds (1960b) employed the same method to determine the number of litters produced. He found an average of 2.82 litters a year for hares in Newfoundland.

The earliest pregnancies apparently began about the first week of April and if these females had been bred again on the same dates that parturition occurred--as seems probable based on findings of Severaid (1942, 1945)--birth of the third litter would have occurred in late July. No birth-dates were estimated to have occurred after mid-August, based on the calculated date of birth of young juveniles caught in August and September. For example, the youngest hare tagged on the main study area (tagged September 6) weighed only eight and one-half ounces and was estimated to be about three weeks old--indicating probable parturition about mid-August. Significantly, a female trapped on an adjacent area, July 13, and necropsied, was carrying five embryos that were judged 20 days old when aged by comparison to

findings of Bookout (1964); indicating parturition normally would have occurred July 30.

Pregnancies have been recorded in snowshoe hares much later. For example, Dodds (1960b) recorded seven extremely late pregnancies in hares in Newfoundland and calculated that breeding had taken place in late October and November, but he was not able to determine whether or not the females were young-of-the-year or adults. Siegler (1954) reported a pregnant hare collected November 28 in New Hampshire that was near term; indicating that breeding occurred in late October. Criddle (1938) also reported that pregnancies may occur as late as October.

Most investigators--Grange (1932), Aldous (1937), MacLulich (1937), Severaid (1942, 1945), Rowan and Keith (1956), Adams (1959) and Dodds (1960b)--have found that August was the last month of pregnancy in the snowshoe hare. However, Adams believed that the reproductive period was terminated earlier in Montana than in other regions. The latest records of palpable pregnancies were July 10-13 and he concluded that pregnancies may be terminated about August 1.

### Size of Litters

On the basis of palpation of females handled on the main study area, counts of fetuses were made of 16 pregnancies presumably in late stages of gestation. Two or three fetuses were counted in each

instance and the average number determined by this technique was 2.4 to a pregnant female. The five pregnant females that were necropsied each had two to five unborn young estimated to be 19 to 29 days old. The mean number of fetuses was 3.2.

Mean litter-size has been reported by several investigators, including a few records for Lepus a. washingtonii, reported by Scheffer (1933). Counts of embryos of 266 pregnant females examined by Aldous (1937) in Minnesota showed an average of 2.84 to a female; the mode was three. The data collected by Aldous over a three-year period showed that only two females carried as many as seven embryos; one carried six, and six each carried five embryos. MacLulich (1937) found an average of 3.4 young to a litter, and Green and Evans (1940c), reported 2.90 embryos to a female, based on 140 pregnant hares examined. Only one litter was found to contain as many as seven embryos. Severaid (1942, 1945) found the average litter-size of captive hares in Maine was 2.92, based on 161 pregnancies observed during two years. He observed seven litters born in captivity, or as determined by post mortem examination, and noted that they varied in size from two to six; each of three of the females examined had five unborn young near term. Rowan and Keith (1956) found one to seven fetuses in each pregnant female examined in Alberta. The average litter size was 3.82.

Adams (1959) reported the average number of young to a litter

as palpated in 32 pregnancies was 2.72 and the following year nine pregnancies had an average of 3.00 embryos, as determined by palpation. Dodds (1960b) reported an average of 3.1 young in each of 16 litters born in captivity, and including records of 52 pregnant females caught in the wild, the average size of litters for hares in Newfoundland was 3.3

## DEVELOPMENT, WEIGHT, AND STANDARD MEASUREMENTS

Estimates of the rate of growth were based on the periodic measurement of trapped samples of juveniles born in 1961 and the repeated remeasurement of many of these tagged hares. Weight and factors that influenced weight-loss, and standard measurements were analyzed for sex and age-groups for each trapping period.

### Development of Juvenile Hares

A growth curve was plotted following the procedure used by Adams (1959) and based on the form of the growth curve developed by Severaid (1942) for hares in Maine. This curve was constructed analogous to the growth curve of Severaid, but with the origin lowered to the level of the mean weight at birth of hares from the study area and with the right-hand end of the curve lowered to the average weight of juvenile hares in winter (Figure 21). Birth-weights of hares were based on a litter of three young born in captivity; weights of juveniles were based on a sample of both sexes tagged in 1961 and recaptured repeatedly during trapping periods in January to March 1962. The rate of growth was assumed to be the same for hares on the study area in western Oregon as that reported by Severaid for captive juvenile hares in Maine.

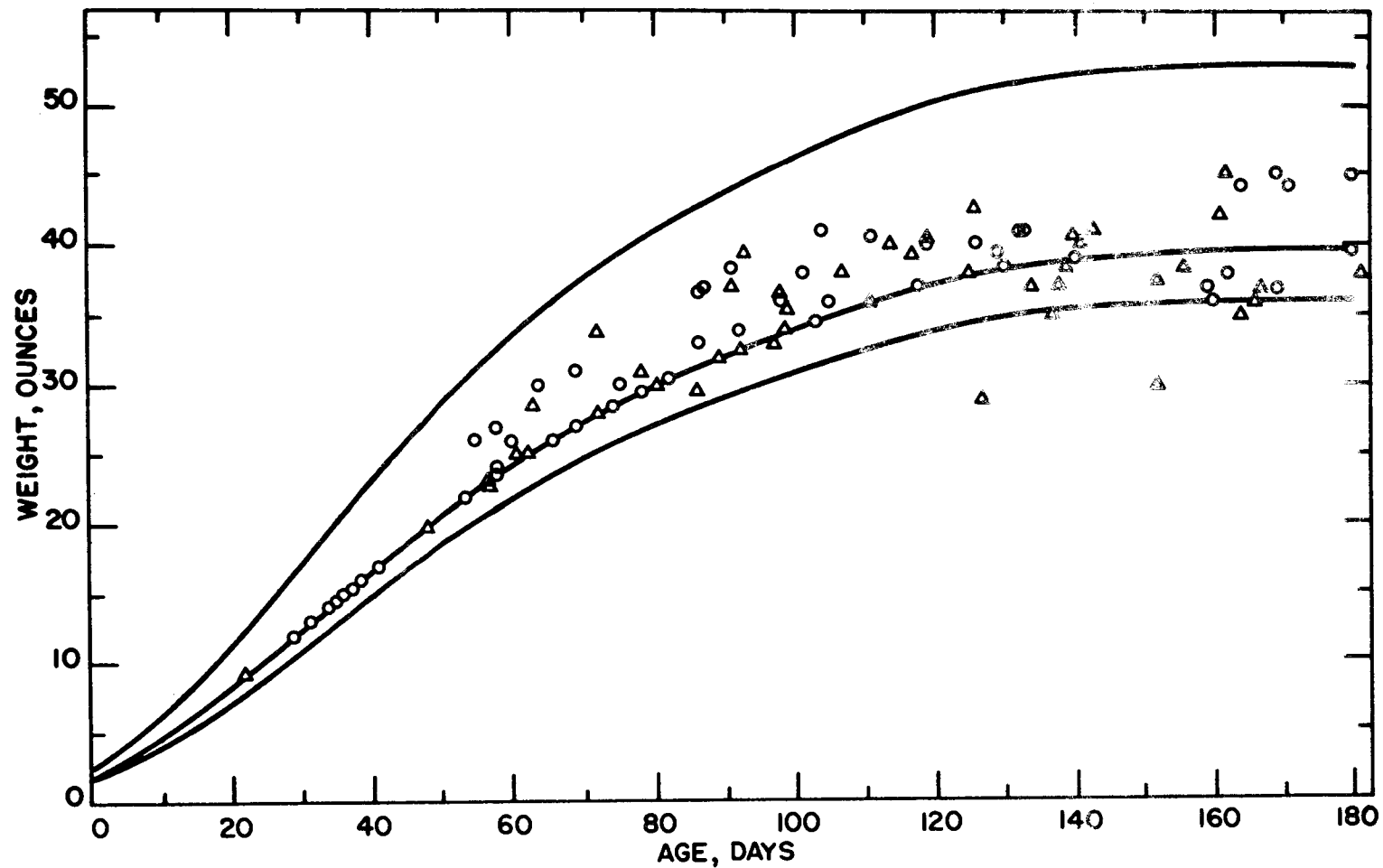


Figure 21. Growth curves for average weights of juvenile snowshoe hares. The upper curve was drawn from Severaid's data for captive hares of known age in Maine. The lower curve was constructed by Adams for live-trapped, juvenile hares in Montana. The middle curve is adapted from Severaid's curve to fit the mean weights of juvenile hares from western Oregon. Weights of hares born in 1961 and caught in two or more trapping periods are represented by triangles for males and circles for females.



The method used by Adams provided an empirical test of goodness of fit of this modified curve for hares from western Oregon. That is, the initial weight of each hare born in 1961 and recaught in one or more trapping periods was placed on the curve at the appropriate weight-ordinate, letting the point fall on whatever date-abscissa it would. An assumption of the method is that all hares fall on the weight-age line at the time of first capture. Their initial weights on each later trapping period in which they were recaught were plotted according to the number of days since the last weighing and at the correct weight-ordinate, irrespective of where the point might be with reference to the curve of growth.

Adams postulated that, if a hare was growing more slowly than the rate indicated by the modified curve, the points subsequent to the one plotted from the first weighing would fall below the line. Conversely, if a hare grew at a more rapid rate than the curve indicated, the secondary points would fall above the line. Therefore, if the rates of growth of hares on the study area coincided with the rate indicated by the modified curve, there would be approximately as many points above the line as below it. Inspection of the distribution of points for juvenile males and females about the modified curve indicates a failure of fit, particularly in the period from 60 to 120 days. The goodness of fit was better after 120 days. Apparently the rate of growth of hares was more rapid than indicated by the modified curve

and it may be inferred that the juvenile hares in this population attained their maximum juvenile-weight sooner than the hares studied by Severaid or Adams. There were no fluctuations in the distribution of weight-at-age data comparable to those found by Severaid and Adams, both of whom reported irregular gains after about the 100th day.

These findings indicate that there is no definite time of cessation of growth for all juveniles, primarily because of differences in growth rate as influenced by time of birth. Those few points that fell widely below the curve represented juvenile males born late in the summer that did not gain at the same rate as hares born early in the summer. Adams (1959) reported a similar observation, as follows: "Those hares born early in the summer reach maximum weight in fall and early winter. Hares born later continue to grow through most of the winter. "

Most juvenile hares nearly attained their maximum weight by 120 days, excepting hares born in later litters. This inference is supported by the mean weights of individual hares caught each trapping period (Figure 22). The mean weight of juveniles of both sexes, born in 1961 and weighed in October of that year was 40.3 ounces. The age of all hares in this sample was presumably less than six months, since there were no indications of parturition occurring before May. The mean weight of juveniles of both sexes remained fairly constant in subsequent trapping periods.

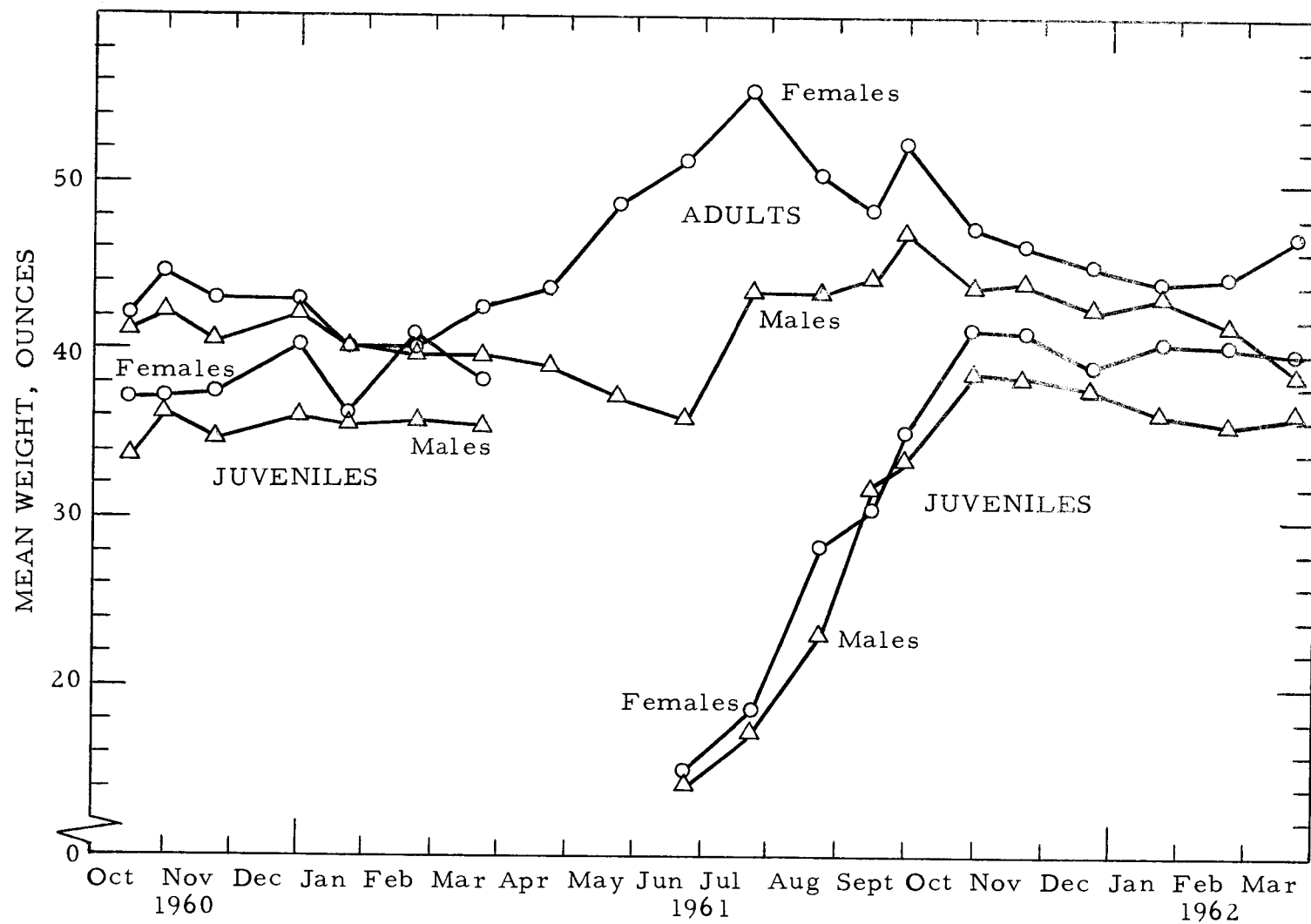


Figure 22. Mean weights of individual hares caught each trapping period.

### Monthly Weights

Mean weights of individual hares caught and weighed each trapping period are shown in Figure 22. Data were divided according to sex and age, because of the marked increase in weight of adult females during the breeding season and the rapid gain in weight of juveniles of both sexes during the summer.

Most monthly samples were comparatively large in all categories, but varied in size as indicated in Table 6, which lists the number of individuals caught in each trapping period. All hares born in a previous year were arbitrarily classified as adults after March, as previously noted. Juveniles born in 1961 were present in samples after June. Mean weights were based on the weight of each individual hare at the initial weighing in each period. Weights of a few hares listed in Table 6 were not recorded.

Mean weights of older juveniles and adults, during the non-breeding season, were comparatively uniform and constant from month-to-month. There was a consistently small disparity between weights of juvenile and adult males and females throughout the annual cycle. This difference was pronounced during the breeding season when many females were pregnant during a given sampling period. Mean weight of adult females increased sharply in May, indicating the influence of pregnancy. Mean weights of adult females caught each trapping period

reached a peak of 55.3 ounces in July, but did not approximate pre-breeding season conditions until October 1961.

Adult males apparently lost weight in late winter, coincident with the beginning of the breeding season. But the decline in mean weight of adult males sampled in April, May, and June is partly due to the inclusion of smaller males that previously had been classed as juveniles. The size of the samples of males also were so small that little significance may be attached to apparent fluctuations in their weight. Samples of adult males remained small through the summer and this may partly explain the greater average weight of adult males handled during that period.

A singular record of fluctuation in weight of an individual is that of male No. 929 that was recaptured 33 times from October 1960 to March 1962. It weighed 40 ounces when first caught, but its weight declined slightly to 36 ounces by spring of the next year. During the summer this animal, now classed as an adult, apparently gained rapidly to a peak of 50 ounces in September. But by March 1962 this adult male weighed 40.5 ounces, the same as it weighed in March 1961.

Rowan and Keith (1959) determined the weights of snowshoe hares from month-to-month over the entire year, based on hares collected in north-central Alberta. Since no attempt was made to distinguish between adult and juvenile hares after the end of August, average fall-weights included both older juveniles and adult hares. They found that

males and females exhibit similar fluctuations in weight during the nonbreeding period, and that hares increase in weight during the fall, culminating in December. This increase presumably was accentuated by the growth of juveniles which had not attained adult weight. A significant loss in weight occurred in January, but fluctuations in monthly weights from February to May lacked significance. Another sharp rise in weight took place in June, followed by a marked reduction in August.

Changes in weight, other than those brought about by the initial growth of an animal or during pregnancy were thought to represent changes in the amount of body fat. These changes were not believed to result from the varying availability of food, but a reduction in nutritive quality of food as winter progresses was considered a possible influence. Rowan and Keith also noted that the increase in weight of hares sampled in June corresponded to the annual "green-up" of vegetation in Alberta.

The progressive decrease in mean monthly weight from February to May tentatively was associated with the onset of reproductive stress, by these investigators. Conversely, the gains in weights of hares in fall were thought to have resulted from the absence of sexual activity.

Dodds (1960b) found that the seasonal trends in weights of 167 adults hares collected in Newfoundland was quite similar to that reported by Rowan and Keith, although the differences among monthly

samples were nonsignificant. The weights of adult males and females were comparatively stable for the months of January to May, but weights of both increased in June. Males handled were heaviest during the fall from September to December. Females sampled were heaviest during June, July, and August, presumably because most were pregnant. He concluded that adult hares of both sexes increase in weight during the fall and early winter in Newfoundland.

Dodds (1960b) speculated that there may be an increase in efficiency in converting food to body fat after the breeding season. Increased losses of body heat and use of stored fat during cold weather, he suggested, may be compensated for by reduction of activity with greater snow cover. The metabolism may again undergo a change with increased endocrine activity that leads to reproductive processes in April and May. This mechanism was proposed by Dodds to explain the apparent loss of weight in January, followed by fairly stable weights during the coldest months of winter, and increased body weight in May caused by availability of green vegetation and pregnancy in females.

The continual decline in weight of adult and subadult hares from January until the onset of the breeding season, and the increase in weight of males and females during the summer were fairly comparable to the findings of this study. The principal differences with these results were found in September when adults probably were near their highest weight in western Oregon, in contrast to the lowest monthly

weights of adults as found by Rowan and Keith (1959). Rowan and Keith, and Dodds (1960b) also reported a rapid increase in weight of adult males and females from September to December, while the results in the present study indicated a gradual decline in weights of adults during the fall and winter.

It seems likely that the disparity between weights found in September in this study and those reported by Rowan and Keith was caused by their combining juvenile and adult hares in the same sample. Also, adult females were significantly heavier in western Oregon during the winter and through most of the reproductive cycle, whereas Rowan and Keith, and Dodds, reported that the difference between the sexes were nonsignificant during this period.

#### Weight-loss in Fall and Winter

Much of the apparent fluctuation in the average monthly weight of hares sampled was due to differences in the sex ratios and age composition of the samples obtained in each trapping period. It was also difficult to compare seasonal differences in weight that were not influenced by growth, or pregnancy in adult females. However, a comparison was made of hares' weights during late fall and early winter after juveniles had nearly attained adult size, and during a period of little or no reproductive activity.

It was observed that most older juveniles and adults weighed



less in early winter than their corresponding weight in late fall. In order to test this observation, the mean weights of all hares caught in one or more trapping periods in both the fall and winter were determined, as is listed in Table 19. Hares sampled each year were different with exception of a few individuals that were handled in each three-month interval during the non-breeding season in both years. In all, analyses were based on 53 records that were subdivided by sex, and years (1960-61 and 1961-62). This procedure afforded an approximate comparison between mean weights in the late fall and early winter.

Table 19. Mean weight of older juvenile and adult hares caught in one or more trapping periods in each three-month interval during the fall and winter of 1960-61, and 1961-62. Weight in ounces.

Year	<u>Juvenile and Adult Males</u>			<u>Juvenile and Adult Females</u>		
	Size of Sample	Oct. - Dec.	Jan. - Mar.	Size of Sample	Oct. - Dec.	Jan. - Mar.
1960-61	11	39.2	38.2	12	41.6	39.4
1961-62	16	41.4	40.1	14	44.0	42.9

The differences between weights in fall and winter were analyzed by t-tests on the paired observations for sexes and years. The mean loss in weight of all hares was 1.4 ounces, and losses in weight were significant for both sexes. Differences between weights of females in fall and winter were highly significant (one-percent level) in 1960-61,

and were significant at the five percent level in 1961-62. The mean difference between weights of males in fall and winter were nonsignificant in 1960-61, but were significant at the five percent level in 1961-62.

#### Mean Weight of Adult Hares

The weight of adults of both sexes was compared during a period of little or no breeding activity. Thus, the mean weight of each adult handled one, two, or three times during January-March 1962 was determined. Mean weights of individual males ranged from 34.5 to 46.5 ounces; range of weights of individual females was from 38 to 49.8 ounces. The mean weight of 21 males was 40.6 ounces and of 18 females, 43.4 ounces. This difference was analyzed by means of a t-test and was significant at the five percent level. The mean weight of adult hares of both sexes in winter was 41.9 ounces, or 1189 grams.

An adult male, No. 892, that weighed 50 ounces in September was the heaviest adult male weighed during the study. The heaviest nonpregnant, adult female, No. 838, weighed 52 ounces in October 1961. A pregnant female, No. 833, whose average weight during the nonbreeding season was 49.5 ounces, weighed 66 ounces in July.

Severaid (1942) recorded an average weight of 1229 grams (43.3 oz) for 153 wild adult hares caught in February 1940 and 1941, while 38 captive hares weighed in February and December 1940 had an average weight of 1636 grams (57.7 oz). Adams (1959) reported

that the average weight of 36 hares of both sexes live-trapped in January and February 1953-54, in Montana, had an average weight of 1132 grams or about 40 ounces.

The mean weight of adult snowshoe hares from the area studied in western Oregon is nearly the same as that reported by Severaid for wild hares in Maine and apparently is not significantly different from hares live-trapped in Montana, as reported by Adams.

Reports from other investigators indicate that mean weights of some subspecies may be substantially larger than the mean weight of wild adult hares sampled in Oregon, Montana, and Maine. For example, Grange (1932) stated that the average weight of adult snowshoe hares in Wisconsin ranged from 1400-1600 gm (49.3-56.4 oz). Green, Larson, and Bell (1939) reported the mean weight of 153 non-pregnant, wild hares from Minnesota as 1402 gm (49.4 oz). Rowan and Keith (1959) found that the mean weight of wild hares in north-central Alberta, from January to April inclusive, was  $1424 \pm 34.0$  gm for females and  $1390 \pm 33.9$  gm for males. The difference between the sexes was nonsignificant. Dodds (1960b) listed the average weight of 167 adult snowshoe hares in Newfoundland as 54.0 ounces; weights were recorded over a 12-month period and included 15 pregnant females. Mean weight of 87 adult males was 50.3 ounces and of 80 adult females was 58.0 ounces. Dodds noted that the largest nonpregnant female weighed 80 ounces and was collected in August. The largest

male weighed 67 ounces and was collected in October.

### Effects of Successive Captures on Weight

It was noticed that hares that were caught two or three times during a trapping period usually weighed less after each successive capture. For example, nearly all hares recaught on successive trap-nights during January - March 1961 lost from one to six ounces after the second or third catch, and only a few showed no change in weight, or were one ounce heavier after the second successive capture. None showed a net gain after the third successive catch. Some of the largest losses in weight were found in adult females during the summer. Thus a pregnant and lactating female, No. 838, lost 5 1/2 ounces after having been caught on the first and third trap-nights during June, and two actively lactating but non-pregnant females -- Nos. 820 and 996 -- that were caught on successive trap-nights during August lost 4 and 4 1/2 ounces, respectively.

To test the significance of these observations, weights of juveniles and adults were divided by sex and the mean weight of hares caught two times during a trapping period were calculated for intervals of three months, as is shown in Table 20. This arrangement of the data also has the advantage of demonstrating the distribution of the records between sexes and among periods. Hares recaught on the first and second, and the first and third nights of a trapping period were

Table 20. Comparison of the mean weight of juvenile and adult hares caught two times during a trapping period, by intervals of three months. Weight in ounces.

Date	Males			Females		
	Size of Sample	First Time Caught	Second Time Caught	Size of Sample	First Time Caught	Second Time Caught
Oct. -Dec. 1960	8	36.1	36.6	6	38.3	36.2
Jan. -Mar. 1961	20	36.9	35.4	13	40.0	38.5
Apr. -Jun.	8	37.6	36.8	11	47.5	45.0
Jul. -Sept.	17	33.6	33.0	20	40.1	38.9
Oct. -Dec.	21	39.6	39.0	18	43.0	42.3
Jan. -Mar. 1962	23	38.9	38.4	20	44.0	43.0

treated alike. Hares recaptured on the second and third trap-nights were treated the same as hares caught on the first two nights of trapping in a period.

The data, which were based on 188 records of weights of hares caught two or more times in a trapping period, were analyzed by analysis of variance and were found highly significant (one-percent level) for weight at first capture compared to weight at second capture, for sex, and for time of year. Since there was a significant interaction between sex and time of year, differences between means of periods of three months were tested by the method of least significant difference. The periods of April-June, and July-September were found significantly different at the one percent level. The probable explanation of these differences is that most females sampled in April-June were pregnant and therefore much heavier than males, and in July-September proportionally more young juveniles of both sexes were caught than were adults, hence the mean weight of all hares caught during this period was much less than the mean weights of hares sampled in April-June or in October-December 1961.

Separate analyses of variance were made for weights of juvenile and adult males, and females that were caught on three successive nights during a trapping period. Rather than calculate mean weights by intervals of three months for the smaller number of individuals that were weighed a third time during a trapping period, the

individual observations were used in the analyses of variance to minimize the effect of the range in weights among individuals. The results of both analyses were highly significant as were the LSD's between mean weight of first, second, and third captures for both sexes at the one percent level, excepting the difference between mean weights of females on the second and third times caught, which was significant at the five percent level.

Only a very few of the hares caught on three successive nights showed a net gain in weight, and losses ranged up to 6 1/2 ounces. mean loss in weight for all males and females caught three successive times during a trapping period, based on 59 records, was approximately one ounce between each successive capture.

During the extended trapping period in February 1962, three hares were caught on six successive trap-nights, two were caught on five successive nights, and five others each were caught four times during the six-day trapping period. The weights of these hares fluctuated following each successive capture, but a downward trend was evident. Each of these hares weighed an average of one and one-half ounces less on its last capture than it had weighed after the third successive catch. An example is that of an adult male, No. 929, that weighed 41 1/2, 39 1/2, and 37 1/2 ounces following the first, third, and sixth successive captures.

Trapped hares probably were confined on the average for more

than half their normal period of activity each night. Thus, the most likely explanation for this small loss of weight after each successive confinement overnight in a trap and subsequent handling is that feeding was interfered with, and that the animals simply failed to ingest normal amounts of food between successive nights of capture. Typically, hares may have entered traps in the early evening, were deprived from feeding until released on the following midday, and may have re-entered traps that evening, before feeding appreciably, etc.

#### Standard Measurements

Standard measurements of juvenile, subadult, and adult hares are summarized in Table 21. Data were tabulated separately for males and females, because of apparent differences in size between adults of the two sexes. Since methods were not available to correctly estimate the ages of young juveniles (and to distinguish among juveniles born in successive litters), it was not possible to report development, based on standard measurements, in the form of a growth curve. However, the mean and standard deviation of the standard measurements were calculated separately for each of three weight-classes of young juveniles handled from June to September 1961. Measurements were averaged for individuals remeasured during a trapping period or remeasured in a second trapping period and while in the same weight-bracket. The smallest category of young juveniles ranged in weight from 8 to 15 1/2



Table 21. Standard measurements of juvenile, subadult, and adult snowshoe hares, Lepus americanus washingtonii Baird, from western Oregon. Mean and standard deviation of measurements of juveniles from June to September 1961, of subadults from October 1961 to March 1962, and of adults from October 1960 to March 1962. Weights are in ounces. Measurements are in millimeters.

Age, and Weight-class of Juveniles	Sex	Size of Sample	Mean and Standard Deviation					
			Weight	Head	Ear	Tail	Foot	Total Length
0-15	♂	15	12.3 ± 2.0	62.4 ± 3.9	53.9 ± 3.4	22.8 ± 4.7	76.7 ± 3.5	259.6 ± 13.8
	♀	13	12.5 ± 2.5	61.6 ± 4.5	52.2 ± 2.4	24.0 ± 4.4	76.4 ± 4.8	259.7 ± 23.0
16-31	♂	29	24.8 ± 3.4	73.9 ± 3.6	68.5 ± 4.2	28.8 ± 3.6	104.7 ± 7.3	344.8 ± 23.0
	♀	30	26.3 ± 3.5	74.0 ± 4.0	68.8 ± 3.0	28.8 ± 4.2	106.9 ± 6.5	355.7 ± 19.2
32-47	♂	14	37.1 ± 3.3	78.2 ± 2.3	73.4 ± 2.5	34.6 ± 5.6	120.2 ± 4.3	398.5 ± 14.0
	♀	15	37.9 ± 3.0	79.9 ± 2.9	74.3 ± 3.0	34.1 ± 6.1	120.7 ± 5.8	402.1 ± 17.9
Subadults	♂	27	--	79.7 ± 2.3	71.9 ± 3.4	37.2 ± 5.3	123.6 ± 4.4	406.1 ± 14.1
	♀	23	--	79.8 ± 3.1	72.0 ± 2.2	38.0 ± 4.7	125.6 ± 4.0	416.8 ± 11.7
Adults	♂	26	--	82.3 ± 2.1	72.4 ± 2.5	35.2 ± 5.5	124.0 ± 2.6	414.2 ± 10.2
	♀	28	--	83.2 ± 2.5	72.9 ± 3.4	35.9 ± 3.5	126.0 ± 4.1	425.1 ± 14.2

ounces and probably were 3 to 5 weeks of age; the next weight-class was 16 to 31 ounces and these hares were estimated to be 5 to 12 weeks in age; and the third category of young juveniles weighed 32 to 47 ounces and were approximately 12 to 20 weeks of age. All estimates of age are based on comparison with the modified weight-at-age curve for hares in this study (Figure 21).

Subadults represent a category of hares that weighed 32 to 47 ounces, and that were caught and measured one to eight times from October 1961 to March 1962. Mean standard measurements of subadult and adult hares are based on the mean of the mean of successive measurements of each individual, in each sample. Juveniles handled in 1960 to March 1961 were omitted from this tabulation, since standard measurements were accomplished only in October 1960 and these hares were not remeasured as juveniles.

Measurements of adults were obtained mainly from August 1961 to March 1962. Most were recaptured and measured repeatedly and the means were based on one to nine measurements of the same individual.

An adult male, No. 929, tagged in October 1960 and measured nine times during eight trapping periods from August 1961 to March 1962, illustrates the reliability of the measurements. The means and standard deviations were as follows: head,  $84.7 \pm 2.0$ ; ear,  $74.2 \pm 1.2$ ; tail,  $32.2 \pm 5.0$ ; foot,  $125.9 \pm 1.1$ ; and total length,  $404.7 \pm 6.4$  (measurements in millimeters). These results indicate that no

important changes in standard measurements occurred and that all measurements were repeated with considerable accuracy. The length of tail was measured with least precision.

There were no marked differences between standard measurements of young juvenile males and females in each of the three weight-categories, but the differences were not tested for significance because of the arbitrary method of grouping.

Juveniles born in 1961 that weighed 32-47 ounces had attained body size comparable to older juveniles (subadults) and adults. Since the first litters in 1961 were born about mid-May, these hares were less than five months of age. However, the mean standard measurements of subadults and adults were slightly greater, particularly, mean length of foot and mean total length. Differences in the mean standard measurements of subadult and adult males and females were tested by use of t-tests. Mean total length and head-length of adults of both sexes were significantly greater than that of subadult males and females. The only significant difference in the standard measurements among subadults was the greater total length of females. Mean total length and hindfoot-length of adult females were significantly greater than in adult males. All tests of significance were made at the five-percent level.

The largest hare handled was an adult female, No. 833, tagged

in March 1961 and measured in each of five trapping periods from August 1961 to March 1962. Mean standard measurements were as follows: head, 86 mm; ear, 78 mm; tail, 37 mm; foot, 131 mm; and total length, 450 mm. This also was the heaviest hare handled and its weight ranged from 48 to 66 ounces; the latter weight was recorded during pregnancy. The total length of four other adult females ranged from 440 to 450 mm. None of the males was this large.

Few published records are available of the standard measurements of Lepus a. washingtonii. Bailey (1936) gave the following average measurements of five adults: head, --; ear, 62 mm; tail, 41 mm; foot, 125 mm; total length, 429 mm. Dalquest (1942) reported the average length of the hindfoot and total length of 58 adults of both sexes from western Oregon and Washington were 117 mm (range 105-135 mm) and 413 mm (range 380-455 mm). The mean hindfoot-length and total length of males and females were not significantly different between sexes. Dalquest noted that Lepus a. washingtonii is the smallest (and darkest) of American snowshoe hares.

The measurements given by Bailey for foot, and total length are nearly identical to those recorded in this study. The mean measurements reported by Dalquest are smaller, but the ranges are equivalent.

Adams (1959) noted the similarity of the standard measurements of hares in Montana and Maine. For example, mean length of ear

(from notch) for 29 adult hares in Maine was 73.0 mm (Severaid, 1942). In Montana it was 72.9 mm. The mean length of the hindfoot of adult hares was 137.0 mm in Maine, compared with 136.7 mm in Montana. These results for length of ear are very similar to those of hares in western Oregon; that is, the mean ear-length of adult males was  $72.4 \pm 2.5$  mm and of adult females,  $72.9 \pm 3.4$  mm. But the mean length of the hindfoot of adult hares in this study was considerably less than that reported in Montana and Maine. The average for 26 adult males was  $124.0 \pm 2.6$  mm and for 28 adult females, the mean length of the hindfoot was  $126.0 \pm 4.1$  mm. The difference between the means was significant at the five-percent level.

Dodds (1960b) reported the average measurements of the snow-shoe hare, Lepus americanus struthopus, in Newfoundland: Based on a large sample taken over a 12-month period (mean weight was 54.0 ounces), the mean length was 455.2 mm; length of ear, 72.2 mm; length of hindfoot, 131.2 mm; and the mean tail-length of five hares was 36.0 mm. The mean length of 88 males was 458.3 mm and of 80 females, 451.9 mm--a reversal of the difference in length found in the two sexes in Oregon. Dodds did not indicate whether or not this difference in length of males and females was significant.

The measurements of ear-and tail-length are similar to findings in this study. But the length of the hindfoot and, particularly, total length (and weight) is much larger for both sexes than the same measurements of hares in Oregon and marks the subspecies in Newfoundland as a much larger-sized hare than Lepus a. washingtonii.

## SEX AND AGE COMPOSITION

Information on sex and age composition of the population was obtained principally from the samples trapped monthly and from the calendar-graph data.

### Sex Determination

Sex of hares was determined by examination of the genitalia. The penis and clitoris were everted for examination by applying downward pressure with a thumb and forefinger placed around the genital region. During the breeding season, adults also could be sexed by secondary sexual characteristics, which were palpable testes in males, and enlarged mammae in females that frequently showed signs of lactation.

Severaid (1942) described and illustrated the distinguishing anatomical characteristics of both sexes, and observed that the location of the urethral opening is the identifying feature that must be determined--the opening is terminal in males and extends farther towards the anus in females. He also noted that these characteristics were distinguishable in new born young.

### Age Determination

Age determination of juveniles during the summer was based on

size and pelage characteristics. The presence of slightly enlarged and palpable teats of females that had borne young the previous summer was used to distinguish adult females. This procedure was based on Adams' (1959) findings that the teats of immature hares were nearly undetectable by palpation. Males tagged when immature were correctly aged thereafter, but an entirely satisfactory technique was unavailable to permit accurate classification of untagged subadult and adult males. Since this subspecies does not change pelage color in winter, the aging technique suggested by Nelson (1909) and used by Adams was inapplicable; i. e. , the feet of adults are white while the feet of young hares before their first molt are brown. However, an approximate age-classification of males in fall and winter was based on weight, and on the character of the penis. Lechleitner (1959) noted that there is an increase in rugosity of the penis with age in the black-tailed jack rabbit. This tendency also appeared slightly in snowshoe hares.

Classification of hares necropsied as juveniles or adults was verified by determination of the degree of closure of the proximal epiphyses of their humeri. This aging technique was developed by Hale (1949) for the cottontail rabbit, and Lechleitner found that the time of closure of the epiphyseal groove is between seven and nine months in the black-tailed jack rabbit. Dodds (1960b) determined approximate dates of epiphyseal closure in a series of humeri obtained from captive, known-age snowshoe hares and found that an epiphyseal cartilage plate

was absent or undeveloped until seven and one-half months.

### Sex Ratio and Age Composition

Sex ratio and age composition of hares trapped during each trapping period are summarized in Tables 22, 23, and 24. Data were tabulated by periods of three months to facilitate analysis in terms of climatic changes, availability of food, and breeding activity. For example, age composition and sex ratios of hares trapped during the breeding season in 1961 are based on hares caught from April through September; the data for October through March 1960-61, and 1961-62 represent the nonbreeding seasons.

Table 23 summarizes the age composition and sex ratios of hares taken two or three times during a trapping period. This analysis was accomplished to determine whether or not seasonal differences may have existed among hares that were recaptured repeatedly.

Table 24 is a summary of the age composition and sex ratios of hares caught for the first time and tagged in each trapping period.

Based on catches of hares in each trapping period, adult females were caught more often than adult males. This tendency was most evident during the breeding season and particularly during July, August, and September, when catches of females were nearly two and one-half times that of males. The sex ratios of adults were comparable during both periods of little or no breeding activity, but the number of



Table 22. Summary of age and sex ratios of hares caught on the main study area--summed by trapping periods--for each period of three months, from October 1960 to March 1962.<sup>1</sup>

Date	Adults			Juveniles			Adults and Juveniles		
	Males	Females	All	Males	Females	All	Males	Females	All
<u>Including Recaptures</u>									
Oct. -Dec. 1960	33	31	64	47	42	89	80	73	154 <sup>2</sup>
Jan. -Mar. 1961	23	19	42	41	23	64	64	42	107 <sup>3</sup>
Apr. -Jun.	27	41	69 <sup>4</sup>	2	5	7	29	46	76 <sup>4</sup>
Jul. -Sept.	17	41	58	86	70	157 <sup>5</sup>	103	111	216 <sup>5</sup>
Oct.-Dec.	22	29	51	60	47	107	82	76	158
Jan. -Mar. 1962	43	40	83	36	20	56	79	60	139
Total	165	201	367 <sup>4</sup>	272	207	480 <sup>5</sup>	437	408	850 <sup>2-5</sup>
<u>Excluding Recaptures</u>									
Oct. -Dec. 1960	29	24	53	30	24	54	59	48	108 <sup>2</sup>
Jan. -Mar. 1961	14	11	25	17	15	32	31	26	57 <sup>3</sup>
Apr. -Jun.	19	30	49 <sup>4</sup>	1	4	5	20	34	54 <sup>4</sup>
Jul. -Sept.	13	31	44	64	58	123 <sup>5</sup>	77	89	168 <sup>5</sup>
Oct. -Dec.	17	19	36	35	33	68	52	52	104
Jan. -Mar. 1962	27	22	49	20	12	32	47	34	81
Total	119	137	256 <sup>4</sup>	167	146	314 <sup>5</sup>	286	283	572 <sup>2-5</sup>

<sup>1</sup>Thirty-nine hares caught at 32 stations on the open area during three additional trap-nights from February 13-15, 1962 are not included in this summary.

<sup>2</sup>One hare was not sexed or aged during October-December 1960.

<sup>3</sup>One hare was not sexed or aged during January-March 1961.

<sup>4</sup>One adult was not sexed during April-June 1961.

<sup>5</sup>One hare was not sexed or aged and one juvenile was not sexed during July-September 1961.

Table 23. Summary of age and sex ratios of hares caught two or three times--summed by trapping period--for each period of three months, from October 1960 to March 1962.<sup>1</sup>

Date	Adults			Juveniles			Adults and Juveniles		
	Males	Females	All	Males	Females	All	Males	Females	All
Oct. -Dec. 1960	5	4	9	15	11	26	20	15	35
Jan. -Mar. 1961	6	6	12	15	8	23	21	14	35
Apr. -Jun.	8	11	19	1	1	2	9	12	21
Jul. -Sept.	4	9	13	16	10	26	20	19	39
Oct. -Dec.	4	7	11	17	11	28	21	18	39
Jan. -Mar. 1962	12	12	24	9	6	15	21	18	39
Total	39	49	88	73	47	120	112	96	208

<sup>1</sup>Hares caught at 32 stations on the open area during three additional trap-nights from February 13-15, 1962, are not included.

Table 24. Summary of age and sex ratios of hares caught for the first time, during each period of three months, from October 1960 to March 1962.

Date	Adults			Juveniles			Adults and Juveniles		
	Males	Females	All	Males	Females	All	Males	Females	All
Oct. -Dec. 1960	18	13	31	16	13	29	34	26	61 <sup>1</sup>
Jan. -Mar. 1961	1	1	2	4	3	7	5	4	9
Apr. -Jun.	4	2	6	1	4	5	5	6	11
Jul. -Sept.	2	0	2	45	39	85 <sup>2</sup>	47	39	87 <sup>2</sup>
Oct. -Dec.	2	3	5	12	10	22	14	13	27
Jan. -Mar. 1962	4	2	6	5	1	6	9	3	12
Total	31	21	52	83	70	154 <sup>2</sup>	114	91	207 <sup>1,2</sup>

<sup>1</sup>One hare was not sexed or aged during October-December 1960.

<sup>2</sup>One juvenile was not sexed during July-September 1961.

adult females caught during the reproductive period exceeded adult males caught by a ratio of 2:1. This applied to total catches, including recaptures, and to the sum of individual hares caught during each of the seven trapping periods from April to September. But catches of juvenile males exceeded catches of juvenile females, particularly in winter. Combining catches of adults and juveniles, the sex ratios were comparatively even, but differed in both winters (Jan-Mar 1961, and 1962) when catches of males were greater than catches of females. This tendency was reversed during Apr-Jun 1961, when catches of females markedly exceeded catches of males.

Sex ratios of catches on each trap-night within a trapping period fluctuated widely, and the tendency for some individuals to be retaken two or more times within a trapping period exaggerated differences in the sex ratios of catches as compared with individual hares caught. This was illustrated during the third trapping period, in November 1960. Of the 26 catches of adults, 17 were females and 9 were males. But the difference was negligible when sex ratios of individual hares were compared. Also, wide disparities in sex ratios favoring the catching of juvenile males were recorded in February and November 1961, but these differences were negligible or reduced when based on individual juveniles caught in each trapping period.

Differences in the sex ratios and age composition of individual hares caught each trapping period were not so large. For example, a

disproportionate number of catches of juvenile males was recorded in Jan-Mar, Jul-Sept, Oct-Dec 1961, and Jan-Mar 1962. But these differences were nullified, except for Jan-Mar 1962, when recaptures were excluded.

Among hares caught two or three times during a trapping period, proportionally more juveniles were recaptured than adults in the first six months of the study. Nearly all of the hares in this category that were trapped in April, May, and June were adults. The near absence of juvenile hares during this period resulted from an arbitrary decision to classify all hares born in the previous year as adults, after March. In all other periods, except Jan-Mar 1962, juveniles in this category outnumbered adults by a ratio of about 2:1.

Sex ratios of hares caught repeatedly in a trapping period were comparable to sex ratios of individual hares caught in each period. Overall, adult females outnumbered adult males and the opposite condition obtained among juveniles, but more males were recaptured repeatedly each trapping period than females. Adams (1959) also found that sex had little influence on the tendency of hares to be repeatedly retrapped.

Sex ratios and age composition of hares caught for the first time, as tabulated in Table 24, probably are most representative of these parameters of the population as revealed by live-trapping. The number of males was significantly greater than females at the five-

percent level for both adults and juveniles. In all, 205 adult and juvenile hares were sexed and found to have a sex ratio of 80 females to 100 males. In each quarter, with one exception, more males were tagged than females. The sex ratio of 84 young juveniles tagged during Jul-Sept was 87 females to 100 males. Males outnumbered females in this sample of the population trapped at a season when movements were comparatively restricted, an abundance of food was available, and juveniles were not influenced by sexual stimuli.

The number of juveniles tagged (154) exceeded adults tagged (51) by a ratio of 3:1. This difference was principally caused by the influx into the population of young hares born during the breeding season of 1961 (Figure 12).

Wide variations in sex ratios were recorded in some trapping periods. For example, during the fifth trapping period, in December 1960, of 12 adult hares caught, 9 were females and 3 were males. But for the first five trapping periods more males were tagged and were caught more frequently than females. A second example was from the first part of the breeding season. Of 18 adults handled one or more times in April, 11 were males and 7 were females, but this ratio was reversed in the next trapping period when 12 adult females were caught compared to only 3 adult males; a disparity that continued in each of the next three trapping periods. Also, in August, eight adults were caught two or three times during the trapping period and seven of these

were females.

Sex ratios within trapping periods were comparable among juvenile hares, except in January 1961, when seven of nine juveniles caught were males and only two were females. Usually the sex ratios of hares caught for the first time during a trapping period were about equal.

Variations in monthly sex ratios shown by the calendar graphs were not comparable to the fluctuations in ratios indicated by trapping data. Adult females apparently outnumbered males throughout most of the breeding season, but sex ratios of juveniles born in 1961 were similar as determined by the calendar graphs.

Adams (1959) also reported that the sex ratios of hares trapped from month-to-month were unbalanced. But the sex ratio of 58 hares known to be alive at the start of his study in northwestern Montana was equal, and the sex ratio of 101 young trapped during one year was 43 females to 58 males (difference from unity is nonsignificant).

Most investigators have reported balanced sex ratios for snowshoe hares in the wild, if sampling was unbiased. They also have noted seasonal sexual variations in response to traps. Severaid (1942) reported that of 219 adult hares live-trapped and sexed in Maine, 108 were males and 111 were females, and of 60 young born in captivity, 28 were males and 32 were females. Of 1625 hares sexed by Aldous (1937) in Minnesota, 54 percent were males and 46 percent were

females. Webb reported a sex ratio favoring males in a sample of 386 hares shot during April and May. But sex ratios favoring females were found by Rowan and Keith (1956) for hares studied in Alberta. Dodds (1960b) found the sex ratio for 764 juvenile and adult hares examined in Newfoundland was 407 males to 357 females, which is a significant difference at the five percent level. But sex ratios of adults only were not significantly different in any of the five years of the study. He concluded that the preponderance of males was caused by their increased movement that resulted in an increased rate of capture.

Webb (1942) analyzed the sex ratios of 3920 hares trapped by Green and Aldous and showed that there was a tendency to catch more males than females in winter while the reverse occurred during the summer. That is, more males than females were caught from December to April, and more females than males were taken from April to December. Adams (1959) also suggested that males are more readily trapped in the spring than females, but during the summer the females become more susceptible to trapping than males. He attributed these differences to the influence of the mating season.

## ACTIVITY AND BEHAVIOR

Recapture data were analyzed to determine the size of home range and to determine whether or not there were differences in home-range size between adults and juveniles, and between sexes. The data also were examined to determine whether or not shifts of range or dispersal movements had taken place. Observations in the field revealed movements of toe-clipped hares, use of forms, and feeding habits.

### Home Range and Movements

Hayne (1949) reviewed the concept of home range and evaluated methods used in calculating size of home range. He noted that each method depended upon the assumption that an animal will be trapped throughout at least the biologically important portions of its home range. Hayne also was the first to present a logical approach to the problem of the relative frequency with which different portions of the home range are visited by a mammal. Stickel (1954) also compared different methods of determining size of home range from grid-trapping data and proposed additional methods of analyzing trapping data. She observed that precision in estimates of range cannot be expected, and that interference of trapping is unavoidable. Hayne(1950) questioned that determination of home range by methods of enclosing



successive points of capture revealed true home range, but rather represented "the working out of a complex relationship between an animal and a set of traps." Adams (1959) concluded that at best some of the methods of analyzing home range are of unknown accuracy, and at worst many are grossly misleading.

Whatever the interpretation placed upon analyses of home-range size, as revealed by trapping data, these data must be interpreted carefully. Furthermore, as Burt (1940, 1943) and others have noted, home range varies with sex and age of the animal, season, weather, breeding conditions, habitat, population density, and available food.

Some minimum number of recoveries of tagged hares is needed in a comparatively short period of time to determine size of home range with reasonable accuracy. Additional recoveries of the same individuals or of animals of the same sex and age are necessary to determine possible seasonal changes in size of range. Recoveries distributed over the annual cycle of an animal and from year-to-year also are needed to detect dispersal movements, or shifting of ranges. These conditions would strengthen interpretations of records of movements based on mark, release and recapture methods, and allow optimal use of recapture data to calculate size of home range. This conclusion is comparable to that made by Calhoun and Casby (1958), who stated: "Ideally, what is desired is a large number of observations of each animal in the sample. Each such set of observations should

cover a short span of time and the taking of observations should in no way disturb the animal or interfere with its movements. "

In this study, it was assumed that dispersal occurred, but this largely was undemonstrated; shifting of range and seasonal expansion of range apparently occurred, but an inability to account for hares that may have moved off the large grid and too few recoveries of most hares precluded separate treatment of these types of movements. The wider spacing of traps also influenced results, since it enabled recoveries over longer distances and allowed potentially larger estimates of range. It also is obvious that interference with the normal behavior and movements of the animals caused by trapping and handling activities may have biased results. Nonetheless, while it is uncertain how much these activities interfered with normal movements, it was assumed that the distribution of catches is significantly related to actual home range.

Records of recapture were treated as an indication of the area over which each animal was active during the period from first to last capture. Only hares caught three or more times were included in estimates of range. Two records--Numbers 680 and 449--were treated as representing dispersal movements. The computed size of range of each was based only on recaptures at the new locations. Hares did not range freely over their entire "home range" each night, but presumably used more or less of their range in winter or summer and also may have shifted their main centers of activity during the

period of the study; others may have been immigrants and moved about more widely than did hares with established patterns of home range.

Determinations of home-range size, as revealed by trapping data, were made by two methods as follows: The inclusive boundary strip method of enclosing successive stations of capture was used to compute size of trap-revealed range for hares caught three or more times, and to demonstrate changes in apparent size of range with successive captures and elapsed time between captures. The apparent size of range as computed by this method also was compared with the range in which a hare will be 90 percent of the time, as calculated by the circular bivariate distribution method of Calvin (Hooven, 1958). (The 10 percent level of significance was used with Calvin's method, because of the small average number of recatches. Size of range was not calculated for hares caught only one or two times, since this few catches did not allow a meaningful measure of "mean" radius of movement by this method.)

An assumption of the boundary-strip method for calculating size of home range is that an animal ranges, on the average, beyond the points of capture over a boundary zone extending one-half the distance towards the next adjacent station (Hayne, 1950). This system accepts the presence within the home range of traps which the animal may not visit during the relatively short series of trapping periods. In the inclusive boundary strip method of Blair (1940), the external

points of capture are considered centers of rectangles, the sides of which equal the distance between traps. The area enclosed by the connected exterior corners of the rectangles is considered to be the "home range" of the animal.

Stickel (1954) demonstrated with artificial populations that the boundary strip method of calculating size of home range provided the closest estimates of the true range among methods tested. The exclusive boundary strip method gave results closer to the true range than did the inclusive boundary strip method. But the latter method provides an objective means of connecting stations of capture and appears more realistic when the range is calculated on the basis of a small number of recaptures.

The circular bivariate distribution method devised by Calvin and used by Hooven (1958), is based on the relative frequency with which different portions of the home range are visited by a mammal. This approach to home range was first proposed by Hayne (1949). As a reference point, he took the mean coordinate point of capture, defined as the "apparent center" of activity within the home range. The distance of each point of capture from its apparent center of activity can thus be calculated for each animal. Hayne then showed that the probability of an animal being caught in a particular area of unit size decreased with its distance from the apparent center of activity.

It is significant that essentially the same premise was used,

apparently independently, by Calhoun and Casby (1958), Harrison (1958), and Calvin, in developing related methods of estimating the home range of mammals. Namely, the expectation of capturing an animal at a particular station depends upon the distance of its center of activity from the trapping stations. The mathematical expressions used by Calhoun and Casby, and Calvin to approximate the density function of the animal about its center of activity were also similar.

Calhoun and Casby (1958) made three assumptions concerning concepts of home range. Namely, the home range is fixed, there is a true center of activity, and the probability of an animal being in a unit of area decreases with increasing distance from the true center of activity. They also noted that this and the second assumption suggested a bivariate normal distribution of the density function. They then derived mathematical expressions for travels of animals between traps, on the basis of the stated assumptions, and the results of their equations were similar to those of Dice and Clark (1953).

Harrison (1958) proposed a concept of "home range" as that of a center of activity surrounded by a series of concentric "probability zones" within which an animal spends varying proportions of its time. Harrison assumed that recoveries were distributed normally about the center of activity, and found that the most satisfactory estimate of the range is the standard deviation of this normal distribution. Thus, the approach used by Harrison to estimate range of movements was

comparable to that used by Calhoun and Casby (1958), and Calvin, to estimate home-range size, although Harrison employed somewhat different mathematical procedures.

Calvin made two assumptions, related to those of Calhoun and Casby, for application of the circular bivariant distribution method. Namely, the range of the animal is circular, and the animal moves freely and at random about its entire range.

These assumptions were not fully met, since the exact shape of the home range is not known, e.g. some tendencies towards linearity of range were shown by hares on the study area. (Stumpf and Mohr [1962] analyzed trapping data for Microtus and for many other animals, and found that linearity of home range is a common condition. But, Calhoun and Casby used data on the captures of male harvest mice, Reithrodontomys, in their analyses of home range and concluded that for most of the mice the home range may be considered circular). Also, there were some indications that the trapping activities interfered with normal movements, and some hares may have developed a habit of entering traps readily, i. e. , a "trap habit". However, Calvin's method provides an objective means of approximating home range based on a comparatively few captures. The "mean" radius of movement, obtained by the standard deviation of traps catching an animal from the apparent center of the home range, may be determined readily without measurements of these radii, etc. , as required by the

methods of Calhoun and Casby (1958), and Harrison (1958). Furthermore, this estimate of the "average" radius is for a given level of significance, and is related to the number of captures. The procedure for determination of home range by this method is outlined in the Appendix.

### Size of Home Range

The computed size of range for each hare caught three or more times is summarized in Tables 25, 26, 27, and 28. The apparent size of ranges was variable and frequently there was a wide disparity between range-sizes calculated by the inclusive boundary strip method as compared with the circular bivariant distribution method. Variation among computed size of range of individual hares was partly due to the small average number of recoveries, but to a greater extent it reflected the temporal distribution of recaptures.

When the number of recaptures was small, estimates of home-range size by the boundary strip method were usually too small, and tended to be too large when made by the circular bivariant distribution method. Tracking of hares in snow and observing released hares supported the larger estimates of home range. That is, there is much evidence to indicate that hares move freely about their range and frequently avoid entering open traps. Thus, enclosing stations of capture, based on a small number of recaptures, cannot be expected

Table 25. Computed size of range of adult male snowshoe hares caught three or more times during the period of the study; includes juvenile males tagged and released from October 1960 to March 1961 and recaptured two or more times during the remainder of the study.

Tag Number	Date Tagged	Times Caught	Days From First to Last Catch	Computed Size of Range	
				Inclusive Boundary Strip Method	Circular Bivariant Distribution Method
999	10-8-60	5	306	2.36 acres	10.91 acres
985	10-8-60	7	197	0.79	1.28
980	10-8-60	7	44	0.79	1.27
972	10-9-60	5	43	3.04	19.26
968	10-9-60	7	105	0.79	.76
958	10-22-60	6	151	1.35	3.64
955	10-22-60	3	2	0.45	2.01
953	10-22-60	6	183	1.24	3.54
951	10-22-60	3	29	0.45	2.02
943	10-22-60	14	183	1.57	2.40
933	10-24-60	3	27	0.45	2.01
929	10-24-60	34	509	8.10	7.36
912	11-19-60	13	155	2.59	3.66
907	11-20-60	11	123	1.35	1.60
901	11-20-60	5	97	2.47	21.50
898	11-20-60	22	484	12.60	19.08
896	11-20-60	9	484	11.25	53.67
894	11-21-60	3	206	3.49	68.33
878	12-22-60	6	420	7.65	47.55
876	12-28-60	5	414	3.60	49.74
859	12-30-60	9	444	3.60	6.79
853	1-21-61	7	61	2.70	7.76
851	1-21-61	17	420	10.35	9.04
818	4-23-61	14	298	13.50	29.78
652	7-13-61	3	217	2.25	16.06
644	7-13-61	5	186	6.75	23.90
325	10-25-61	9	145	4.50	5.43
Mean		8.8	220	5.76	10.15



Table 26. Computed size of range of adult female snowshoe hares caught three or more times during the period of the study; includes juvenile females tagged and released from October 1960 to March 1961 and recaptured two or more times during the remainder of the study.

Tag Number	Date Tagged	Times Caught	Days From First to Last Catch	Computed Size of Range	
				Inclusive Boundary Strip Method	Circular Bivariant Distribution Method
996	10-8-60	21	306	3.37 acres	3.61 acres
994	10-8-60	8	141	0.45	0.73
991	10-8-60	7	44	0.90	1.40
989	10-8-60	5	197	2.25	12.52
982	10-8-60	14	495	6.30	14.25
964	10-9-60	6	165	2.92	13.58
962	10-22-60	8	369	2.70	6.80
960	10-22-60	5	234	0.45	0.96
947	10-22-60	13	478	2.25	5.33
946	10-22-60	5	152	0.45	0.64
939	10-23-60	4	29	1.46	9.79
916	11-19-60	6	124	1.80	4.97
914	11-19-60	6	484	1.80	1.92
905	11-20-60	4	263	2.81	32.31
903	11-20-60	7	313	4.39	45.68
892	11-21-60	4	122	1.80	9.79
890	11-21-60	4	260	0.45	0.98
888	11-21-60	23	451	6.30	11.96
884	12-21-60	10	176	0.90	1.07
874	12-28-60	4	116	1.12	4.57
872	12-28-60	16	446	3.60	5.35
855	1-21-61	5	37	3.49	15.40
843	2-25-61	5	350	3.60	29.20
841	2-25-61	11	165	2.02	3.33
838	3-21-61	11	275	2.70	4.55
835	3-21-61	11	362	4.50	6.11
833	3-21-61	11	362	6.30	11.76
820	4-22-61	7	110	3.15	11.32
805	5-20-61	5	159	3.15	30.81
311	10-24-61	8	146	1.80	2.72
347	11-21-61	11	86	6.30	27.99
Mean		8.5	239	3.30	7.38

Table 27. Computed size of range of male snowshoe hares born in 1961 and caught three or more times during the remainder of the study.

Tag Number	Date Tagged	Times Caught	Days From First to Last Catch	<u>Computed Size of Range</u>	
				Inclusive Boundary Strip Method	Circular Bivariant Distribution Method
593	6-14-61	8	190	4.05 acres	11.88 acres
682	7-11-61	14	250	4.95	6.55
680	7-11-61	6	58	1.80	1.92
512	8-8-61	20	223	5.85	8.80
514	8-8-61	3	52	1.12	10.04
518	8-8-61	5	190	4.50	20.86
526	8-8-61	4	51	1.01	3.60
528	8-8-61	6	52	1.24	2.78
532	8-8-61	3	2	0.67	4.02
536	8-8-61	3	30	1.35	42.21
36	8-10-61	6	50	1.80	9.28
42	8-10-61	4	131	1.35	1.96
577	8-9-61	4	105	1.35	2.29
405	9-6-61	3	2	0.45	2.01
409	9-6-61	4	77	2.70	14.04
449	9-27-61	4	90	0.90	--
303	10-24-61	11	146	7.65	12.65
307	10-24-61	4	58	4.05	18.28
313	10-24-61	6	29	0.90	--
332	10-26-61	4	56	4.50	20.88
349	11-21-61	13	118	1.80	0.69
374	2-11-61	3	35	2.70	36.18
Mean		6.3	91	3.37	6.17

Table 28. Computed size of range of female snowshoe hares born in 1961 and caught three or more times during the remainder of the study.

Tag Number	Date Tagged	Times Caught	Days From First to Last Catch	Computed Size of Range	
				Inclusive Boundary Strip Method	Circular Bivariant Distribution Method
598	6-14-61	7	57	2.59 acres	8.40 acres
668	7-12-61	3	56	2.25	46.22
664	7-12-61	3	57	0.67	4.02
656	7-12-61	10	248	2.25	3.64
646	7-13-61	4	57	1.46	5.22
530	8-8-61	4	51	0.79	2.28
534	8-8-61	7	190	4.50	8.53
538	8-8-61	6	133	1.35	1.53
547	8-8-61	5	77	1.35	1.60
403	9-6-61	3	23	0.67	4.02
425	9-7-61	9	161	8.55	38.58
427	9-7-61	12	193	4.50	7.66
435	9-7-61	4	192	4.05	15.34
447	9-8-61	4	74	1.35	9.79
454	9-27-61	6	85	5.40	12.43
462	9-29-61	4	108	4.95	33.61
319	10-24-61	6	29	1.80	1.92
324	10-25-61	6	109	3.15	5.36
345	11-21-61	3	30	1.80	8.03
Mean		5.6	102	3.59	7.21

to have encompassed the principal range of an animal.

Lengthy intervals between recaptures may have resulted partly from hares whose main centers of activity were outside the periphery of one or both grids; some records undoubtedly represent dispersal movements; others may represent shifting of ranges. In all cases, failure of hares to be caught frequently even over a long period of time probably contributed to the many records of dispersed catches. It also seems likely that some hares may have become "trap shy" and continued to live on the area occupied by the grid, but mostly avoided entering traps. Extended movements during some part of the annual cycle, as revealed by successful trapping of hares in the open area in February 1962, also tended to increase the estimated size of range, especially as computed by the circular bivariate distribution method.

The average size of range, as computed by the inclusive boundary strip method and weighted according to number of catches, and as computed by the circular bivariate distribution method and weighted according to the number of catches by pooling the variances; i. e.,  $\text{mean } s^2 = \frac{\Sigma(SSX + SSY)}{\Sigma(n-1)}$  showed adult males to have a larger trap-revealed range than adult females. Results are indicated in Tables 25 and 26.

This procedure of weighting the individual records was used since it logically assigned more weight to records with a larger number of catches; e. g., the number of times each hare was caught varied

widely to a total of 34 catches out of a possible 67 trap-nights, for one adult male.

The differences in mean size of apparent home range of juvenile males and females may have been influenced by slightly more recatches of juvenile males on the average. Nonetheless, the results indicate that juvenile females may have a slightly larger range than juvenile males.

The apparent size of the trap-revealed ranges of all hares caught three or more times during the period of the study is indicated by cumulative captures, in Figures 23 and 24, based on the inclusive boundary strip method. The mean size of range of all hares recaptured during each trapping period was plotted. Thus, the curves represent composite values based on times caught and season of catch, which also may have been affected by shifting of ranges and wider seasonal movements. The fact that the sample of adult hares was on the average becoming older possibly influenced the estimated size of range. The wider spacing of traps used from October 1961, also had a marked affect and the influence of the longer movements revealed as a result of alteration of the trapping program in February 1962, is evident. However, there is no indication that the estimates of size of home range of adults or juveniles have reached an asymptotic value.

The apparent size of range of juveniles born in 1961, as determined by this procedure, shows on the average a small initial size of

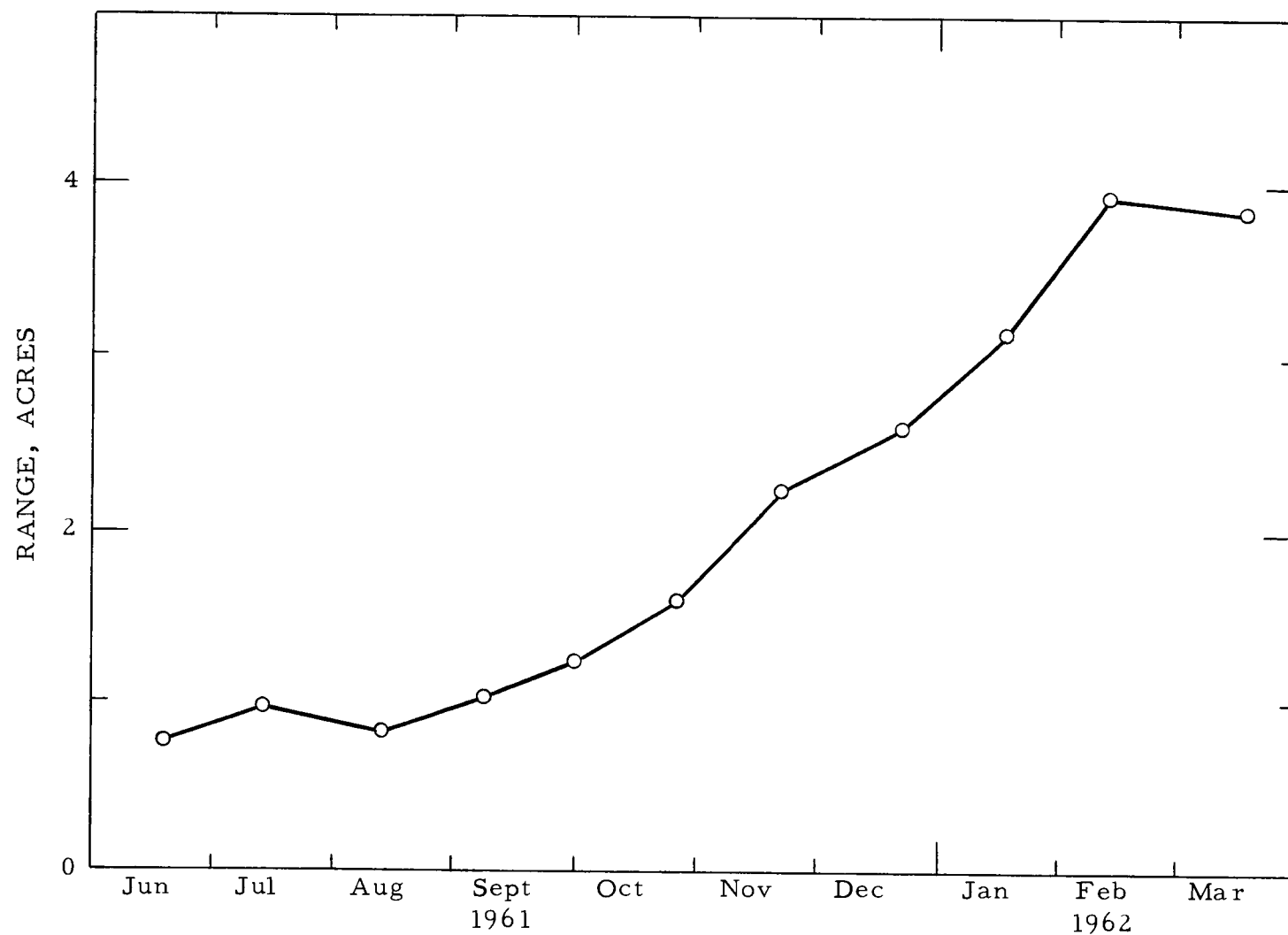


Figure 23. Apparent size of trap-revealed range of juvenile snowshoe hares born in 1961, tagged and released, and recaptured two or more times during the remainder of the study as indicated by cumulative captures.

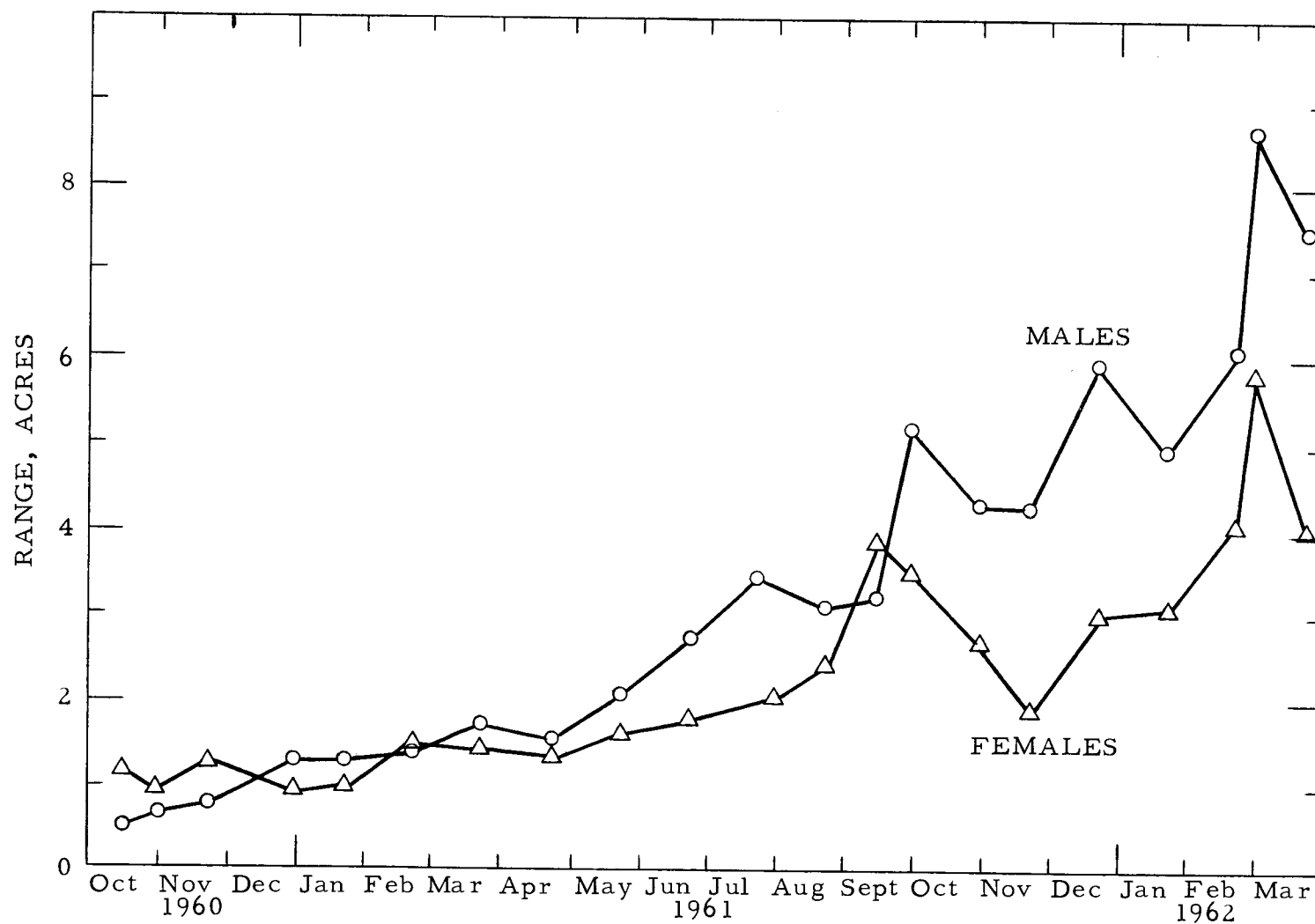


Figure 24. Apparent size of trap-revealed range of adult male and female snowshoe hares caught three or more times during the study, as indicated by cumulative captures. Data include subadults tagged from October 1960 to March 1961 and recaptured two or more times.

range (inherent in the method) that increases rapidly (Figure 24). It is not possible on the basis of these data to differentiate between changes in actual size of range and changes caused by the increased number of catches. Other factors that also may have influenced size of range were the maturation of the juveniles, changes in seasonal feeding habits, and changes in behavior preliminary to the approaching breeding season. Thus, it is misleading to interpret this curve as indicating that the mean size of range of young juvenile hares do not exceed one or two acres. But it also is evident that the size of range of older juveniles during winter is larger on the average than that of young juveniles.

The cumulative mean size of range of adult males recaptured from October 1961 to March 1962 is larger than the corresponding size of range of adult females. A corresponding difference is evident from mean size of range of adult males and females as calculated by the circular bivariant method.

The cumulative size of range of juvenile males and females did not show marked differences and the maximum mean size in 1962 of about 4.0 acres is considerably less than the estimates obtained by the circular bivariant method. By the latter method, the mean size of ranges of juvenile and adult females are nearly the same. However, mean size of range of adult males is larger than that of juvenile males.

Adams (1959) calculated size of range of snowshoe hares in



northwestern Montana by the exclusive boundary strip method, excluding occasional movements, dispersals and shifting of range, and plotted apparent mean range size as indicated by cumulative captures. He found that the home range of individuals was largest for adult males (25 acres), second largest for adult females (19 acres), and smallest for immature hares (14 acres). All values given for a range size were regarded as minimal.

Comparing data from Figure 23, which is computed in a manner approximating that used by Adams, it is apparent that the home range of hares on the study area in western Oregon was much smaller, and possibly less than half the size found by Adams. This result is probably due to more favorable habitat on the area studied in western Oregon. Some of the differences in size of range also may be attributed to differences between the two subspecies studied, since Adams presumably worked with either Lepus a. pineus or Lepus a. bairdii.

Dodds (1960b) obtained a few observations of movements of snowshoe hares, Lepus a. struthopus, in Newfoundland, by live-trapping. Six marked hares were retrapped a total of 10 times. The average distance between trap and retrap-sites was 46 yards, and was comparable to findings in this study. Dodds also noted that if the traps were not moved, hares were often retaken at the original trap-site within a few days.

Bider (1961) studied the ranges of hares in an area in Quebec

characterized by a heterogeneity of vegetative structure, and found (by live-trapping) that the daily range of males and females in summer and winter was about four acres. Daily ranges were modified in both sexes by reproductive activities.

Seton (1909, 1929) estimated the home range of snowshoe hares to be about 20 to 30 acres in brushy woods and twice that large in more open woods. He also reported that some individuals will pass their lives within a radius of 200 yards. Criddle (1938) also gave the radius of movement within the home range as a few hundred yards in dense woods to a mile or more in thin woods. MacLulich (1937) noted a few random observations of movements of hares that are in a similar category with those of Criddle (op. cit.). Aldous (1937) found by re-trapping hares in Minnesota that most of the recaptures were within one-eighth mile of the point of release. This shows a tendency towards a restricted size of range, but may indicate a much larger value than calculated in this study, since few "mean" radii of movement (at the 10 percent level of significance) exceeded 10 chains. Grange (1932) tracked a hare in snow in Wisconsin and could not drive it beyond an acre of 10 acres in size, which he concluded gave an indication of the hare's home range. Dodds (1960b) also followed two hares on the snow after they were flushed in March. Both hares circled in arcs from 60 to 200 yards in diameter. He also observed that hares occasionally travel considerable distances prior to the

breeding season and gave an example of following a single hare's track for over a quarter of a mile in mid-March.

### Centers of Activity

The trap-revealed centers of activity of hares caught three or more times are shown in Figure 25. Most were located within the second growth, reflecting the preponderance of catches in that habitat. The concentration of calculated centers of range within the area that had been occupied by the smaller grid is a result of the greater amount of trapping there.

The apparently random distribution of the centers of activity within the second growth indicates an absence of territorial behavior. This conclusion is in accord with observations of Calhoun and Casby (1958), who postulated that where there is no territorial behavior and the environment is uniform, the centers of the home range of individual animals should be distributed at random.

The overlapping of ranges is also indicated by inspection of Figure 25. Since the "average" radius of movement of adult hares was approximately five chains, the range of movements of each may have extended on the average over an area roughly equivalent to that occupied by the entire smaller trapping grid.

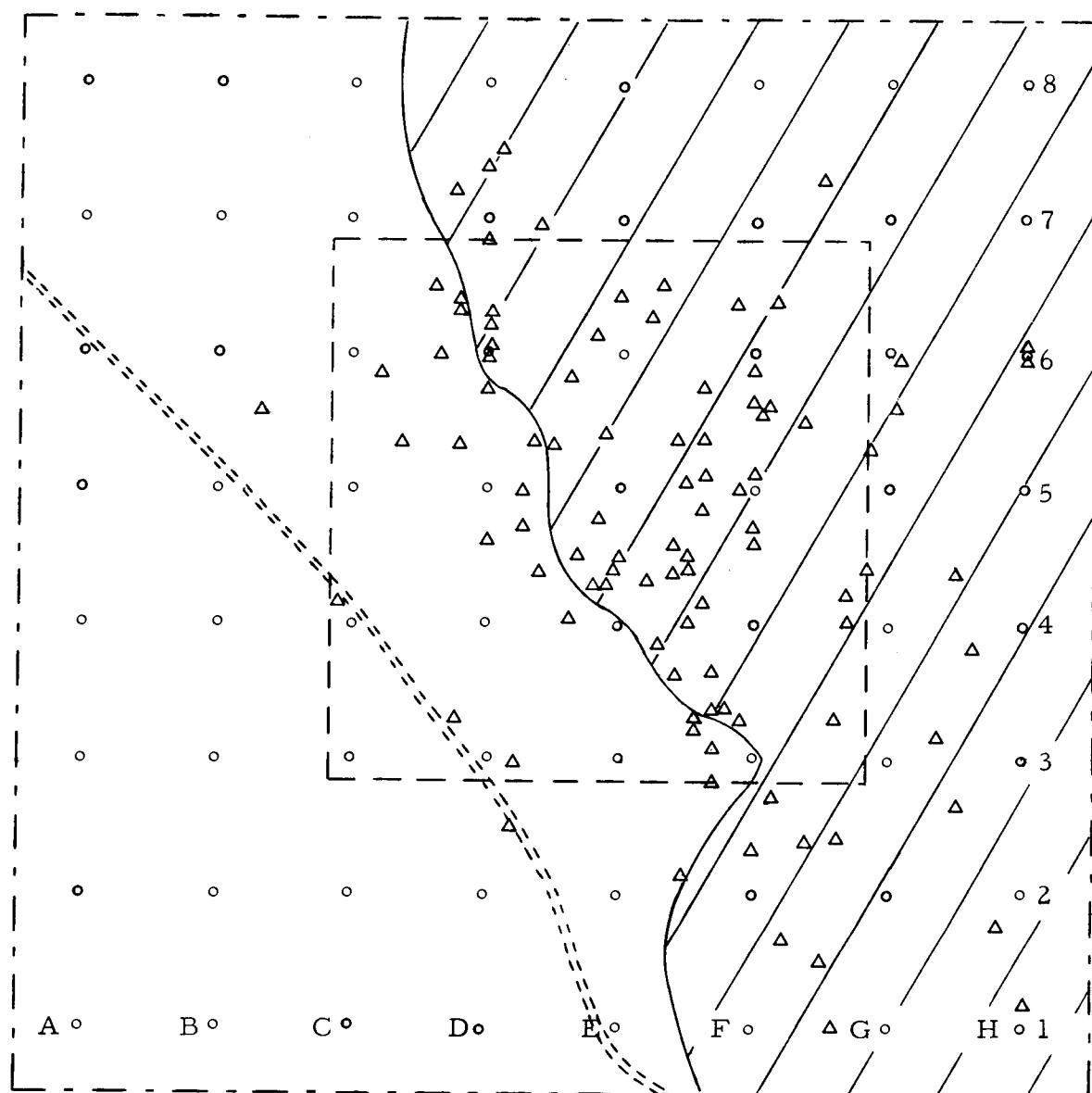


Figure 25. Trap-revealed centers of activity of hares caught three or more times. Each triangle represents the apparent center of activity of one hare. Trapping stations on the larger trapping grid are designated by open circles, and the area that had been occupied by the smaller trapping grid is indicated by a broken line. The second growth is represented by shading, and the unshaded part represents the open area.

### Examples of Movements

Many hares were recaught only one or two times and the distribution of so few catches revealed little about their movements, but the following examples illustrate typical trap-revealed movements, and some of the principal kinds of problems that were encountered: Hares repeatedly recaught over a period of several months at a small number of adjoining stations; hares caught infrequently at stations near the perimeter of the small grid and later recaught at nearby stations on the large grid, but in a portion of the area previously unoccupied by traps; hares caught at stations near the center of both grids, but seldom recaught in periods of a year or longer; hares that apparently ranged more widely in winter than at other times of the year; and hares repeatedly recaught at only one or two stations.

The most frequently caught animal was a male, No. 929, that was tagged during the first trapping period, in October 1960, and recaught in all but four trapping periods, a total of 33 times. Its apparent center of activity was near Station E-4 (on both grids) and on the edge of the second growth. Its range-size as calculated by the inclusive boundary strip method was 5.4 acres after 22 captures on the small grid and was unchanged by 11 additional captures on the large grid. However, it was caught one time at a station not encompassed by its earlier places of capture on the small grid and its

calculated range-size was expanded to 8.1 acres. The estimated size of range as determined by the circular bivariate distribution method was comparable--10.7 and 7.4 acres at the five and ten percent levels of significance, respectively. All stations of capture were contained within the "average" radius of movements--of approximately five chains--about the apparent center of activity, as calculated by the circular bivariate distribution method, but enclosing points of capture as in the "minimum area" method resulted in a trapezium-shaped figure.

An adult female, No. 996, recaptured 20 times from October 1960 to August 1961 is representative of a hare with an apparently stable range. This animal was caught repeatedly in each of 11 trapping periods during this 10-month period. It was caught from one to four times at each of ten adjoining stations within the second growth that were centrally located on the small grid; the trap-revealed center of activity was near Station E-4. The shape of its range as indicated by enclosing stations of capture was roughly circular and all but one of the points of capture lay within the circular area enclosed by its range of 3.6 acres as calculated by the circular bivariate distribution method. This estimate was comparable to the estimated range-size of 3.4 acres as determined by the inclusive boundary strip method.

The movements of an adult male, No. 898, may indicate a shifting of range, or possibly the true center of its activities may have

been outside the perimeter of the small grid. It was tagged in November 1960 at Station E-4 on the small grid and subsequently recaptured eight times on or near the boundary of that grid. It was not recaptured on the small grid after July, but was recaptured on the large grid 13 times, from October 1961 to March 1962, at stations adjacent to the previous stations of capture.

An adult male, No. 896, apparently had a home range near the perimeter of the small grid and within the second growth. It was recaptured only two times in nearly a year, after having been tagged at Station G-7 on the small grid in November 1960. But, it was recaptured at F-7 on the large grid in October, at G-7 in February 1962, and twice more in February at Stations A-5 and B-5, after traps within the second growth had been closed following the first three days of trapping. It also was recaptured at G-7 during the last trapping period, in March. This pattern of captures seems to indicate that the traps may have interfered with wider movements, but it also supports a concept of constancy of spatial occupancy that is implicit in relating movements to a center of activity. Alternately, it may indicate that hares range farther in winter.

An adult male, No. 894, was tagged in November 1960 at Station B-5 in the open area, recaptured in December at Station F-6 within the second growth, and recaptured for the last time in June at Station A-2, again in the open area. These movements suggest that

the probable center of activity was located within the small grid, but there is no explanation for its not being caught more frequently. Presumably some hares may have avoided entering traps entirely and others, as this example, seldom may have entered traps.

An example of a hare whose principal range apparently lay outside the small grid was that of an adult male, No. 859, that was tagged at Station H-1 on the small grid in December 1960. This hare was not recaptured on the small grid, but it was recaptured eight times at Stations G-2, 3 and H-2, 3 on the large grid from October 1961 to March 1962. A similar record was that of an adult female, No. 835, tagged at Station H-1 on the small grid in March 1961 and recaptured nine times within one year at four adjacent stations on the large grid; namely, Stations E-2, F-2, G-2, and G-3. There were many hares that evidenced this kind of movement, i. e., their home ranges were apparently stable for a year or longer and their movements were not influenced noticeably by trapping activities on the small grid.

An older juvenile male, No. 349, that was tagged at Station F-6 on the larger grid in November 1961, probably represents an example of a hare that had acquired a "trap habit", since it was subsequently recaptured 12 times, and in each of the remaining trap-nights, at the adjoining station (F-5).

An unusual record of movements was that of an adult female, No. 903, that was caught seven times from November 1960 to



September 1961. It was tagged at Station C-3 and recaptured four times at Station H-8 during the summer of 1961, and also at Stations A-2 and D-3 during the summer. The shape of the trap-revealed range was extremely elongate and there was a wide disparity between the estimated size of range as calculated by the two methods (Table 26).

A subadult female, No. 803, that was tagged in the fifth trapping period and recaptured only one time may have been a transient. The hare was first caught at Station H-8, in the southeast corner of the small grid and within the second growth, and recaptured three months later at Station B-1, in the northwest corner of the grid and in the open area. On the other hand, this hare may simply have been trap-shy.

The record of an adult female, No. 820, that was caught six months after trapping began and near the center of the small grid, suggests that it may have moved into the area. It subsequently was recaptured six times during the summer at six stations extending diagonally across the grid from B-2 to G-6. This unusual pattern of movements may represent the usage of an unoccupied habitat caused by mortalities on the grid during the winter of 1961.

Examination of the distribution of catches of hares recaptured one or more times, shows that the trap-revealed ranges are related to the true ranges and that the ranges of most hares are comparatively stable. These records also tend to support Brant's (1962) findings that live-trapping does not appreciably disturb movements of small

mammals in adjacent areas.

### Dispersal Movements

Dispersal movements were treated as a type of shifting of range applicable to young juveniles; e. g. , immature hares were not caught in traps before about three to five weeks of age and were assumed to have a very small home range that was confined to the area in the vicinity of the place of birth. Subsequent recaptures and, particularly, repeated recaptures of these individuals at stations widely removed from the initial stations of capture were construed as dispersal movements.

The apparent dispersal movements of juveniles hares born in 1961 are listed in Table 29, and diagrammed in Figure 26. These immature hares were all recaptured one to five months after tagging and six to 13 chains from the stations where first tagged. Hares numbered 593, 680, and 449 each were caught repeatedly over a period of three to five months at the new locations that presumably were their new centers of activity.

This interpretation of the data is necessarily tentative, since observations are based on so few recoveries. However, it is supported by the time elapsed between tagging and recapture at the new locations, and the repeated recaptures of some individuals at the new centers of activity. Also, all of these hares were tagged on the

Table 29. Apparent dispersal movements of juvenile snowshoe hares born in 1961.

Tag No.	Sex	Date Tagged	Weight (ounces)	Distance Moved (feet)	Times Recaught at New Locations, and Dates	Days Elapsed From Tagging to Recapture at New Location
593	♂	Jun. 14	14	602	(6) Jul. 11-Dec. 19	27
680	♂	Jul. 19	14	852	(6) Oct. 24-Dec. 21	105
536	♂	Aug. 8	27	495	(1) Sept. 11	30
623	♂	Aug. 9	27	602	(1) Nov. 21	104
449	♂	Sept. 27	30	634	(4) Dec. 19-Mar. 19	83
590	♀	Jun. 15	16	396	(1) Aug. 8	54
587	♀	Jun. 15	15 1/2	664	(1) Nov. 20	159
583	♀	Jun. 15	15 1/2	420	(1) Oct. 25	132
668	♀	Jul. 12	14 1/2	495	(1) Sept. 6	56

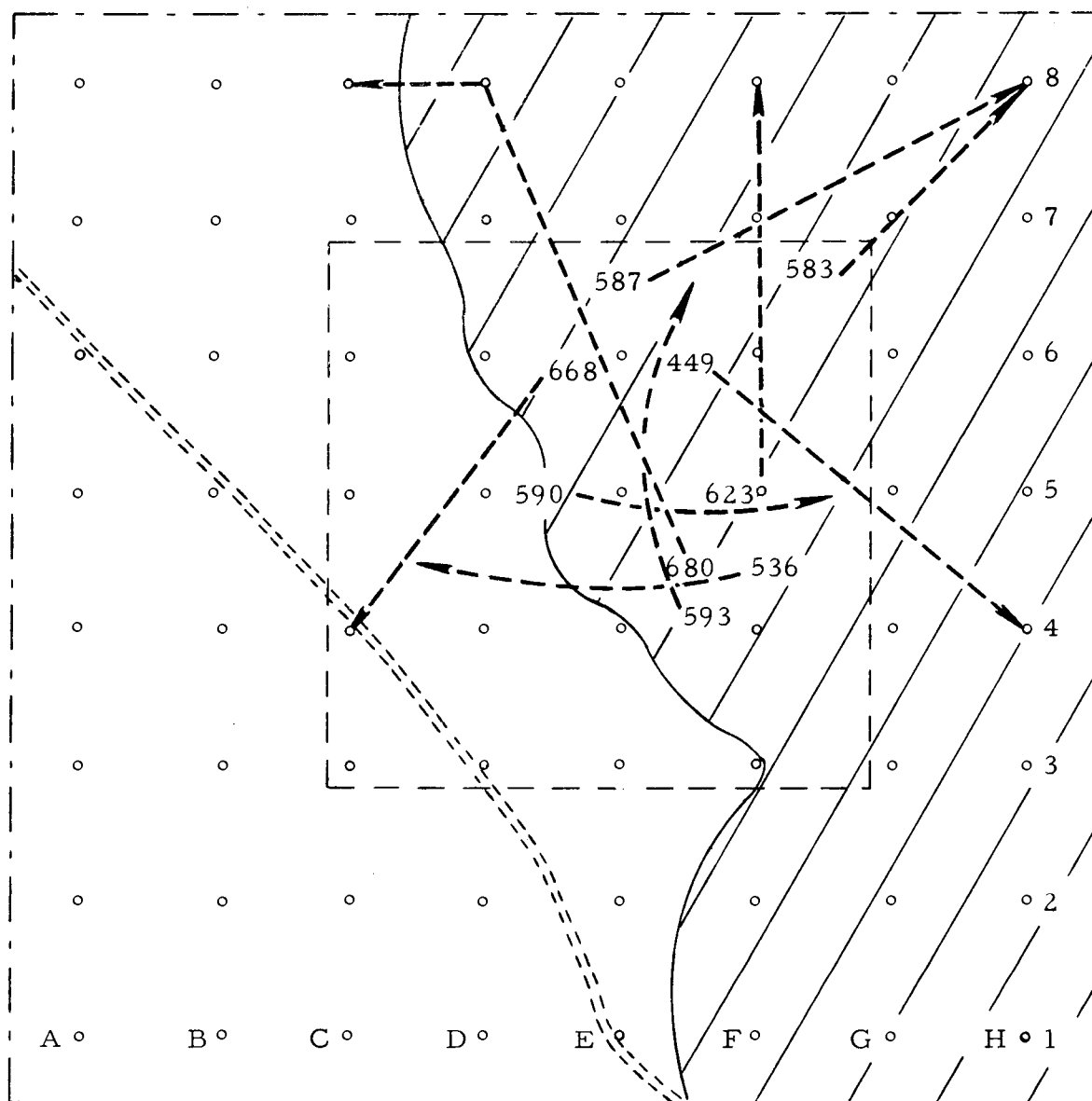


Figure 26. Apparent dispersal movements of juvenile hares born in 1961. The numbers in parentheses designate the number and the place where each hare was first tagged. The wide, broken lines indicate apparent dispersal to new centers of activity. The area that had been occupied by the smaller trapping grid is indicated by a narrow, broken line. The second growth is represented by shading, and the unshaded part represents the open area.

smaller grid, but five were only recaught after trapping stations were spaced farther apart and in that part of the second growth that had not been occupied by the smaller trapping grid.

Comparable movements were not observed in older juveniles that were first tagged during the fall and winter. Rather, these sub-adults that were recaught one or more times apparently had established ranges. Also, unlike the young juveniles, a larger proportion remained in the trapped sample. Another reason that this type of movement may not have been recorded was the small size of the grid used in 1960-61, which virtually precluded detection of dispersal or shifts in range. These observations tend to indicate that dispersal movements may have occurred mostly among young juveniles and during the summer, partly accounting for the small percentage of these hares that were recaught.

#### Movements of Hares in February 1962

An unusual series of records were obtained during the three additional days of trapping in February 1962. (The 32 traps in the second growth were closed after the usual three days of trapping, but traps at stations in the open area were set for an additional three days.)

During the first three nights of this successful trapping period an unusually large number of catches occurred in the open area-- nearly one third of the 63 catches in the first three days were recorded

at stations in that cover type. (None of the 26 hares caught one, two, or three times in January 1962 had been caught at stations in the open area.) Nonetheless, 22 individual hares were caught 39 times during the additional trapping, including three hares tagged for the first time.

An adult male, No. 929, was recaptured on six successive nights at Station D-4 in the open area near the edge of the second growth.

A subadult male, No. 512, was caught at Station C-6 in the open area and released about 11:00 a.m. It ran directly to the second growth following release and may have immediately entered the trap at Station E-8. In any case, this hare had been recaptured when Station E-8 was checked about 1:00 p.m. of the same day. This is the only record of a hare having been recaptured during the daytime and soon after handling. It is interesting that this same hare was recaptured at C-6 on the following day, and on the third trap-night was recaptured again at E-8.

Of particular interest, however, were those records of hares that had only been caught at stations within the second growth during the first three days of trapping. For example, an adult male, No. 818, had been caught at E-5 on the third trap-night, but subsequently was recaptured at A-2, and twice at C-4 on the fourth, fifth, and sixth nights of trapping, respectively. The movements of selected hares are diagrammed in Figure 27; the nights of capture are numbered.

The results indicate a tendency towards linearity of movements,

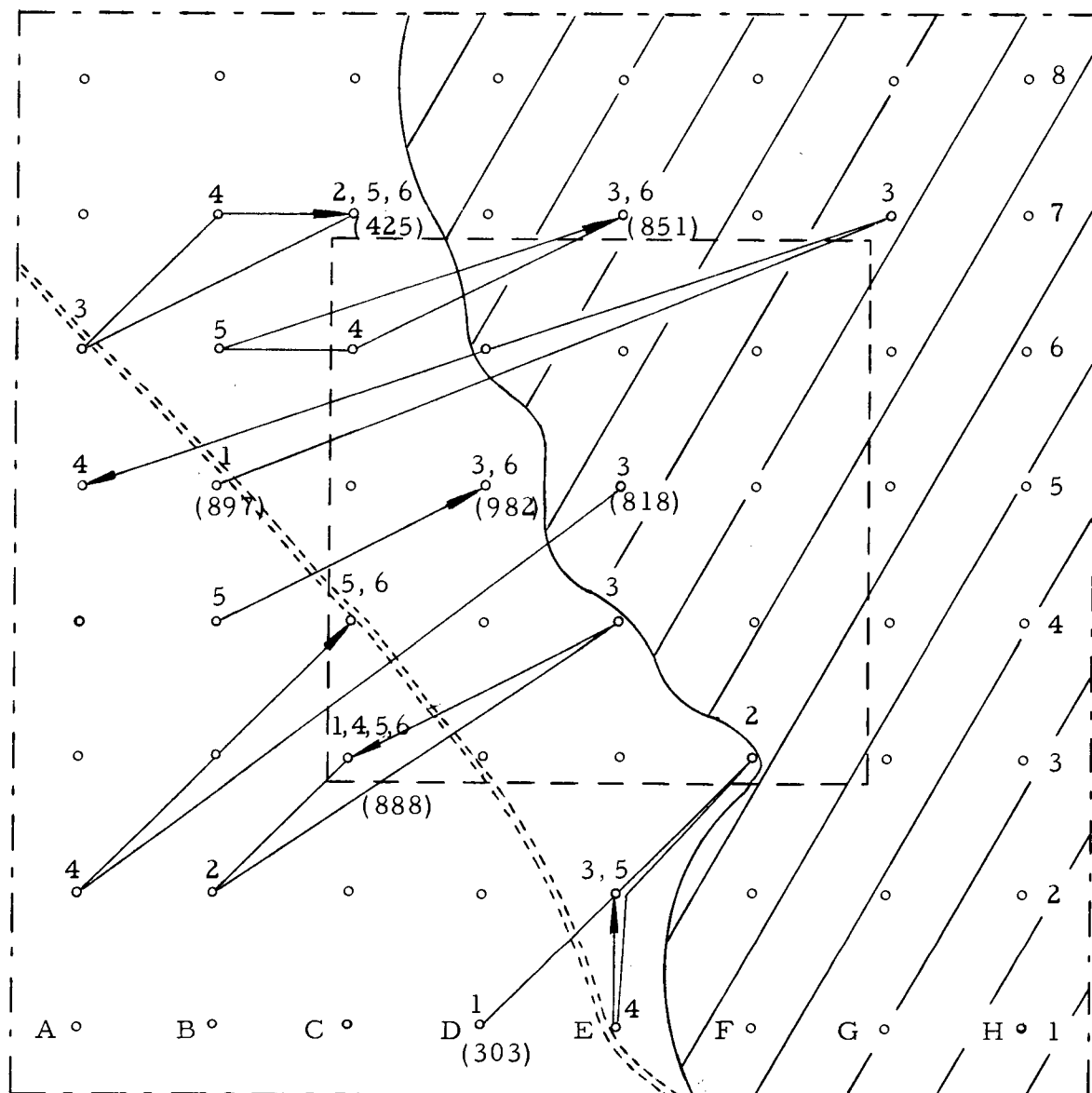


Figure 27. Examples of movements of hares repeatedly caught during the extended trapping period in February 1962 that indicate a tendency towards linearity of movements. The 32 traps in the second growth were closed after the usual three days of trapping, but each trap at the 32 stations in the open area was set for three additional days. The number of each hare is indicated in parentheses; the nights of capture are numbered.

e. g. , the trap-revealed ranges of each of the hares figured (with exception of No. 898), based on all recaptures, were approximately elliptical and the ratio of length to width was more than 2:1. There is also an indication that hares may have tended to enter traps close to their forms. Since hares apparently remained within the second growth during the daytime, they generally entered traps at stations within that portion of the area and hence were taken infrequently at stations in the open area. The data also demonstrates that hares may range farther in winter, since movements of this extent were seldom recorded in other trapping periods.

#### Movements of Toe-clipped Hares

Notched tracks of toe-clipped hares allowed identification of individuals under favorable tracking conditions, as is illustrated in Figure 7. Tracks of marked hares were readily distinguishable from tracks of unmarked hares and the identification of marked individuals was verified by examining tracks made by these hares following their release from traps.

There was little time to track hares marked by this technique during the study, but movements of several marked hares were recorded during trapping periods in February, March, and April 1961, and in March 1962. In each case that tracks of marked hares were identified along "trap lines", movements were within the area



encompassed by the stations of capture, as enclosed by the boundary-strip method. An exception was that of an adult male, No. 943 (also identified by toe-clipping as "2L, 3R"), that was tracked on the small grid for approximately 600 feet. Tracks of this hare were encountered about midday on April 21. The animal was identified, backtracked to its resting place near Station H-2, within the second growth, and followed to where it had taken shelter near Station H-6. It was uncertain whether the hare made this excursion during the early morning or during the day, but there was no indication that it was disturbed. It followed a circuitous path in traveling a straight-line distance of only 300 feet, circled twice around Station G-5 and continued in a wide loop that passed near Stations F-6 and G-7, before terminating near H-6. This animal was retrapped 13 times on the small grid after tagging in October 1961. Its home range as calculated by both the inclusive boundary strip and the circular bivariate distribution methods did not encompass its observed movements beyond the rectangle enclosed by Station G-5. Also, its trap-revealed range tended to be elliptical, and the movements described extended along the long axis of its range.

An unforeseen application of the method enabled identification of a tagged hare that escaped during removal from a trap in March 1962.

Tracking was not possible on crusted snow and the technique is limited seasonally. But hares may be quickly and permanently marked

and thereafter the existence and identification of individual hares in a population can be determined readily from their tracks in the snow. Dell (1957) described potential applications of the method and emphasized that unlike many sampling procedures which disrupt the normal activities of animals, most activities ascertained from observations of tracks reflect normal behavior.

Effects of marking hares by toe-clipping. Slight bleeding occurred following severing of the toe-ends, but snow on the ground at the time of marking may have hindered clotting of blood. Some of the hares also may have reopened their wounds while confined in traps. Five of the toe-clipped hares that were recaught during the same trapping period showed little or no bleeding. The condition of the clipped toes of the eight marked hares recaught in March was good and wounds were fully healed, with exception of the partial exposure of the first metatarsal joint on the hindfoot of one hare. No changes were noted on subsequent examinations. Dell (1957) also found no evidence of infection in any wounds made by toe-clipping, even during summer.

The sample of hares marked by toe-clipping was comprised of about equal numbers of subadults and adults. Twelve of the 15 had been tagged previously and had been recaught one or more times before marking by this method. One of this groups succumbed two days after marking and after the third successive capture. Three other marked hares were included among the five mortalities, apparently caused by

trapping and handling, that occurred in March 1961. But it is believed that any injurious effects of toe-clipping were negligible and probably did not contribute materially to the cause of death.

Concern was felt that the open wounds caused by toe-clipping might attract predators and thereby expose marked hares to added predation, but no evidence was found to support this contingency. Only one of the 15 toe-clipped hares was not recaptured. Eleven of the 15 were retrapped one or more times during the trapping period following marking, and five were recaptured repeatedly later in 1961, and 1962.

#### Use of Forms

A search was made for the forms of hares that were seen or flushed while we were checking traps. Those located were recorded, and marked with plastic tape. Since hares usually were flushed within the second growth, nearly all forms that were found and those observed regularly were near the partially cleared trap-lines within the coniferous reproduction. Significantly, no hares were seen or flushed in the open area, with exception of those that had been released after handling and were disturbed later.

Forms commonly were located in clumps of bear grass. For example, a typical form, situated midway between Stations G-3 and G-4, was located in a small opening in the second growth within dense

clumps of bear grass and bracken fern. It consisted of a cavity at the base of a bunch of bear grass and was obscured from view by overhanging leaves; access was by distinct passageways through the vegetation. Blades of bear grass had been clipped within the cavity and runways, but there was no depression in the ground, nor was vegetation matted-down in the form (Figure 28). Also, within the second growth, many forms were located in thickets of huckleberry and others were found next to fallen logs. Most of the forms appeared to provide protection from predators and stormy weather, e. g. , hares sitting in forms within clumps of bear grass usually were not visible even at close range.

In the open area, hares may have occupied forms that were secreted under logs or stumps and thus were not flushed when we passed nearby.

It was impossible to determine whether or not the same or different individuals were occupying particular forms on successive dates. It also was not determined how many forms were used by an individual hare. But it seems probable that the same form may have been used by more than one hare at different times, and that an individual used several forms. (Seton [1929] found that certain individual hares that he watched throughout the year used the same three or four forms in winter as were used in the warmest days in summer.)

Grange (1932) observed that forms of hares were sometimes



Figure 28. A form, or resting place, of a snowshoe hare located among clumps of bear grass, Xerophyllum tenax, in the second growth. The lack of structure of the form used by the snowshoe hare is characteristic.

sheltered by sedges or grasses, and were commonly located in dense cover. He also found that hares in Wisconsin made frequent use of hollow logs and occasionally entered burrows in the ground. MacLulich (1937) also reported that hares in Ontario made use of holes in the ground, and Morse (1939) noted that hares in Minnesota regularly used woodchuck burrows. Dalquest (1942) reported trapping a hare, Lepus a. washingtonii, in a burrow of a mountain beaver, Aplodontia rufa, and tracks in the snow twice led down burrows of this mammal.

Severaid (1942) reported that hares used forms regularly throughout the year in Maine. He found that forms were located in a wide variety of places and in different types of cover, but always seemed to be in a spot that provided protection from predators and inclement weather.

Adams (1959) noted that a form usually had no particular structure, but that a slight oval depression may develop in the ground or litter where the hares rested. Most forms were located in or near good cover, but occasionally hares were seen resting in exposed situations. Forty-eight forms that were observed 710 times during a year, were occupied an average of 15.2 percent of the times observed, but 38 percent were used only once. One hare used a form on 10 of 11 successive observations on different days in winter. Adams also reported that sometimes two or more hares used the same form, though never more than one at a time.

Dodds (1960b) reported that all forms observed in Newfoundland in winter were close to the base of an alder or young fir. Hares also made use of holes and depressions in the snow, but did not use holes in the ground. During the summer, he found forms randomly distributed in diverse types of cover.

### Feeding Habits

The small number of species of abundant herbaceous plants, shrubs, and trees, and seasonal limitations on the availability of palatable forbs made it possible to obtain an indication of the feeding habits of hares by indirect observations. For example, signs left by hares feeding, particularly on twigs of shrubs and trees, provided unmistakable clues to their feeding activities. Little evidence was obtained by direct observations of hares feeding in the field, aside from a few that were seen to feed after handling.

Douglas-fir, western hemlock, oval-leaved, huckleberry, Vaccinium ovalifolium, and red huckleberry, Vaccinium parvifolium, and willow, Salix coulteri, apparently represented the preferred foods of hares in winter and constituted the bulk of their diet in that season. Salal and long-leaved Oregon grape occurred sparsely in the second growth, apparently were of low palatability, and were not heavily utilized by hares. Each of the three species of Rubus had been clipped by hares, but only the western dewberry, R. vitifolius, was sufficiently

abundant to have been of importance in the diet of hares. None of the other species of trees or shrubs was abundant on the area, and none contributed significantly to the hare's winter diet. Western rhododendron was abundant on good habitat near the study area and was sometimes clipped, but seldom eaten by hares. This type of behavior also was reported by Bider (1961) and deVos (1964) for hares in Quebec and Ontario. Both found that twigs of an unpalatable fir, Abies balsamea, frequently were cut and left uneaten on the ground. deVos also observed that young shoots of juniper, Juniperus communis, were often cut and left uneaten during early spring--this apparently was caused by hares attempting to keep their runways open.

Numerous observations were afforded to compare the palatability of Douglas-fir and western hemlock in the fall of 1961. Boughs of both coniferous species had been cut to clear trails along the trap-lines within the second growth. Needles and twigs on cut-branches of Douglas-fir were immediately consumed by hares and within two weeks some of the boughs were completely denuded of twigs and several were stripped of bark. Piles of fresh droppings were noted on or about the boughs of fir, although fecal pellets typically were not distributed in this manner. (Dodds [1960b] noted that, if undisturbed, hares may remain in one spot for a full evening's feeding period.) The hemlock boughs were not eaten to any comparable degree. Branches were untouched or only the outer tips clipped. On the basis of these and other



observations, Douglas-fir was estimated to be several times more palatable than western hemlock and is a preferred species in winter of hares in this region.

Grange (1932) observed that the winter diet of snowshoe hares in Wisconsin and Minnesota may consist entirely of the needles and bark of jack pine. Baker, Korstian, and Feterolf (1921) reported that the food of snowshoe hares in Utah during winter consisted principally of conifers, including Douglas-fir, and Adams (1959) also found that Douglas-fir was heavily used by hares in winter in northwestern Montana.

The bark of live trees or shrubs seldom was eaten by hares, although a few Douglas-fir saplings within the second growth were "barked" in winter. Dodds (1960b) reported that balsam fir frequently was girdled by snowshoe hares in Newfoundland. Bider (1961) noted that young maples, Acer spicatum, were stripped of their bark in the spring. deVos (1964) listed a large number of species of deciduous and coniferous trees, shrubs, and herbs, on which barking by snowshoe hares was observed during the winter. Girdling by hares was also noted, but was considered relatively insignificant as compared to barking.

Browse above 36 inches high generally was not available to hares, as is illustrated in Figure 29, unless the items of food could be reached from logs or stumps, etc. Dodds reported that stumps or



Figure 29. All of the available, palatable twigs on this oval-leaved huckleberry, Vaccinium ovalifolium, a preferred species of food, have been utilized by snowshoe hares. The upper portion of the shrub was beyond reach and escaped clipping.

rocks were used by snowshoe hares in Newfoundland to enable them to reach higher branches. He also noted that hares would climb up gently sloping birches, which had been cut, to obtain twigs unavailable from the ground.

A conspicuous "browse line" was present on Douglas-fir reproduction on the area, but was less evident on hemlock. However, hares were able to reach palatable browse, previously unavailable, from the surface of deep or drifted snow, as is shown in Figure 30. (The amount of snow that accumulated on the study area ranged from one to three feet, depending on the location and amount of exposure.) While snow covered herbaceous foods for weeks at a time, it also weighed down branches of Douglas-fir and hemlock, and huckleberry, bringing an abundance of palatable browse within reach of hares during critical periods. Bider (1961) and deVos (1964) also found that the availability of woody stems used by hares for food is modified during winter not only by the accumulated depth of snow, but also by the weight of snow on branches.

Short sedge was potentially an important food item to hares, since this perennial was abundant and available throughout the year. But there was no indication that it was more than lightly utilized. Two other species of sedge on the area were not abundant, nor were any of several species of grasses or rushes abundant and there was no indication that hares utilized them extensively.



Figure 30. A Douglas-fir seedling clipped by a snowshoe hare. The snow covered many alternative sources of food and made the terminal leaders of this seedling accessible. The clean, oblique cuts on the remaining portions of the stem are characteristic of the clipping injury caused by snowshoe hares.

Western sword-fern, Polystichum munitum, and bracken fern were fed upon by hares, but the bracken fern apparently had a low palatability similar to rhododendron. Bracken fern was abundant in the open area and within openings in the second growth (Table 4), but indications rarely were seen of hares having clipped fronds. During early September, a patch of bracken fern about 10 feet in diameter was clipped one to one and one-half feet from the ground, apparently by a hare. The only other sign of hares feeding on bracken was infrequent nipping of the outer tips of fronds or an occasional stipe that had been clipped. Tender stipes occasionally were clipped soon after emergence in May and June.

Bear grass was the most abundant forb, particularly within the second growth, and there was evidence of hares having frequently clipped the outer parts of the coarse grass-like leaves. Outer leaves of a few small plants were completely consumed, but most of these plants apparently were undisturbed by hares. However, hares frequently clipped leaves of bear grass within forms and runways, but it was uncertain that this material was eaten. Stems of this plant were not disturbed by hares, but were readily eaten by deer before the inflorescences opened.

Evidence of feeding by hares on stems and leaves of dwarf dogwood or bunch-berry, Cornus canadensis, was found in December, but this plant was not abundant on the area. Dodds (1960b) also

reported this species was utilized by snowshoe hares in Newfoundland.

False dandelion was palatable to hares, abundant, widely distributed, and was green and available at all seasons of the year, except when the basal rosettes of leaves were covered by snow. Hares fed lightly on unopened heads, stems and leaves during the summer. New stems and leaves of white-flowered hawkweed, were occasionally consumed by hares in summer. Pearly everlasting apparently was unpalatable; only the stems and leaves of new shoots were observed to have been clipped by hares.

Green stems, leaves and petioles of fire-weed, Epilobium angustifolium, were consumed by hares, but the plant only occurred sparingly. However, the same parts of the more abundant small fire-weed were utilized frequently.

Neither of the legumes occurring on the area was used extensively by hares. Leaves, petioles and tender stems of the broad-leaved lupine, Lupinus latifolius, occasionally were consumed by hares, but it was apparently of low palatability. This large perennial lupine was fairly common and retained some green leaves throughout the year, but little evidence was seen of hares having eaten it. The newly emergent shoots of yellow lupine seldom were clipped by hares and the mature plant was not used.

Seedlings or emergent fronds, new stems and stipes, buds, and green leaves of ferns and forbs were apparently favored by hares

in summer. Generally the forbs and bracken fern were little used after reaching maturity or after they were in a dried condition.

Phenological observations indicated that rapid growth of herbaceous plants began about the first of May and that forbs were abundantly available and most palatable from that date. Several of the species of shrubs had begun to leaf out by that time, but bud-burst in Douglas-fir at the elevation of the study area was delayed on the average until the end of May.

Dodds (1960b) noted that with the first evidence of green herbaceous vegetation, the snowshoe hare in Newfoundland shifts from a woody diet to herbaceous vegetation. He also reported that wild snowshoe hares ate white clover, Trifolium sp., grasses, Gramineae, sedges, Cyperaceae, ferns, Polypodiaceae, marsh marigold, Caltha palustris, and dandelion, Taraxacum sp., in summer. Other investigators have also reported that the hare's diet throughout the summer is comprised of a wide variety of herbaceous plants: Seton (1909, 1929), Grange (1932), Aldous (1936), Criddle (1938), Adams (1959), Bider (1961), and others. For example, deVos (1964), in a study of the feeding habits of hares in southern Ontario, observed that hares begin to feed on woody vegetation soon after the arrival of the first frosts and remain on the diet until spring when green, succulent vegetation reappears.

Competition between black-tailed deer and hares for food was

probably unimportant, since usage of the area by deer was limited in winter and there was no indication of a scarcity of summer foods.

Several hares were kept in captivity at the Forest Research Laboratory, at Corvallis, for varying lengths of times, over a period of several months. No feeding experiments were conducted on these animals, but some observations were made of their feeding preferences. The captive hares accepted alfalfa hay; readily consumed several species of grasses, Gramineae, in fresh condition and freshly picked red clover, Trifolium pratense. Apples also were eaten readily by captive hares in traps and in the pens. Pelleted rabbit rations frequently were shunned or only taken in small quantities by juvenile and adult hares.

Severaid (1942) found that grasses were utilized first, then alder, Alnus rugosa, by snowshoe hares kept in large outdoor enclosures. The twigs and young shoots of white birch, Betula papyrifera, also were a preferred food.

Direct observations of hares feeding. Ten juvenile and adult hares that began feeding immediately after they were handled and released in the field were watched closely for one to several minutes, and plants eaten were noted when possible. The adults were all females; sexes of juveniles were four males and one female. Four of the hares were each observed feeding on two or three trapping periods.

These hares fed on Douglas-fir and western hemlock twigs and



needles, huckleberry, false dandelion, and other composites. One hare fed on western dewberry leaves for two minutes following release.

Only one young juvenile hare was seen to feed following release, in July. This immature hare ate dry bracken fern fronds--possibly an indication of a depraved appetite; it also nibbled on blades of bear grass, small fire-weed, and ate other forbs that were not identified.

This abnormal behavior observed in winter and summer may have represented a depraved hunger, but the plants eaten, with the possible exception of dried bracken fern, were all species commonly utilized by hares.

## POPULATION FORCES

Mortality

Adams (1959) described mortality in terms of the probability of survival, i. e. , the number of hares alive at the end of a period divided by the number alive at the beginning of the period. Dodds (1960b) calculated annual productivity of hares in Newfoundland and used this as a measure of survival, i. e. , annual productivity equalled reproductive potential minus the mortality. Both methods were used in this analysis. Both crude and age-specific rates are presented following procedures used by Adams. Sex-specific rates are not given since the sex ratios were comparable.

Survival of the marked sample of the population is indicated in Tables 30 and 31. These tables clearly show a tendency for a high "disappearance rate" among young juveniles and the comparatively stable nature of the adult portion of the population. Figure 31 shows the percentages of the 1960-cohort recaptured in each subsequent trapping period--indicating the continued survival of these adult hares. An interesting trend is revealed by inspection of this figure, which shows a high initial "disappearance rate" for newly tagged hares that drops to a fairly stable level after the sampling period in which hares were marked.

Table 30. Decline and replacement of the snowshoe hare population on the area studied as indicated by hares tagged, and recaptured from previous trapping periods. For example, of the 39 hares handled during the third trapping period, 10 had been tagged during the first trapping period, 12 had been tagged during the second trapping period, and 17 were tagged for the first time. Of the 17 tagged in November 19-21, only one was recaptured in the next trapping period, etc.

Date of Trapping Period																				
1960					1961											1962				
Oct. 8-10	Oct. 22-24	Nov. 19-21	Dec. 20-22	Dec. 28-30	Jan. 21-23	Feb. 25-27	Mar. 21-23	Apr. 22-23	May 19-20	June 13-15	July 11-13	Aug. 8-10	Sept. 6-8	Sept. 27-29	Oct. 24-26	Nov. 20-22	Dec. 19-21	Jan. 13-15	Feb. 10-15	Mar. 17-19
13	10	10	2	3	3	1	3	3	3	3	2	3	1	0	0	0	0	0	1	0
	20	12	0	3	4	3	6	4	2	3	1	2	1	1	2	0	2	2	2	1
		17	1	5	5	5	6	4	3	4	4	4	3	2	3	2	2	1	4	3
			4	1	0	1	1	1	1	1	0	0	0	0	0	0	0	1	2	0
				7	1	1	2	1	1	0	1	0	0	0	2	2	1	2	2	2
					4	3	2	1	0	0	0	1	0	0	1	0	0	1	1	1
						2	1	1	1	0	2	2	0	0	0	0	1	0	1	0
							3	0	1	2	2	2	0	1	2	0	3	2	2	2
								3	2	1	1	2	1	1	0	1	0	0	1	0
									1	0	1	1	0	0	1	0	0	0	0	0
										7	2	3	1	1	1	1	1	0	0	1
											26	9	4	1	3	3	3	2	3	2
												33	10	6	3	4	5	1	3	2
													20	2	2	4	1	2	3	2
														8	2	1	3	1	1	1
															18	6	6	3	4	3
																7	3	3	2	1
																	2	0	0	0
																		4	0	0
																			5	1
																				3
1	5	2	2	1	1	0	0	1	0	1	12	16	12	5	9	3	2	4	4	3
0 <sup>2</sup>	0	1	0	0	0	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0
13 <sup>3</sup>	30	39	7	19	17	16	24	18	15	21	42	62	41	23	40	31	33	25	37	25

<sup>1</sup>Hares tagged and released, but not recaptured in a later trapping period. <sup>2</sup>Hares caught and not released. <sup>3</sup>Hares caught (excluding recaptures).

Table 31. Juvenile snowshoe hares born in 1961, tagged, and recaught from previous trapping periods. For example, of the 44 juvenile hares handled in August, three had been tagged in June, nine had been tagged in July, and 32 were caught for the first time. Of the 32 caught in August, only 10 were recaught in the next trapping period, etc.

Trapping Period	Date of Trapping Period										
	1961							1962			
	Jun. 13-15	Jul. 11-13	Aug. 8-10	Sept. 6-8	Sept. 27-29	Oct. 24-26	Nov. 20-22	Dec. 19-21	Jan. 13-15	Feb. 10-15	Mar. 17-19
11	5	2	3	1	1	1	1	1	0	0	0
12		22	9	4	1	3	2	2	1	2	2
13			32	10	6	3	4	5	1	3	2
14				19	2	2	4	1	2	3	2
15					8	2	1	3	1	1	1
16						14	5	4	1	2	1
17							6	2	2	1	1
18								2	0	0	0
19									3	0	0
20										3 <sup>4</sup>	1
21											0
-- <sup>1</sup>	0	12	16	12	5	7	3	2	3	2	0
-- <sup>2</sup>	0	2	1	1	0	0	0	0	0	0	0
-- <sup>3</sup>	5	26	45	35	18	25	23	20	11	15	10

<sup>1</sup> Hares tagged and released, but not recaught in a later trapping period.

<sup>2</sup> Hares caught and not released. (An untagged female was sacrificed and an untagged male was found dead in a trap in July; and an untagged female and male were each found dead in traps in August and September respectively.)

<sup>3</sup> Hares caught (excluding recaptures).

<sup>4</sup> Sex of a juvenile tagged in February was unrecorded.

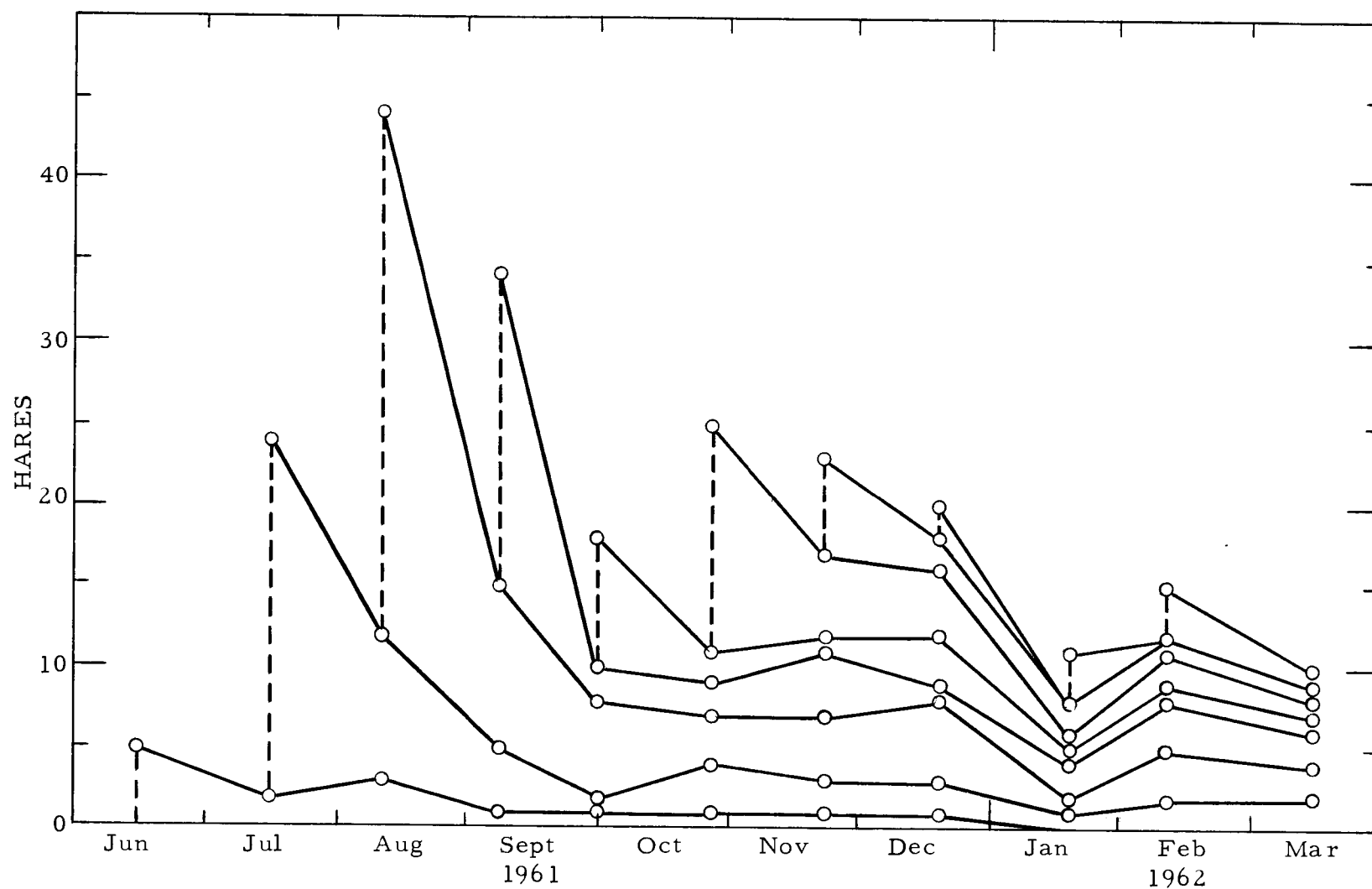


Figure 31. Juvenile hares born in 1961, released, and recaptured from previous trapping periods. For example, of 44 juvenile hares handled in August, 3 had been tagged in June, 9 had been tagged in July, and 32 were newly tagged and released, etc.

To estimate the probability of survival from birth to the following February, the average number of adults present during the breeding season was estimated (recapture method) and it was assumed that half were females. Thus there was an average of 28 adults, or 14 females during the breeding season. Using an assumed biotic potential of 7.54 (derived from Adams's data), these females produced an estimated 106 young.

A total of 113 juveniles born in 1961 was caught and all but four were tagged and released (85 of these were caught during July, August, and September), but by February 1962 the 1961-cohort of young was reduced to an estimated (recapture method) 19 individuals. Therefore, the probability of survival from birth to the first breeding season was  $19/106 = .18$ .

Inaccuracies in the population-estimates and in estimates of the sex ratios of adults during the breeding season, plus the uncertainty of the assumed biotic potential, emphasizes the hypothetical nature of this approximation of survival. For example, the calendar-graph estimates of the adult population during the breeding season were slightly higher and indicated a higher ratio of females. Also, the number of young produced during the breeding season in 1961 probably was higher than estimated, since 113 juvenile hares born in 1961 were caught, of which 109 were tagged and released. Thus, it is likely that the probability of survival of young to the next breeding

season is less than the calculated value.

An indication of the survival and longevity of hares in Minnesota is provided by the records of Aldous (1937). He reported that of 454 hares trapped, marked, and released in 1932, 70 were recaptured in 1933; that 22 of the 1932-cohort were taken in both 1933 and 1934; and that four of the original 454 hares were retaken in 1933, 1934, and 1934. Aldous also reported that of 797 marked hares released in 1933, 152 were recaptured in the following year. These data show that the "disappearance rate" of trapped hares was approximately 80 percent during the first year after marking.

Green and Evans (1940b) found that the probability of young hares surviving from birth to February of the following year was highly variable--and ranged from .08 to .91 over a seven-year period in Minnesota. They also found that the average annual mortality of adults was 70 percent.

Adams (1959) found that the probability of young hares surviving from birth to 53 days was .67, on his study area in northwestern Montana. But from age 53 days to the first breeding season (6.5 months later), the probability of surviving was only .11. Adams also compared the survival rate of young with that of adult hares for the same period. He found that the survival rate for adults from the midpoint of the breeding season to the following February was .31, or considerably higher than the rate (.09) for young hares.

An approximation of the crude survival rate<sup>6</sup> was obtained for hares in this study by using the estimates of the population (recapture method) for February 1961, and 1962. There were an estimated 30 hares on the area from which the population was trapped in February 1961, and 49 hares were estimated on the area trapped by the larger grid in February 1962. (On the basis of proportionate area, there were an estimated 22 hares present on an area comparable to that trapped in February 1961.) Therefore, the crude survival rate was  $22/30 = .73$ .

Adams calculated that the crude survival rate for hares in Montana, from February 1953 to February 1954, was .47. This was determined by use of population estimates obtained from the calendar-graph; data that had a downward bias in February 1954. In other words, the crude survival rate was probably higher than indicated.

Green and Evans (1940b) found that crude survival rates of hares in Minnesota were extremely variable. The rates for a seven-year period were: 1932-33--.48; 1933-34--.95; 1934-35--.69; 1935-36--.61; 1936-37--.21; 1937-38--2.28.

Dodds (1960b) calculated annual productivity of hares in Newfoundland and used this as a measure of survival. He determined

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<sup>6</sup>Crude survival rate, as defined by Adams (1959), is the number of hares of all ages alive in February divided by the number alive in the preceding February.



annual productivity ratios from large samples of humeri of hares snared from mid-October to mid-December for a six-year period. In all, 81.2 percent of the hares collected were juveniles, from which Dodds derived an average productivity index of 8.6. The calculated productivity indexes varied from 5.7 to 12.3--a highly significant difference.

Dodds also constructed a theoretical survival curve from which he estimated annual mortality. He found a high annual mortality for each age class in the population, and noted that mortality was higher in the very young and very old. On the average, he reported about 20 percent of hares of all ages may be expected to survive annually.

Biotic potential was not calculated for hares in this study, but for comparative purposes an approximate productivity index was calculated using an assumed BP of 7.54 derived from Adam's data for hares in Montana. (Reported biotic potentials of snowshoe hares have ranged from 6.82 [Green and Evans, 1940b], to 10.51 [Rowan and Keith, 1956].)

Using mean-population estimates as determined by the recapture method for October-December 1961, the mean percentage of juveniles in the population during this period was 70.8 percent and the calculated productivity index was 5.8. (Figure 12 shows the percentage of juveniles in the trapped samples of the population for the

entire study.) This is lower than the productivity indexes reported by Dodds--notwithstanding the average BP of Newfoundland hares was 9.3--and suggests a higher rate of mortality among juvenile hares in Oregon. It may be significant that these parameters reported by Dodds (1960b) were applicable to a population in "...an increasing phase of a population fluctuation..."

#### Predation and Other Mortality Factors

Mortalities were caused by mammalian and avian predators, diseases, parasitism, accidents, and man. The latter category included the occasional shooting of hares during big game and upland bird hunting seasons and, on the study area, trapping and handling accounted for the loss of several hares.

Neither disease nor parasitism apparently constituted serious decimating factors to the population during the study, and no pathological conditions were diagnosed among the hares necropsied. Most hares were infested with ticks during part of the year and also harbored one or more kinds of internal parasites, without noticeable affects. However, infections of internal parasites may have contributed to some losses among juveniles and adults; normal internal parasitic infections may also have been debilitating to the extent that infected individuals were more susceptible to predation, exposure, and "trap sickness".

All evidence pointed to predation as the most important source of mortality among hares of all ages. Avian predation was suspect throughout the study, but little direct evidence was obtained to support this assumption.

Adams (1959) attributed more than one-third of the deaths of young hares born on his study area in northwestern Montana to great horned owls: "The preponderance of evidence points to owl-predation as the primary mortality factor. Of course other factors, such as disease and the cover-food relationship may have affected prey-vulnerability."

Mortalities caused by predators. The remains of several hares were discovered on the grid during the study. Most of these mortalities were presumably the victims of predators, rather than having succumbed to disease, parasitism, or other natural causes.

The carcass of an adult hare was found on the grid in mid-June; death was estimated to have occurred since the previous trapping period, in May. Both hindfeet were present plus remnants of skin and hair, and most of the gut was intact (the hare had not been toe-clipped).

The only immature hare found dead, except for losses directly associated with trapping and handling, was a 24-hour-old-kill found in mid-August. This animal apparently had been eaten by a bobcat, as revealed by perforations made by a predator's teeth in a patch of skin

from the back. One hindleg, chewed-off at the distal end of the femur, was the only other part of the carcass found. Measurement of the hind-foot indicated that the hare was probably no more than three weeks old.

On August 28, 1961, the head of an adult female hare was found at the base of a low snag near Station C-4 (Figure 32). The condition of the head, which had been severed at the third cervical vertebra, indicated that death had occurred within 24 hours. This animal, No. 904, had been tagged in November 1960 and recaptured three times; it appeared in good condition when released on August 10, at Station H-5, within the second growth.

A carcass of a hare found in the vicinity of Station G-4, in mid-March 1962, was believed to have been eaten by a bobcat; one foot had been chewed-off and the head was missing, but the hide and gut were intact. Bobcat tracks were found about the carcass.

Mortalities represented only by remnants of the gut (usually the stomach and part of the small intestine) or gut contents, accounted for losses of three hares; one each in December 1960, and in February and March 1962.

A few older skeletal fragments of hares also were found on the study area; the presence of broken bones indicated that the animals may have been consumed by mammalian predators.

In all, the recent remains of seven juvenile and adult hares were found, and the evidence indicated that they were killed by



Figure 32. The recently severed head of an adult female snowshoe hare, Number 905, as found lying at the base of a low snag on the study area on August 28, 1961. The head, which had been severed at the third cervical vertebra, was found in the vicinity of Station C-3, in the open area. This hare had been live-trapped and released in good condition at Station G-5, in the second growth, two and one-half weeks before, on August 10.

mammalian predators. But these few mortalities, mostly found in winter and within the second growth, represented only a mere fraction of the hares trapped, tagged, and later unaccounted for. For example, only one immature hare was found dead, although less than half of the juvenile hares born in 1961 and tagged were subsequently recovered.

Mortalities caused by trapping activities. The live-trapping and handling activities unquestionably constituted an important decimating factor, since 16 hares were known to have died as a result of these activities during the 18 months of the study. All losses occurred between November 1960 and September 1961.

An adult male hare was severely wounded by an adult female, when both were caught together in a double-door trap. The male died, apparently as a result of the injuries and exposure.

An adult male was accidentally caught in a trap prior to the trapping period in February 1961 and died. The traps had been hooked-open and possibly the hare had dislodged the hook and released the door when it entered the trap. This practice of fastening the traps open between trapping periods was discontinued after the trapping period in February 1961.

Ten hares succumbed in traps during the trapping periods in February, March, and April 1961; six adult females, one adult male and two subadult males were found dead in the traps and an adult male died two and one-half hours following release. All but one of these

hares had been recaught on two or three successive trap-nights.

Cause of death was not established. However, a prolonged period of cold, wet and snowy weather prior to the trapping periods when the losses occurred may have restricted movement and feeding.

This decimation of the adult population near the lowest point in its annual cycle, and particularly the loss of adult females, may have reduced the total number of young produced on the study area in 1961. But the effects of these mortalities probably were diminished by hares moving onto the area. Five adult females were caught on the study area for the first time and tagged during March, April, and May 1961, none of which was subsequently known to have died.

A pregnant female, No. 861, died in a trap on July 12, 1961. This hare had been partially exposed to direct sunlight and may have succumbed because of heat exhaustion; the air temperature at the time the trap was checked was 93°F.

Three additional mortalities caused by trapping were young juveniles, one of which had been injured during handling and was subsequently sacrificed. The other two were found dead in the traps of undetermined causes.

#### "Trap Sickness"

Traps were checked in midday, and hares caught had been captive for less than 24 hours--they were probably confined about 12

hours on the average. Hares were handled quickly and released quietly after weighing, the last step in the handling procedure. Behavioral observations were almost entirely limited to hares caught in the open area, because of the thickness of cover within the second growth.

The normal reaction of released hares consisted of an immediate escape. Flight of hares released in the open area was deliberate and oriented, with few exceptions, directly towards the second growth. The initial direction of escape may have taken a hare away from dense cover, but most hares simply circled back and continued into the coniferous reproduction. Some hares apparently continued to travel in a direction away from the second growth and were lost to view. A few took cover momentarily under logs or stumps, but readily flushed when approached.

Some hares simply paused for a short interval after release, before bounding away. Others did not attempt to escape promptly, permitted us to approach within a few feet, and frequently began feeding in our presence (Figure 33). This type of atypical behavior was considered abnormal and apparently resulted from the adverse effects of prolonged and repeated confinement within traps.

Abnormal behavior of this type is commonly encountered in live-trapped animals, e. g. , Adams (1959) described similar behavior in hares released following trapping and handling. He referred to it as "trap sickness" and noted the similarity of symptoms to those of





Figure 33. A juvenile male hare, Number 528, feeding quietly on forbs following trapping and handling in August 1961. This animal repeatedly was approached to within four feet. This atypical behavior was shown by several hares immediately upon release.

shock disease, as described in hares by Green and Larson (1938), and Green, Larson, and Bell (1939). But Adams concluded that in the absence of pathological diagnosis it was uncertain that the observed syndrome was identical to that defined by Green et al.

Very mild symptoms of "trap sickness" (hares pausing before flight) were noted in six hares from August to December. Five of the six animals observed were males. Mild symptoms, characterized by hares stopping to feed when released, were shown by 10 hares on 15 occasions, and four of these hares each showed this behavior on two or three trapping periods. Among adults, only females were seen to behave in this manner, in each trapping period from April through September. For example, Hare No. 841 behaved atypically after a second handling in April and May, and after a third handling in August. Conversely, of five juvenile hares that stopped to feed after release, four were males. Two of the older juveniles showed mild symptoms of "trap sickness" in January and February, and the other three juveniles that showed this type of feeding-behavior were young males handled in July and August.

Hares that died in traps or seen after handling were about equally divided between adults and juveniles. But it is a moot question whether or not the hares which succumbed in traps, or soon after handling, died from severe "trap sickness" or from some other undiagnosed, pathological condition. Chitty (1959) reviewed the

evidence about the nature of shock disease and concluded: "It seems more probable that trap-deaths merely reflect variations in the intensity of trapping, handling, and other procedures."

Throughout the study, the incidence of "trap sickness" varied in males and females (Table 32) and it was higher in adults than in juveniles. Thirteen, or 11 percent, of the 118 juvenile hares that were born in 1961 and captured showed symptoms of "trap sickness". Of 89 adults trapped--including juveniles caught from October 1960 to March 1961 and later classed as adults--16, or 18 percent, showed symptoms, including 8 that died. These findings differ from the results of Adams (1959), who reported symptoms of "trap sickness" in 25 of 101 young-of-the-year (25%), while only three of the 58 adults trapped (5%) showed symptoms. But these observations are in accord with those of Green, Larson, and Bell (1939), who concluded that shock diseases afflicted both immature and adult hares with about the same frequency.

A higher incidence of "trap sickness" was observed in adult females than in adult males. For example, of 15 adult females trapped 41 times from July to September 1961, 4 exhibited mild symptoms (unwariness and feeding upon release) and one died in a trap. Of all older juveniles and adults handled and sexed, 11 of 40 females or 27.5 percent as contrasted to only 5 of 47, or 10.6 percent, of males trapped, showed symptoms. Differences noted between sexes of

Table 32. Seasonal incidence and frequency of "trap sickness" in hares handled on the main study area.

Date	Hares Caught (Including Recaptures) <sup>1</sup>		Number of Times "Trap Sickness" Observed <sup>2</sup>		Symptoms Per Capture	
	Males	Females	Males	Females	Males	Females
Oct. -Dec. 60	80	73	3	0	.04	0
Jan. -Mar. 61	64	42	4(2)	5(5)	.06	.12
Apr. -Jun.	29	46	1(1)	5(1)	.03	.11
Jul. -Sept.	103	111	6(2)	7(2)	.06	.06
Oct. -Dec.	82	76	1	0	.01	0
Jan. -Mar. 62	79	60	0	2	0	.03
All	437	408	15(5)	19(8)	.03	.05

<sup>1</sup>One hare was handled, but not sexed in each of the first three quarters and two hares were handled but not sexed in Jul. -Sept. 1961; in all, 889 catches were recorded.

<sup>2</sup>Number of hares found dead in traps or that died soon after handling is shown in parentheses.

juveniles born in 1961 were smaller.

In summary, symptoms of "trap sickness" were exhibited by 29 of 207 hares that were handled 889 times during the study. This includes 13 hares that were found dead in traps or that died soon after handling. The condition was most frequently observed from January through September 1961, and most deaths occurred in February, March, and April 1961.

Adams (1959) noted that the only period when adults showed symptoms was from January to April. But the prevalence of symptoms was highest during the summer in his study of hares in Montana, and was apparently related to the large proportion of juveniles trapped in that season.

Dodds (1960b) found that a small percentage of live-trapped hares in Newfoundland were dead when the traps were examined, although in no cases were traps left unattended more than 30 hours and nearly all were placed in protected spots. Three adult males and one adult female trapped in February, March, and June were found dead in traps. Pathology was normal and no heavy parasitic infestations were found. Three juveniles trapped during July and August also died in traps for no obvious causes, according to Dodds.

The reported occurrence of mortality among adults in winter and juveniles in summer, in Newfoundland, corresponds to the seasonal occurrence and frequency of losses resulting from live-

trapping and handling activities in this study.

The behavior classified as very mild "trap sickness", i. e., hares remain motionless for a half-minute or longer following release, is similar to that of hares, in forms, that perceived an observer, but did not attempt flight even when closely approached. It seems probable that this type of behavior may not have been indicative of any physiological anomaly. Only one of the six hares that behaved in this manner had been handled previously during the trapping period in which the behavior was noted.

The behavioral influence of repeated captures during a trapping period is inconclusive, based on the 10 hares that stopped to eat following release. These animals had each been handled one or two times in a trapping period, before symptoms were noted in 10 of the 15 recorded observations.

Atypical behavior was observed in an adult female, No. 841, that was handled twice during each of three trapping periods in April, May, and August. This female was actively lactating in May and August, but was not palpably pregnant. In each period she behaved abnormally the second time she was handled.

A subadult male was caught five times during the extended trapping period in February 1962, but did not show atypical behavior until the fifth and sixth trap-nights. However, nine other hares were trapped on four to six consecutive nights during this period with no

apparent inimical effects. Most hares tagged during the study were repeatedly handled with no apparent adverse effects. For example, male No. 929 was caught 34 times in 16 trapping periods from October 1960 to March 1962; a period of 509 days from first to last capture.

Of the nine subadult and adult hares that died in traps or soon after handling from February to April 1961, all but one had been caught previously one or two times during the trapping period that death occurred. But the weather had been continually cold and snowy, movement of hares mainly was restricted to the second growth, and less than normal amounts of food were available. Reproductive activity had also begun. This combination of factors seems to indicate an apparent adverse effect of repeated captures and prolonged confinement during cold weather. The other adult and three immature, untagged hares that died had each been caught only once during the period that mortality occurred. (The death of a pregnant female, No. 861, in a partially protected trap on July 12 likely was caused by overheating.)

### Pathology

Hares that were found dead in traps or that died soon after handling on the main study area were necropsied to determine if they were normal, or whether or not a diseased condition may have caused death. Of the 16 hares in this category, nine were

necropsied under the direction of Dr. Dean H. Smith of the Veterinary Diagnostic Laboratory. Gross pathology of four others was determined by necropsies made in the field, and three were not examined pathologically. Twelve other hares trapped at sites one to one and one-half miles north of the main study area in December and January 1961 also were necropsied at the Diagnostic Laboratory; seven were necropsied at time of capture, and five that died after being held in captivity for one to four months were examined soon after death. In addition, an adult male and female, trapped off the main study area in April and July, also were necropsied at the Laboratory. In all, 23 hares were necropsied at the Diagnostic Laboratory between November 1960 and July 1961, and represented six subadults and 17 adults; the sexes were equally divided (sex of one adult was not recorded).

Gross pathology also was noted of each hare in which intensive parasitological examinations were made. In all, this sample included 14 adults and 30 juveniles. An equal number of males and females were represented among adults sampled, but juvenile males outnumbered juvenile females by a ratio of 2:1. The juveniles were all trapped during July, August, and September; adults were caught during the spring and summer of 1961.

Diagnosis of all hares necropsied at the Diagnostic Laboratory, or examined more superficially prior to parasitological examinations,



was normal and no evidence of disease was found.<sup>7</sup> An adult male caught in a trap with a second hare in November 1960 was badly lacerated around the back and over the head. An adult female and sub-adult male that had been penned together in January 1961 were found mutilated from wounds incurred while fighting. The female had severe lacerations of the head around the jaws, eyes, and ears. The male had puncture-type wounds over the body, especially around the abdomen.

The diagnosis of the five hares that were found dead in traps on the main study area during the trapping period in March 1961 is pertinent: "These rabbits appeared to be in fairly good condition. The reason for their dying in the traps could not be found." One kidney on an adult male of this group showed atrophy, but cultures of the kidney and spleen were negative.

### Parasites

Protozoa. Dr. Stuart E. Knapp of the Department of Veterinary Parasitology examined the blood smears and found them negative

Oocysts of Eimeria stiedae were present in fecal materials of

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<sup>7</sup>Data extracted in part from reports on file at the Animal Diagnostic Laboratory at O.S.U. : Accession Numbers 10255, 10352, 10396, 10478, 10641, 10768, 10939, 10973, 11009, and 11193.

all hares examined. Namely, in five juvenile males and one juvenile female examined September 19-21, in a juvenile female examined in October 9, and in an adult female necropsied at the Diagnostic Laboratory in July 1961.

Severaid (1942) reviewed the occurrence of coccidia in snowshoe hares as reported by other investigators, and discussed the etiology and significance of coccidiosis as a cause of mortality of captive juvenile hares in Maine. For example, coccidiosis caused 40 percent of all juvenile mortality, compared with nine percent adult mortality among hares studied in 1940. Five species of Eimeria were identified from fecal materials of three hares that died of coccidiosis. Scheffer (1933) also reported that 12 immature snowshoe hares apparently died of coccidiosis while held in captivity during the summer in western Washington.

It seems likely that coccidiosis may be a cause of mortality of juvenile hares in western Oregon. However, Lechleitner (1959) concluded that Eimeria sp. had little effect upon black-tailed jack rabbits, Lepus californicus, under normal environmental conditions.

Cestoda. Tapeworms of the species, Mosgovoyia pectinata americana (Goeze), were found in 12 of the 44 hares examined for endoparasites. They were encountered only in young juveniles of approximately three to four months of age and were equally distributed between the two sexes. From one to five tapeworms, mostly in the

adult stage, were recovered from each of the infested hares, with exception of one juvenile female whose small intestine contained 19 cestodes. All of the tapeworms were recovered from the small intestine excepting one that was present in the stomach--presumably representing a movement after death of the host.

Dalquest (1942) found specimens of Lepus a. washingtonii usually were lightly infested with tapeworms, ticks, fleas, and one heavy infestation of ectoparasites was seen.

Boughton (1932) found that young hares in Manitoba became infested about three weeks after birth and that all juveniles examined were infested during the summer. However, he found that only one of 388 adults examined was infested. Philip (1938) encountered mature tapeworms of this species in the small intestine of 16 of 172 varying hares examined in Alaska. Green, Larson, and Bell (1939) recovered adult tapeworms, M. pectinata americana, from many apparently normal hares examined in Minnesota. Severaid (1942) found this cestode in only four hares out of a large number examined. The infested hares were juveniles of the same litter that were autopsied at five to 12 weeks of age and were each found to contain five to 11 cestodes. The first of these hares, which died at the age of 32 days, contained 11 immature cestodes approximately one inch in length. Erickson (1944) recovered M. pectinata americana from 62 of 720 hares examined. He noted that five large Mosgovoyia completely

occluded the intestine of a hare collected in July. Dodds and Mackiewicz (1961) found no adult hares infested in Newfoundland, but 17 percent of 203 juvenile hares were infested. They also reported that as many as seven mature cestodes were found in a single animal and although the small intestine appeared occluded, the infested hares seemed normal. Boughton (1932) and Erickson (1944) found that infestation in young hares induces a high degree of immunity.

Records of occurrence of bladderworms (Taenia pisiformis Bloch) in hares necropsied at the Diagnostic Laboratory were incomplete. However, cysticercus-stage larvae were found in a subadult and adult male, and two adult females examined in January; two adult males and an adult female also were found heavily parasitized with bladderworms in April; and occurrence of tapeworm cysts was recorded in each of three adult males and one female examined in May 1961. In only one hare, an adult female necropsied in July 1961, was absence of larval stages of tapeworms noted. In summary, bladderworms were found in seven subadult or adult males and four adult females examined at the Diagnostic Laboratory from January to July 1961; absence was recorded in only one of the 12 hares examined. Of the four hares necropsied in the field, tapeworm cysts were recorded in two adult females, trapped in February and July, but tapeworm larvae were not noted in two juvenile females examined in July and August. Records of occurrence of T. pisiformis were also

available for 35 of the 44 hares examined parasitologically in the laboratory, including records for 13 of the 14 adults examined.

Larval stage of T. pisiformis were found in 24 of 50 hares examined, as is shown in Table 33. These larvae were found only in adults with exception of one juvenile estimated to be approximately four months of age. Twenty-two of 27 subadults and adults examined, or 81 percent were infected, but infections were comparatively light and 31 larvae were the most found in an individual hare. The larvae mainly were encysted to the mesenteries of the abdominal cavity, although three cysticercus-stage larvae were found on the lungs.

Boughton (1932) found larval stages of T. pisiformis in 14.7 percent of hares examined in Manitoba; MacLulich (1937) reported them in 40 percent of hares examined in Ontario; Philip (1938) found one to many larval T. pisiformis in 29 of 172 hares examined; Green, Larson, and Bell (1939) reported the presence of tapeworm cysts (T. pisiformis and T. serialis) in 25 to 30 percent of the hares examined at any period of the year; and Severaid (1942) found bladder worms of this species in 32 percent of hares autopsied during his study in Maine. The number of these cysts found by Severaid varied from a few per animal to 296. Their distribution was similar to that found in the present study, although Severaid noted that they were particularly abundant within the cavity of the pelvic girdle. Dodds and MacKiewicz (1961) also reported bladder worms were more common in adult hares than in juveniles, and found instances of heavier infections than

recorded in this study. These authors described occurrence of larvae in the muscles, about the lung and heart, on the liver, and embedded in the mesenteries.

In the region of the study area in western Oregon, the host of T. pisiformis is probably the coyote. It may also be found in the bobcat; both carnivores occur in moderate numbers in the vicinity.

Nematoda. Two trichostrongylid nematodes,<sup>8</sup> Trichostrongylus affinis (Graybill) and Nematodirus triangularis (Boughton) were found, and identified by S. E. Knapp. These identifications were confirmed by the Beltsville Parasitological Laboratory. The number of T. affinis found in each hare was variable, but they were markedly more abundant in adults and were absent in young juveniles. Trichostrongylids were found primarily in the cecum and large intestine, as is indicated in Table 34, but three larvae were found in the lungs of a juvenile hare.

A total of 3300 T. affinis were found in an adult male that had been placed in cold storage prior to necropsy. All of these nematodes, which were about equally divided as to sex, were found in the cecum and large intestine. The next largest number of T. affinis (636) also was recovered from an adult male that had been handled in a similar manner.

Nematodirus triangularis was found principally in the small intestine. The largest number was recovered from an adult female

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<sup>8</sup>Specimens of each of these parasites were entered in the U. S. N. M. Helm. Coll. and assigned numbers 58795, and 58796.

and only 18 of 468 nematodes of this species were found in the cecum and large intestine; the remainder were found in the small intestine of this hare. Infestations of N. triangularis were comparable to T. affinis, as were the significantly larger numbers in adults, but distribution within the gut was dissimilar, as is shown in Table 34. In addition, a few larvae of N. triangularis also were found in half of the 35 hares parasitized with adults of this species.

Boughton (1932) found N. triangularis and Trichostrongylus sp. in 25.3 percent of hares examined, and noted that these were potentially dangerous parasites to the health of a population of hares. Erickson (1944) found that the heaviest infections of helminths occurred in late winter and early spring, and that the percentage of adults infected by strongylids and the average number of worms per infected adult was greater than among immature hares. He listed T. affinis, N. triangularis, and larvae of Taenia pisiformis among several helminths considered significant in causing mortality to hares. He also noted that these and other helminths may be important in reducing the resistance of hares to other decimating factors.

In summary, trichostrongylid nematodes were found only in the small and large intestines, and ceca; none was found in the stomachs of hares examined, nor were any endoparasites found in two immature hares estimated to be approximately four weeks of age.

It is noteworthy that one of the most commonly reported

Table 33. Occurrence of endoparasites in snowshoe hares from western Oregon examined in 1961.

Parasite	Hares in Sample	Hares Parasitized	Percent Parasitized
<u>Taenia pisiformis</u>	50	24	48
<u>Mosgovoyia pectinata</u>	44	12	27
<u>Trichostrongylus affinis</u>	44	36	82
<u>Nematodirus triangularis</u>	44	35	79

Table 34. Occurrence, distribution, and mean number of adult Trichostrongylus affinis and Nematodirus triangularis in each infested hare in which all strongylid nematodes were counted.

Hares in Sample	<u>Trichostrongylus affinis</u> Parasites in Each Hare			<u>Nematodirus triangularis</u> Parasites in Each Hare		
	Hares Parasitized	Cecum and Large Intestine		Hares Parasitized	Cecum and Large Intestine	
		Small Intestine			Small Intestine	
25 Juveniles	20	12	15	18	42	2
10 Adults <sup>1</sup>	10	4	175	10	205	16

<sup>1</sup>Mean number of T. affinis is based on nine hares; an exceptionally heavily parasitized adult male collected in June was omitted.

Table 35. Juvenile and adult hares infested with ticks, Haemaphysalis leporis-palustris, and mean number of ticks on each infested hare during the period of general infestation.

Date of Trapping Periods	Hares Handled Each Period	Amount of Infestation				Percent of Hares Infested
		None (0)	Light (1-4)	Medium (5-9)	Heavy (10 or more)	
Aug. 8-10, 61	62	14	22	14	12	77.4
Sept. 6-8	41	11	16	5	9	73.2
Sept. 27-29	23	8	8	5	2	65.2
Oct. 24-26	40	19	17	2	2	52.5



nematodes in snowshoe hares, Obeliscoides cuniculi (Graybill), was not found. Severaid (1942) reported that 97 percent of 132 hares autopsied in Maine contained an average of 300 to 400 of this parasite. This also was the most commonly encountered nematode in hares in Newfoundland examined by Dodds and Mackiewicz (1961). They found it in 58 percent of 286 hares collected in one region.

Acarina. The presence of ticks, Haemaphysalis leporis-palustris (Packard), was markedly seasonal and the principal infestations occurred from August to October 1961. The seasonal nature of the infestations is demonstrated by the fact that only one hare, among 42 handled in July 1961, was found infested and no ticks were detected on the 31 hares handled in November 1961.

Only two ticks were discovered on all hares examined from October 1960 to March 1961; one was found on a hare in October and one was found in March. During this six-month period, 70 hares were handled one, two, or three times, on one or more of each of the eight trapping periods.

For the four trapping periods from April to July 1961, an average of 15 percent of the hares handled each month were infested and, with two exceptions, infestations were light.

Most hares handled during the four trapping periods from August to October 1961 were infested with ticks (Table 35). During this period of three months in late summer 108 individual hares were

handled repeatedly, including 79 which were caught for the first time. The numbers of ticks carried on each hare apparently was not influenced by sex of the host, but it is pertinent that few ticks were found on immature hares, estimated to be two months or less old.

Three of 30 young juvenile hares were infested with ticks; however, only eight of this total were caught during August, when a high incidence of infestation was first encountered. Of the 22 immature hares in this category that were caught in June or July only one carried ticks, but nine of these hares were recaptured during August and eight were infested with ticks. Others were either not recaptured or were not recaptured during the period of general infestation.

There was no opportunity to examine nestlings, since the youngest hares taken in traps likely were about three-weeks old.

The highest frequency of infestation was observed in August, when 77 percent of the 62 hares handled were found infested. Most of the heavy infestations were recorded during the trapping periods of August 8-10 and September 6-8. About half of the hares infested with ticks on both of the trapping periods were each found with five or more mostly nymphal ticks. Approximately 30 ticks, distributed about the eyes, were counted on each of two hares in August--the highest infestations encountered.

Most infested hares had less than 10 ticks each, which were always located on the head and mainly about the eyes and base of ears,

as is illustrated in Figure 34. No ticks were detected on any other parts of the body. However, in addition to the preferred sites of attachment, ticks were found attached beneath the chin, at the corner of the mouth and, in one case, to the ear. Severaid (1942) also found ticks most frequently about the ears, head, and neck of infested hares examined in Maine.

For the remaining five months of the study, from November 1961 to March 1962, no ticks were seen on hares examined during the trapping periods in November, December, and January. A single tick was found on each of six hares during February and March.

It is not known why more hares were found infested with ticks in October 1961 than in October 1960. Only one tick was seen on hares handled in October 1960, but about half of the 40 hares handled in October 1961 were each infested with a few ticks. A similar observation was made by Bacon, Drake, and Miller (1959). These investigators observed that ticks (H. leporis-palustris) were not taken in some collection areas during the first year of a study in Washington, but appeared there later. They also noted that the activity of adult ticks of this species began in late February and infestation of rabbits (Lepus townsendii and Sylvilagus nuttallii) increased in March, and continued at a lower level in summer. MacLulich (1937) reported over 100 ticks to a hare during a period of high density of hares in Ontario.

Severaid (1942) reported that in Maine ticks of this species



Figure 34. Common rabbit ticks, Haemaphysalis leporis-palustris, attached about the head of a juvenile female snowshoe hare, Number 598, in June 1961. The ticks are engorged, adult females and represent a typical infestation.

were particularly abundant on all hares obtained in May and June 1939, but occurred infrequently on hares handled in April. None was noted on any of a large number of adult hares examined in February 1940, and only three engorged female ticks were seen on hares handled during the spring and summer of 1940. No explanation was made for the difference in infestation between years. Philip (1938) noted that infestations of H. leporis-palustris were remarkably localized in varying hares examined in Alaska; only 47 of 172 hares were infested. H. leporis-palustris also was found on 12 percent of 122 hares examined from one region in Newfoundland, from May 1 through November, by Dodds and Mackiewicz (1961). Infestation of hares by ticks was widespread and common, and from one to 28 ticks in various stages of development were collected from each infested hare. Adult ticks were found on hares as late as November 16, but prevalence of ticks were highest in June and July. Infestations of ticks were found on seven of 18 hares examined during this period.

Adams (1959) found Dermacentor andersoni (Stiles) as an ectoparasite of snowshoe hares in northwestern Montana, in addition to the common rabbit tick, but made no distinction between them in the field. He observed that ticks first appeared in March and that all hares examined were infested with 50 to 150 ticks per hare; the maximum range encountered. In late August the incidence of infestation and number of ticks on each hare decreased, and by the end of October

the hares were free of ticks and continued so through the winter.

Siphonaptera. Few of the hares handled were infested with fleas and examination of hares in the field failed to reveal more than one or two fleas on any one hare. Fleas were observed once on only 19 of the 208 hares handled during the 21 trapping periods on the main study area, with one exception; one or two fleas were seen on one hare on three successive trapping periods in August and September 1961. Fleas were found about equally on adults and older juveniles and on males and females. But no fleas were found on immature hares estimated to be two months or less old, and only one flea was discovered on one of 30 juveniles examined during the summer. Of the seven hares on which one flea each was discovered from October 1960 to March 1961, five were males and two were females; conversely, of eight hares with one flea each, infested during the breeding season in 1961, only two were males.

Two species of fleas, Cediopsyllus simplex (Baker) and Hoplosyllus affinis (Baker) were found and identified by S. E. Knapp, and most were of the former species. Kohls (1940) had recorded the occurrence of both species of fleas on Lepus americanus. He noted that H. affinis is the less common of the two species.

Hares that were transported live from the vicinity of the main study area to the laboratory and necropsied showed a higher frequency of infestation and more fleas on each of the infested hares

than hares examined in the field. It seems likely that the low incidence of infestation observed in the field may reflect the inadequacy of that examination. However, there was no indication that any of the hares handled were heavily infested with fleas.

Adams (1959) reported the absence of fleas on hares studied in Montana, and of 122 hares examined for ectoparasites by Dodds (1961) in Newfoundland, only one provided a single flea and that was believed an accidental occurrence.

## APPENDIX



### Description of Standard Measurements

- Length: The total length was measured from the tip of the snout to the end of the fleshy tip of the tail, while the hare was held in an extended position.
- Head: The length of the head was measured from the tip of the snout to the back of the head, over the posterior edge of the external occipital protuberance.
- Tail: The length of the tail was measured from the base of the tail on the top to the end of the fleshy tip; a scale was placed at the base of the tail on the dorsal surface and the tail was bent upward to measure.
- Ear: The length of the ear was measured from the notch at the base of the ear to the tip of the ear-cartilage.
- Hindfoot: The length of the hindfoot was measured from the back of the heel to the tip of the nail on the second toe (longest toe); a scale was laid flat against the foot-pad, while the hindfoot was pressed back on the leg to measure.

### Determination of Home Range by the Circular Bivariant Distribution Method

The circular bivariant distribution method of calculating the area upon which an animal is likely to be found was devised by Dr. Lyle D. Calvin, Chairman of the Department of Statistics, O. S. U., and used by Hooven (1958) to estimate size of home range of Peromyscus maniculatus in northwestern Oregon. The "average" radius of points of capture of mice caught 10 or more times from the center of activity was determined by the standard deviation of a circular bivariant distribution in which each animal ranged 95 percent of the time.

The method is based on the standard deviation of the stations at which a given animal is caught from the center of activity, as defined by Hayne (1949). Standard deviation is given by:

$$s = \sqrt{\frac{\sum (Z - \bar{Z})^2}{n - 1}}$$

where  $Z$  is the center point and  $Z - \bar{Z}$  is the distance from the center point in units. The number of catches is  $n$ .

Using the rectangular coordinate system, with the columns denoted as  $X$  and rows as  $Y$ , the formula for the standard deviation reduces to:

$$s = \sqrt{\frac{\sum (X - \bar{X})^2 + \sum (Y - \bar{Y})^2}{n - 1}} = \sqrt{\frac{X^2 + Y^2 - \frac{(\sum X)^2}{n} - \frac{(\sum Y)^2}{n}}{n - 1}}$$

$$s = \sqrt{\frac{\sum (Z - \bar{Z})^2}{n - 1}}$$

Assuming that an animal moves from the center of activity, and follows a circular bivariate normal distribution, the radius of the 90-percent range (range in which it will be 90 percent of the time, realizing the limitation of capture at greater distances because of closer traps) is given by  $st_{.05}$  where  $t_{.05}$  is Student's  $t$  at the five percent level with  $n-1$  degrees of freedom.

In the computation of size of range,  $X$  was designated by an arbitrary number assigned to each station in the columns; similarly  $Y$  was designated by the actual number of the stations in the rows. A frequency table was then set up for both  $X$  and  $Y$ -values, which also allowed determination of the center of activity following the method outlined by Hayne (1949):

$$X = \frac{\sum fX}{n}, \quad Y = \frac{\sum fY}{n}$$

Size of range was calculated by determining the standard deviation of these values and multiplying by the value of  $t$  for the given degrees of freedom; the product represents the radius of range at the 10 percent level of significance. The area is then readily available.

A minor change was made in the computational method, since number of catches ( $n$ ) were comparatively small on the average. (The procedure suggested by Calvin was for application to individuals caught ten or more times.) The  $X$  and  $Y$  coordinates for each station of capture were recorded in a table and the sum of squares for both

coordinates were calculated. The sum of these values divided by the degrees of freedom ( $n-1$ ) gave the variance. Since the F-distribution follows the  $t^2$ -distribution, the value for a given degree of freedom from the F-distribution was multiplied by the variance to give radius squared ( $r^2$ ) directly. Moreover, since the interval between stations on both grids was larger than one chain, it was necessary to convert the area (computed in units) to square chains. This was accomplished by multiplying area (in units) by 2.25 (for 1 1/2-ch trap-spacing) or by 9.0 (for 3-ch spacing).

The following is an example of the use of the method to calculate the home range of a juvenile male, No. 528, tagged in August 1961 and recaptured five times. This hare was caught at stations F-3, F-2, F-1, G-1, G-2, and G-1 on the small grid.

The computed center of activity was:  $X = 6.5$  and  $Y = 1.7$  units.

Computation of size of range:

X	Y
—	—
6	1
6	2
6	3
7	1
7	1
7	2
—	—

$n = 6$

$\Sigma X = 39$      $\Sigma Y = 10$

$$\Sigma X^2 = 255 \quad \Sigma Y^2 = 20$$

$$SSX + SSY = 4.83$$

$$s^2 = \frac{SSX + SSY}{n - 1} = \frac{4.83}{5} = 0.97$$

$$r^2 = s^2 F_{.10} = 0.97 (4.06) = 3.93$$

$$\text{Area} = \pi r^2 = 12.34 \text{ units}$$

Conversion to chains:

$$12.33 (2.25) = 27.75 \text{ sq ch} = 2.78 \text{ acres}$$

Table 36. Plants identified on the main study area.<sup>1</sup>TREESPinaceae, Pine FamilyPseudotsuga menziesii (Mirb.) Franco, Douglas-fir.Tsuga heterophylla (Raf.) Sarg., Western hemlock.Salicaceae, Willow FamilySalix coulteri Anders, Coulter's willow.Betulaceae, Birch FamilyAlnus oregona Nutt., Oregon alder (Red alder).Fagaceae, Beech FamilyCastanopsis chrysophylla (Dougl.) A. DC., Chinquapin.Rosaceae, Rose FamilyPrunus emarginata (Dougl.) Walp., Bitter cherry.Aceraceae, Maple FamilyAcer circinatum Pursh, Vine maple.SHRUBSBerberidaceae, Barberry FamilyBerberis nervosa Pursh, Long-leaved Oregon grape.Ericaceae, Heath FamilyRhododendron macrophyllum G. Don., Western rhododendron.Gaultheria shallon Pursh, Salal.Arctostaphylos columbiana Piper, Bristly manzanita.Vaccinium ovalifolium J. E. Sm., Oval-leaved huckleberry.Vaccinium parvifolium J. E. Sm., Red huckleberry.Rosaceae, Rose FamilyHolodiscus discolor (Pursh) Maxim, Ocean-spray.Rubus leucodermis Dougl., Western blackcap.R. vitifolius C. & S., Western dewberry.R. laciniatus Willd., Evergreen blackberry.Caprifoliaceae, Honeysuckle FamilyLinnaea borealis L. var. americana (Forbes) Rehd., American twin-flower.

Table 36. Continued

FORBSLiliaceae, Lily FamilyXerophyllum tenax (Pursh) Nutt., Bear-grass.Trillium ovatum Pursh, Western trillium.Smilacina sessilifolia (J. G. Bak.) Nutt., Few flowered false solomon's seal.Iridaceae, Iris FamilyIridaceae tenax Dougl., Oregon iris.Polygonaceae, Knotweed FamilyRumex acetosella L., Red sorrel.Caryophyllaceae, Pink FamilyStellaria longifolia Mulh., Long-leaved starwort.Cerastium glomeratum Thuill., Sticky mouse-ear (Chickweed).Berberidaceae, Barberry FamilyAchlys triphylla (J. E. Sm.) DC., Vanilla-leaf.Saxifragaceae, Saxifrage FamilyBoykinia elata (Nutt.) Greene, Slender boykinia.Leguminosae, Pea FamilyThermopsis gracilis How., Slender thermopsis (Yellow lupine).Lupinus latifolius Ag. var. columbianus (Hel.) C. P. Sm., Broad-leaved lupine.Oxalidaceae, Wood Sorrel FamilyOxalis oregana Nutt., Oregon oxalis (Wood sorrel).Hypericaceae, St. John's-Wort FamilyHypericum perforatum L., Common St. John's-Wort.Violaceae, Violet FamilyViola sempervirens Greene, Evergreen violet.Onagraceae, Evening Primrose FamilyEpilobium angustifolium L., Fire-weed.Epilobium adenocaulon Haussk., Common western willow-herb (Small fire-weed).Cornaceae, Dogwood FamilyCornus canadensis L., Dwarf dogwood (Bunch-berry).Scrophulariaceae, Figwort FamilyVeronica serpyllifolia L., Thyme-leaved speedwell.Compositae, Composite FamilyAnaphalis margaritacea (L.) B. & H., Pearly everlasting.Senecio sylvaticus L., Wood groundsel.Senecio jacobaea L., Tansy ragwort.Cirsium vulgare (Savi) Airy-Shaw, Common thistle.

Table 36. Continued

- Cirsium arvense (L.) Scop. , Canada thistle.  
Hypochaeris radicata L. , Hairy cat's-ears (False dandelion).  
Taraxacum officinale Weber, Dandelion.  
Hieracium albiflorum Hook, White-flowered hawkweed.

## GRASSES, SEDGES, AND RUSHES

### Gramineae, Grass Family

- Festuca megalura Nutt. , Western six-weeks fescue.  
Festuca rubra L. , Red fescue.  
Elymus glaucus Buckl. , Western rye-grass.  
Deschampsia caespitosa (L.) Beauv. , Tufted hair-grass.  
Deschampsia elongata (Hook.) Munro ex Benth, Slender hair-grass.  
Aira caryophylla L. , Silvery hair-grass.  
Holcus lanatus L. , Velvet grass.  
Agrostis exarata Trin. , Western bent-grass.

### Cyperaceae, Sedge Family

- Carex subfusca W. Boott , Rusty sedge.  
Carex brevipes W. Boott , Short sedge.  
Carex mertensii Presc. , Mertens' sedge.

### Juncaceae, Rush Family

- Juncus effusus L. var. pacificus Fern. & Wieg. , Common rush.  
Luzula multiflora (Retz.) Lej. , Common wood-rush.  
Luzula divaricata Wats. , Forked wood-rush.

## FERNS

### Polypodiaceae, Fern Family

- Polystichum munitum (Kaulf.) Presl. , Western sword-fern (Bracken fern).  
Struthiopteris spicant (L.) Weis. , Deer-fern.  
Pteridium aquilinum (L.) Kuhn. var. pubescens Underw. , Western brake-fern.

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<sup>1</sup> Nomenclature follows that of Peck (1961) ; locally used common names are in parentheses.



Table 37. Synopsis of the observed weather conditions as compared to the catches of hares and the percent trapping success.

Date of Trapping Period	Catches of Hares on First, Second, and Third Trap-nights <sup>1</sup>	Trapping Success (Percent)	Range of Mean Daily Temperature (Degrees F.)	Precipitation (Inches)	Synopsis of Weather Conditions
Oct. 7-10, 60	9, 8, 3	19.6	--	0	Fair. Partial overcast on first two trap-nights, but clear Oct. 9-10; moderate temperature.
Oct. 21-24	14, 7, 24	26.4	--	0.5-1.0	Stormy. Overcast Oct. 21, and 23-24, but clear on second trap-night; light rain first trap-night and light to hard rain during third trap-night.
Nov. 18-21	11, 24, 25	33.3	28-37.5	0.8	Stormy. Overcast and light rain on first and second trap-nights; 5 in. of snow on third trap-night; nighttime-temperature below freezing on each trap-night.
Dec. 19-22	0, 3, 4	3.6	34-51	0	Fair. Mild and stable weather; clear, warm days--maximum daily temperatures ranged from 42-68° F--and cold nights--minimum daily temperatures ranged from 24-34° F; calm to light wind; no snow on ground.
Dec. 27-30	6, 2, 14	11.5	32-38.5	0	Fair. Clear, cool days--maximum daily temperatures ranged from 40-52° F--and cold nights--minimum daily temperatures ranged from 22-26° F; calm to light wind; no snow on ground.
Jan. 20-23, 61	11, 9, 14	17.8	40-56.5	T	Fair and Stormy. Clear Jan. 20-22, but changed on third trap-night to foggy, rainy and cooler; maximum daily temperatures ranged from 52-69° F; no snow on ground.
Feb. 24-27	11, 5, 8	15.2	28.5-37	> 2.0	Stormy. Continual overcast at nighttime; rain and snow Feb. 24-25; cold with little change in temperature; 10-12 in. of snow on ground. (Trapping period preceded by three weeks of extremely rainy weather; 18 in. of pptn. from Feb. 1-24.)

Table 37. Continued

Date of Trapping Period	Catches of Hares on First, Second, and Third Trap-nights	Trapping Success (Percent)	Range of Mean Daily Temperature (Degrees F.)	Precipitation (Inches)	Synopsis of Weather Conditions
Mar. 20-23	12, 19, 18	25.7	33-45.5	1.0	Stormy. Overcast and light snow or rain on each trap-night; ground covered with 6 in. of snow in open area. 12 in. within second growth. (Weather continually wet and stormy since Feb.)
Apr. 21-23	13, 14	33.7	29.5-32	1.0	Stormy. Heavy overcast and snow and light rain each day; ground covered with 4 in. of snow Apr. 21 and 8 in. of snow fell during first trap-night; snow melted rapidly Apr. 22-23. (Period preceded by two weeks of cold, snowy and rainy weather.)
May 19-21	10, 14	20.5	43-64	0.3	Fair and Stormy. Partially clear first trap-night, but overcast, cool, and light rain on May 19-20.
Jun. 12-15	4, 6, 15	14.5	56-75.5	0	Fair. Clear and hot in daytime and warm at night; maximum daily temperatures ranged from 81-97° F; minimum daily temperatures ranged from 42-54° F.
July 10-13	12, 16, 16	26.0	63-76	0	Fair. Clear and hot in daytime and warm at night; maximum daily temperatures ranged from 84-94° F; minimum daily temperatures ranged from 50-58° F. (Weather had been continually hot and dry since previous trapping period.)
Aug. 7-10	33, 25, 30	44.4	57-65	0	Fair. Warm, and clear day-and nighttime, except for light ground-fog in early morning; minimum daily temperatures ranged from 39-43° F.

Table 37. Continued

Date of Trapping Period	Catches of Hares on First, Second, and Third Trap-nights	Trapping Success (Percent)	Range of Mean Daily Temperature (Degrees F.)	Precipitation (Inches)	Synopsis of Weather Conditions
Sept. 5-8	16, 19, 18	25.1	50-51	T	Fair. Partial overcast first trap-night--clear Sept. 7-8; moderate temperatures in daytime, but minimum daily temperatures ranged from 32-39° F.
Sept. 26-29	9, 9, 13	15.5	42-52	0.3	Fair. Mostly clear, but overcast and light rain in a. m. of Sept. 28; cool--minimum daily temperatures ranged from 26-38° F.
Oct. 23-26	20, 19, 22	32.6	35.5-44	0.8	Stormy. Overcast and cool; rained first trap-night and light rain Oct. 24 and 26; minimum daily temperatures ranged from 31-36° F.
Nov. 19-22	15, 23, 11	25.9	26-36	3.9	Stormy. Overcast and foggy, except partial clearing second trap-night; 3 in. of snow on ground first two trap-nights; moderate to hard rain melted snow Nov. 21 and rains mixed with snow continued through Nov. 22; daytime-temperatures mostly near freezing; minimum daily temperatures ranged from 19-30° F.
Dec. 18-21	7, 20, 21	25.1	32.5-41	5.6	Stormy. Overcast and foggy; hard rains mixed with snow each day; 2.9, 1.4, and 1.3 in. pptn. Dec. 19, 20, and 21 respectively; 8-in. of snow on ground Dec. 18, melted in open area Dec. 19, but patches in second growth; 2-in. of new snow on open area Dec. 21; minimum daily temperatures ranged from 28-38° F.
Jan. 12-15, 62	9, 8, 21	19.8	25.5-26.5	0.5	Stormy. Continual overcast and cold; snowed on first trap-night and on Jan. 14-15; 2 in. of snow on ground at beginning of period and 8 in. at end; minimum daily temperatures ranged from 20-24° F.

Table 37. Continued

Date of Trapping Period	Catches of Hares on First, Second, and Third Trap-nights <sup>1</sup>	Trapping Success (Percent)	Range of Mean Daily Temperature (Degrees F.)	Precipitation (Inches)	Synopsis of Weather Conditions
Feb. 9-12	18, 20, 25	32.8	37-38.5	0.2	Stormy. Partial or complete overcast, with occasional fog and intermittent light rain on Feb. 10, 11 and 12, and hard rain during night Feb. 13-14 (1.8 in.); minimum daily temperatures below freezing 1st, 2nd, 4th, and 5th trap-nights; no snow on ground.
Feb. 12-15	11, 15, 13	40.6	34.5-44	1.8	
Mar. 16-19	7, 16, 15	19.8	31.5-39	T	Fair. Probably clear on partially clear on all three trap-nights, but changed to overcast and rain on Mar. 19; 12-18 in. of granular snow on ground--drifts to 30 in., and snow crusted each night; minimum daily temperatures ranged from 22-29° F.

<sup>1</sup>The 32 traps in the open area were set and all traps within the second growth were closed for three additional trap-nights from February 12-15, 1962.

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