SNOWSHOE HARES IN ALASKA. II
HOME RANGE AND ECOLOGY DURING AN
EARLY POPULATION INCREASE

A THESIS

Presented to the Faculty of the University
of Alaska in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

by

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Not for Publication

Frontispiece. Snowshoe Hare track. February 1962,
College, Alaska.

PREFACE

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I am sincerely thankful for the direction and counsel given by the following professors at the University of Alaska: Dr. Frederick C. Dean, Head of the Department of Wildlife Management, Acting Leader of the Cooperative Wildlife Research Unit, and my major advisor; Dr. Brina Kessel, Head of the Department of Biological Sciences; Dr. James Morrow, Associate Professor of Fisheries; Dr. William O. Pruitt, Jr., Associate Professor of Mammalogy; and Dr. L. Gerard Swartz, Assistant Professor of Zoology.

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Peter Dzikiewicz and Rex Thomas, students in the Department of Wildlife Management, contributed valuable field assistance and data.

I am deeply grateful for the help of my wife, Carolyn Trapp, who served as field and laboratory assistant during the summer and fall of

1961. She contributed many logical ideas, spent long hours working on illustrations, and critically edited, typed, and retyped the manuscript.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

LIST OF TABLES

Table		Page

ABSTRACT

A segment of a continuing study of Snowshoe Hares was conducted from May 1960 to November 1961, near College, Alaska. Objectives regarding home range, reproduction, behavior, age-determination criteria, and census methods were achieved by live-trapping and snaring.

The Schnabel (Krumholz) formula and Petersen ratio for estimating population size were invalidated by differential trap response. The calendar graph, Webb strip-census, Hartman toe-clip ratio, pellet count, and road survey all proved poor or useless as used during this study for estimating hare abundance in this area. An increase in hare sign in marginal habitat between 1958 and 1961 indicated an increase in population density.

Some hares were caught many times in succession in the same trap. Many more avoided traps, some for periods of nearly two years. Inclement weather restricted movements of hares.

Adult and juvenile sex ratios were 1:1. The season of births extended from mid-May to early August. There was a mean of 4.6 fetuses per female per pregnancy.

Hare parasites noted were: Mosgovoyia pectinata, Taenia pisiformis, Dirofilaria scapiceps, Obeliscoides cuniculi, Protostrongylus boughtoni, Haemaphysalis leporispalustris, and Hoplopsyllus glacialis.

Exclusive-boundary-strip home range decreased significantly at the .01 level from 14.5 acreas at a low population density to 13.1 acreas at a higher density.

A juvenile female hare made the maximum despersal movement noted, 1.6 miles.

Snow collected on vegetation formed winter cover for hares. Hares used burrows occasionally.

A sound resembling a low click ("tch") was observed in hares.

Possible displacement behavior was observed in hares.

Two litters were found in simple depressions in the leaves, and one in a nest-like form. Leverets less than 24 hours old could move from their place of birth.

A hare's foot color cannot be used as an age criterion in Alaska in summer, since adults may have brown, white, or mottled hind feet. The epiphyseal groove appears to close at approximately seven months. Juvenile males can be recognized until December by a short, stubby penis, and juvenile females by a short, blunt vulva and lack of palpable teats. A combination of body weight and hind-foot length is recommended for determining the ages of juvenile hares. A lens weight of 160 mg. can be used to separate hares less than a year old from older hares.

INTRODUCTION

This study is second in a series of ecological investigations of a subarctic Snowshoe Hare population which was originated in 1955 by the Alaska Cooperative Wildlife Research Unit as part of a long-term study of the patterns and causes of hare population fluctuations in Alaska. Thomas P. O'Farrell studied a hare population on a 160-acre plot two miles north of the University of Alaska, from June 1958 through April 1960. I studied the same population from May 1960 to November 1961.

Lepus americanus macfarlani Merriam is the subject of this study. (Mammal names are from Hall and Kelson, 1959.) According to Hall and Kelson, this subspecies is distributed throughout Yukon Territory; a large portion of Northwest Territories; the northern half of British Columbia; and Alaska, southeast of a line passing approximately through the following villages: Arctic Village on the south slope of the eastern Brooks Range, Kokrines in the Kokrine Hills, Takotna in the Beaver Mountains, Itulilik on the Holitna River, and Togiak on the northern coast of Bristol Bay. There are no Snowshoe Hares on the Alaska Peninsula west of the Naknek Lake region. There have been hares on Kodiak and Afognak Islands since they were transplanted there in 1934 (Elkins and Nelson, 1954). In 1954, Hares were transplanted from Kodiak to Woody and Long Islands nearby (ibid.), and Hensel (1960, notes on file at Alaska Cooperative Wildlife Research Unit, College, Alaska) introduced some hares on Deranof Island. These transplants have been successful. Several transplants made to the islands of Southeastern Alaska were not (Elkins and Nelson, 1954). Hares are absent from the Southeastern mainland, except on river deltas such as the Stikine and Taku. Elkins and

Nelson also mentioned that there is a population of hares on the moraine of Mendenhall Glacier and adjacent portions of Douglas Island, near Juneau. Presumably this isolated population resulted from a natural movement of the species from the interior.

Lepus americanus dalli Merriam is the only other subspecies of Snowshoe Hare in Alaska and is distributed to the west and northwest of L. a. macfarlani. Its range extends to the coast, north to the Brooks Range, and south to the lake-dotted Kuskokwim Delta. No Snowshoe Hares are found on most of the Kuskokwim Delta or north of the Brooks Range.

The history of Snowshoe Hare population fluctuations in Alaska can be traced through various records and observations. The following data are from Gasser (1935), Buckley (1954), Hopla (1960), and Dr. Frederick C. Dean (viva voce). Gasser said there was a high hare population in 1901-05 in the vicinities of Rampart, Copper Center and Fairbanks. Hares were very numbrous and destructive again near Fairbanks in 1913. Gasser and Buckley both reported a general population high in Alaska in 1924-26, and Buckley reported a low in 1928. In 1935-36 there was a high near Fairbanks. Buckley mentioned highs in 1942-43 and 1947, and lows in 1938-40, 1943-45, and 1948-50. In the fall of 1954 hares were very abundant in the Fairbanks area. Apparently they suffered a population crash that winter, because in the spring of 1955 the hare population was very low (Dean, viva voce). In 1956 it was still very low; Dr. Cluff Hopla of the Arctic Aeromedical Laboratory in Fairbanks attempted to trap hares at that time for his study of tularemia. He said, "In spite of numerous snares and live-traps plus endless hours of searching, no hares were obtained." Although hare studies were formally initiated in 1955 at the Cooperative Wildlife Research Unit, hares were not abundant enough to be studied effectively until 1959. From 1959 through 1961 the hare population in the vicinity of Fairbanks seemed to the casual observer to be increasing rapidly. The present study is temporally situated when the population is beginning a steep ascent.

The objectives of this study were: (i) to determine the effect of population density on home range size of Snowbhoe Hares in interior Alaska; (ii) to study reproduction, behavior, ecology, and age-determination criteria of Snowshoe Hares in a taiga habitat; (iii) to continue compilation of data on this particular hare population; and (iv) to test various census methods which might prove useful under sub-arctic conditions.

Field assistant, Peter Dzikiewicz, operated the trap lines from 1 May until 10 June 1960, after which he continued to help me for about one month, and at other times in the fall of 1960. During the winter of 1960-61, field assistant, Rex Thomas, occasionally operated the trap lines when I was unable to do so. Field work was terminated in mid-November 1961, although a few observations were made during the succeeding three months.

DESCRIPTION OF STUDY AREA

Location and Geological History

The 160-acre study area is located in the taiga of Interior Alaska, near Fairbanks (64° 50' N lat., 147° 50' W long.) (Fig. 1). The area lies two miles north of the University of Alaska, on a south-facing slope on the north edge of the Tanana River Valley. It occupies the northeast quarter of Section 30, T1N, R1W of the Fairbanks Meridian. This plot is situated in good hare habitat and is easily accessible by road from the University. The plot was established by O'Farrell (1960), who studied its hare population from the summer of 1958 through April 1960.

A minor amount of reconnaissance live-trapping and tagging was carried out in an additional area one-half mile north of the University. When the area proved to be unsatisfactory for further Snowshoe Hare study, its use was discontinued.

Black (1958) has described the geological history of Interior Alaska in a general manner; Péwé (1958) has described that of the Fairbanks area in greater detail. O'Farrell (1960) adequately related Péwé's description of geology and soils to the study area.

Climate

The extremes of climate common in Interior Alaska are important in the ecology of its inhabitants. Fig. 2 illustrates the temperature and precipitation regimes for the period during which this study was conducted. The weather of the Fairbanks area was recorded at Fairbanks International Airport, at an altitude of 436 ft. above sea level. This is 114 ft. lower than the lowest point on the study area. Since the

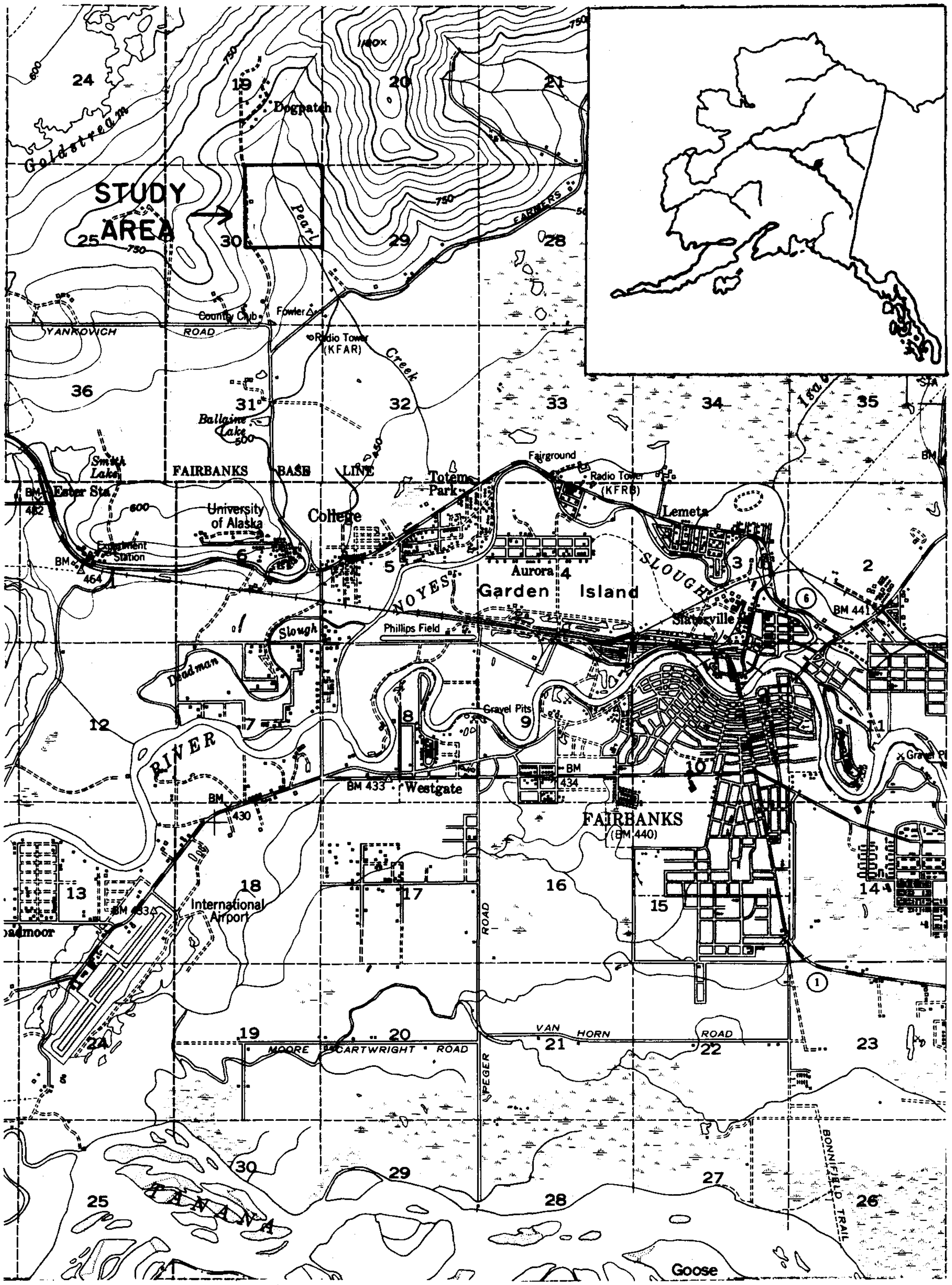


Fig. 1. Location of the Ballaine study area. Insert shows location of this area in Alaska.

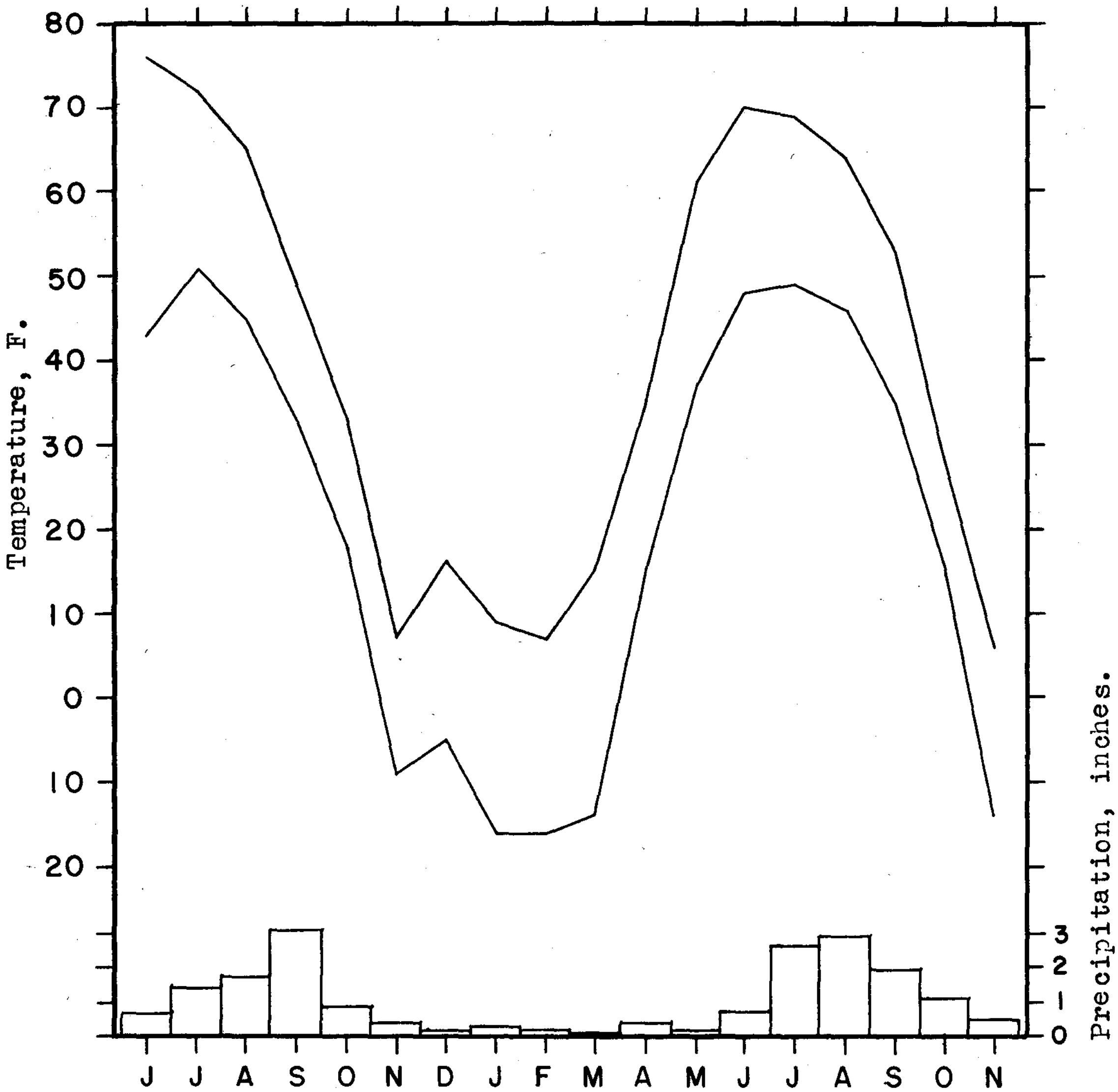


Fig. 2. Fairbanks temperature and precipitation regimes, June 1960 through November 1961.

airport is at a lower elevation one might expect the temperatures there to be slightly lower due to cold air flow and accumulation, but this was not always the case. Temperatures recorded on the study area were frequently more extreme at both ends of the scale than those recorded at the same time at the airport. The difference was generally no more than a few degrees. I have used the weather records taken at the airport chiefly because they are more complete than my own observations on the study area. Adequate time and equipment were not available for a detailed microclimatic study of the plot.

The first snowfall on the study area in the fall of 1960 occurred in late September. Snow was almost entirely melted by mid-April, having lasted about 6.5 months. The mean depths of snow during the months in which it was measurable are shown in Table 1 below. Snow depths were measured on 20 yardsticks, graduated in inches. Each stick was located half way between two live-traps.

TABLE 1. MEAN MONTHLY SNOW DEPTHS ON THE BALLAINE STUDY AREA

Month	Mean depth in inches	Month	Mean depth in inches
October 1960	2.5	January 1961	11.3
November 1960	4.5	February 1961	10.9
December 1960	6.8	March 1961	12.4

An ecologically important snow formation in taiga is _qali_ (Pruitt, 1958), the snow that collects on trees. During the winter in Interior Alaska the increasing weight of qali on small trees and shrubs often bends them over, providing forms with "roofs" for hares. The presence of qali depends upon lack of wind in winter, small amounts of incoming solar radiation, and continuously low ambient air temperatures (ibid.). The low density of the taiga snow allows it to accumulate on branches.

Vegetation

The study area supports mixed coniferous and ddciduous vegetation stands. These are apparently late regeneration or early climax stages of the northern coniferous forest biome, or taiga. The area was separated into nine stands (Fig. 3) chiefly on the basis of physiognomy. The stands were analyzed using a modified version of Dansereau's (1957) pictorial technique. Life form, height, stratification, and coverage can be depicted by this method. Dansereau's method, or modifications of it, have proved more useful than many tabular techniques in giving the reader a rapid idea of the character of the vegetation in an area. Several biologists (Weeden, 1960; Bider, 1961; and Getz, 1961) have used variations of this technique.

Detailed descriptions of the stands are given in the Appendix. Included with these descriptions are pictorial graphs, tables of coverage, and photographs of each stand.

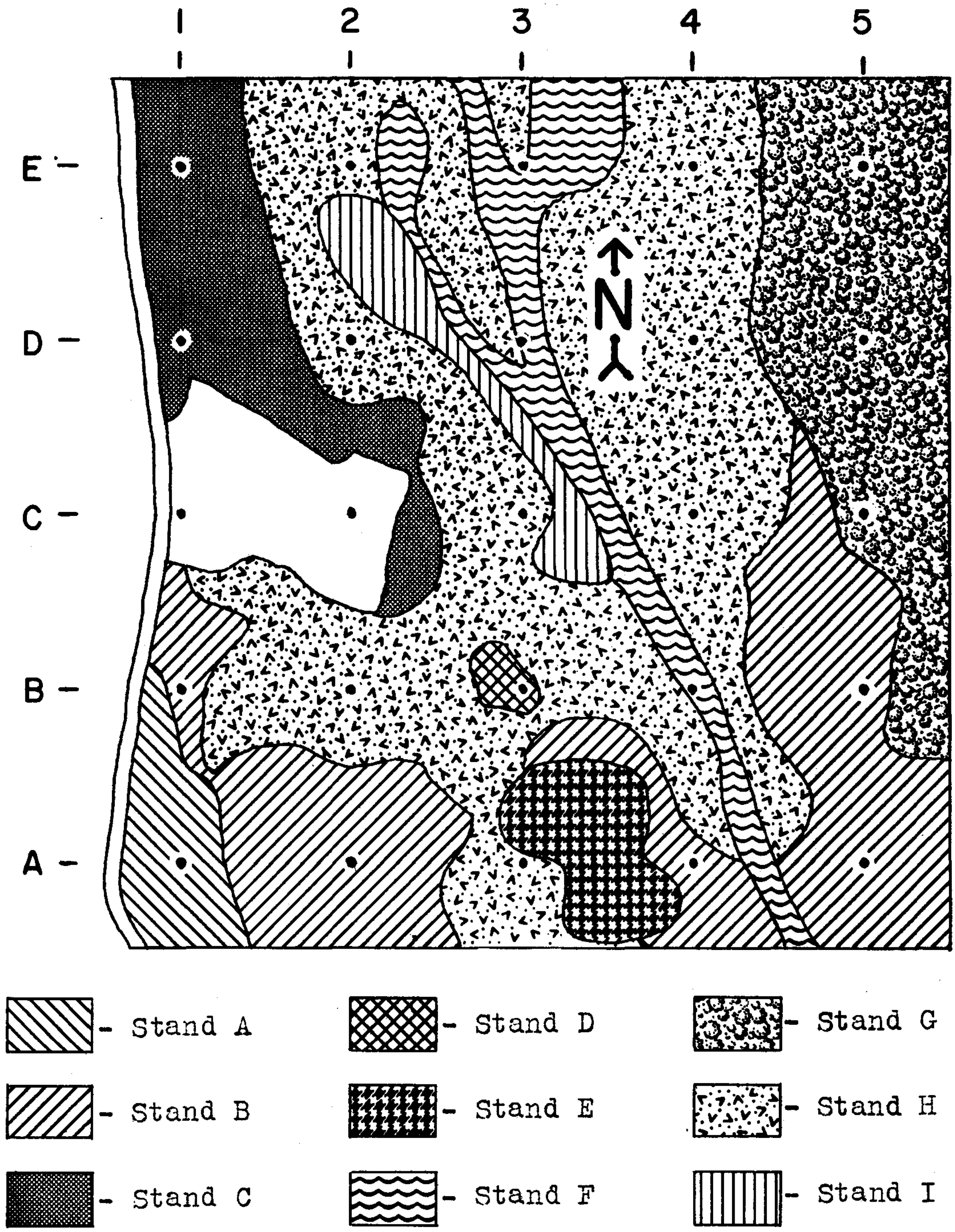


Fig. 3. Vegetation stands and trap sites on the Ballaine study area, College, Alaska. Letters A-E and numbers 1-5 on the map indicate trap lines.

CENSUS METHODS AND POPULATION DENSITY

A major attempt was made to determine the level of density of the hare population on the Ballaine study area. Unfortunately, few reliable data were obtained because the methods used were biased by heterogeneous trap response among hares. Each method and its results are described below. This is followed by a discussion of the response of hares to traps and weather conditions, both of which affect a here's trapability.

An attempt was made to determine the regional population density by counting the number of hares seen along certain roads at certain times, continuing a system of estimating used by Paul E. Tovey (1956, 1957, 1958, data on file at Cooperative Wildlife Research Unit, College, Alaska).

Ballaine Plot Population Level

O'Farrell (1960) surveyed the 160-acre study area and established trap lines. The grid consisted of 25 National double-door live-traps (9 x 9 x 32 in.) placed at 500 ft. intervals. The trap sites were lettered A through E from south to north, and numbered 1 through 5 from west to east (Fig. 3). This gave each trap site a binomial, e. g. A-1, B-3, E-5. Each trap was located within 50 ft. of the surveyed trap site (except trap C-2). Traps were occasionally moved to different places within this radius. There was no trap at site C-1, since this site was in a hay field not frequented by hares. Trap C-2 was located about 100 ft. east of the surveyed site, in the edge of woods bordering the hay field.

Special equipment used in tagging included a supply of hay with which to bait live-traps; a Chatillon spring scale with a 4 lb. capacity graduated in ounces; a steel measuring tape graduated in inches and millimeters; National Band and Tag Company monel metal ear tags, style 1005, size 3; special tag-crimping pliers; a burlap sack in which to weigh hares; and gloves to protect hands while handling hares.

The brome hay contributed by the University Experimental Farm probably was relatively unattractive to hares when green plants were abundant and hare food was not covered by snow. However, it provided food for hares in the traps.

The traps were camouflaged with burlap sacks, moss, and small branches. Most traps were situated in runways (Fig. 4). Funnels were constructed by sticking twigs into the ground near the trap entrances, and placing branches so as to guide the hares into the trap.

Methods used for determining relative abundance of hares were of two types: estimates and indices. The estimates used and their results were as follows.

<u>The Schnabel (Krumholz) formula.</u>-- This method, originated by Schnabel (1938), is based on tagging, releasing, and recapturing animals. It may be called a multiple census, since each day's catch may be regarded as a separate census.

When methods based on recapture are used to estimate population size, several conditions must be met. There should be no loss or gain of marks; no births, emigration, or immigration; no difference in mortality between marked and unmarked individuals; and the same susceptibility to capture in marked and unmarked individuals. The first condition was met in this study. Ear tags were seldom missing from

Fig. 4. A live-trap situated in a hare runway. Note logs and sticks placed so as to funnel hares into the trap.

TABLE 2. APPARENT TRAP AVOIDANCE IN HARES ON THE BALLAINE STUDY AREA, COLLEGE, ALASKA

Tag No.	Sex	No. Captures Previous To A	A		B		No. Days Between A and B	Distance In Feet Between A and B
			Date Of Capture	Site Of Capture	Date Of Capture	Site Of Capture		
2139	F	0	20 May 1959	A-4	26 April 1960	B-4	340	500
2147	M	0	18 June 1959	C-4	28 May 1960	B-4	343	500
2151	M	0	19 June 1959	A-5	9 July 1960	A-5	383	0
2169	M	0	25 June 1959	E-4	24 April 1960	E-5	301	500
2511	F	1	11 Nov. 1959	A-4	8 Nov. 1961	snare	723	336
2513	F	0	18 July 1959	D-2	5 May 1960	E-5	289	1600
2531	F	0	31 July 1959	B-1	9 Oct. 1960	*	433	336
2551	M	2	11 May 1960	B-3	11 Nov. 1961	B-3	547	0
2559	M	0	9 Aug. 1959	E-3	26 June 1960	E-3	319	0
2577	M	1	25 Nov. 1959	D-3	6 Nov. 1961	snare	707	336
2579	F	0	16 Aug. 1959	B-1	10 April 1960	B-2	312	500
2617	M	2	10 Aug. 1960	C-2	1 Nov. 1961	*	446	336
2713	F	0	19 April 1960	D-5	12 May 1961	D-5	386	0
2763	F	0	31 May 1960	B-5	30 June 1961	B-5	396	0
2219	M	0	22 June 1960	E-4	20 May 1961	E-4	330	0
2245	F	0	14 July 1960	B-2	18 May 1961	A-3	306	672
2249	M	0	15 July 1960	D-4	23 May 1961	B-1	310	1844
3739	F	0	30 July 1960	*	12 May 1961	D-4	284	336
3947	F	0	29 Oct. 1960	A-5	25 Oct. 1961	B-5	359	500

*Live-trap placed off regular grid.
**Many trap-nights occurred between all A and B dates.

recaptured hares. An attempt was made to correct for the second condition by conduction censuses when there was no natality. The censuses occupied a short time (14-24 days), reducing the emigration and immigration factors. Most hares which had been captured and released appeared to suffer little, other than becoming excited during the tagging operation. A few hares, however, died while being handled from what appeared to be hypoglycemic shock. The fourth condition could not be met. Some hares developed a "trap habit" and were captured again and again in the same trap; others became trap shy after the first capture, and were not caught again for several months (Table 2). (See discussion of trap response.)

Four Schnabel censuses were conducted, and the population estimates derived from them are shown in Table 3.

TABLE 3. ESTIMATES OF HARE POPULATIONS ON THE BALLAINE STUDY AREA USING THE SCHNABEL (KRUMHOLZ) FORMULA

Census period	No. hares per 160 acres	No. hares per acre
16 August - 16 September 1960	246	1.5
24 December 1960 - 6 January 1961	127	0.8
11 May - 24 May 1961	114	0.7
20 October - 4 November 1961	122	0.8

The Schnabel censuses indicate a decrease in population density throughout the study period. Some decrease might be expected between the first and third estimates given in Table 3, because of winter mortality, however, I find it difficult to believe that the hare population density consistently decreased from August 1960 6o November 1961. During the study I noticed an increase in the amount of hare sign (viz. tracks, pellets, and tree barkings) in areas formerly not frequented by hares. In the winter of 1960-61 I saw comparatively little hare sign in areas which probably were marginal habitat for hares, e. g., the more open upland stands and more densely settled areas in the College community. By the winter of 1961-62 hare sign had increased greatly in these marginal areas. Although the downward trend of the Schnabel estimates may reflect some winter mortality, I believe that any population estimate, or even indication of a trend, would be biased far too much by the effects of differential trap response. Therefore, the Schnabel method is unsatis= factory for determining either the relative or absolute abundance of hares.

The Petersen (1896) ratio.-- Often called the "tagging ratio", "Petersen-Jackson method", or "Lincoln index", this method is also based on the recapture of marked individuals. The population (N) is supposed to be related to the number marked and released (M) in the same way the total caught at a subsequent time (n) is related to the number of recaptures (m).

$$\frac{N}{M} = \frac{n}{m}, \text{ whence } N = \frac{Mn}{m}$$

Confidence limits can be calculated for this estimate.

Since the Petersen (1896) ratio requires the same conditions as the Schnabel method, it did not contribute any more valid information on the number of hares in the study area. To overcome the difficulty of varied trap response, I decided to use a recapture procedure different fromtthe method of capture. The 45 hares captured in live-traps and marked during the last Schnabel census (20 October to 4 November 1961) were used as "precensus" hares. From 4 November to 12 November, 64 snares were systematically distributed over the study area. A total of 34 "census" hares was snared, four of which were recaptures. Using these data in the Petersen ratio, I obtained an estimate of 383 hares on the 160-acre study area, or 2.4 hares per acre (confidence limits $\pm$ 360 at the 95% level). The broad confidence limits are probably due to the small number of recaptures obtained by snaring.

O'Farrell"s (1960) population estimates for October and November 1959, using the Lincoln Index (Petersen ratio), were 215 hares (confidence limits 0 and 636) and 55 hares (confidence limits 11 and 105), respectively. Unfortunately, from the information this method provided, it is impossible to tell if the hare population changed between October 1959 and October 1961.

<u>The Calendar Graph used by Adams (1959)</u>.-- With the abscissa marked off by calendar periods, horizontal lines are plotted across a graph. One line is entered for each animal tagged. The line starts at the date of the first capture and ends at the date of last capture. The number of animals known to be present at a given date is determined by erecting a perpendicular at the point on the abscissa representing that date. The number of horizontal lines intercepted by this vertical line is the number of animals known to be present. Adams used this method successfully on an island population. O'Farrell (1960) found the method useful only as an index to the minimum hare population of the Ballaine study area.

The calendar-graph method indicates the following (minimum) numbers of hares on the study area during the four Schnabel censuses mentioned above:

14 August - 17 September 1960	115 hares
18 December 1960 - 7 January 1961	89 hares
7 May - 27 May 1961	69 hares
15 October - 4 November 1961	54 hares

The apparent decrease in the number of hares between 14 August 1960 and 4 November 1961 is an artifact produced by the calendar graph. If I had not trapped again after 17 September 1960, the calendar graph would have shown 69 hares on the study area during the period 14 August - 17 September. Many hares tagged previous to 14 August 1960 were first recaptured between 17 September 1960 and 4 November 1961. Nine hares tagged previous to 1 May 1960 were not caught again until the last census period in 1961. Most of these were taken by snare, indicating that they had successfully avoided live-traps for more than a year. The minimum number of hares present on the study area during the period 14 August-17 September 1960 (115 hares) is the best population figure the calendar-graph can provide. O'Farrell (1960) obtained calendar-graph estimates of 80 to 85 hares for the summer of 1959. Perhaps this indicates in a rough way that the hare population had increased. The calendar-graph has no value in indicating the true size of a hare population unless nearly all animals are handled frequently, and the method is used over an extended period.

Webb's (1942) strip census.-- This method consists of counting the animals observed while the observer is walking along an arbitrary line. The distance at which an animal is flushed is recorded. The angle between the flushing site and the line walked (observer at apex) is noted. The formula is:

$$P = \frac{AZ}{2XY \text{ Sine } D},$$

where P is the population, A the total area of study, Z the number of animals flushed, Y the average flushing distance, X the length of the walk-line, and D the average angle in degrees. On many occasions I attempted to use this method while walking the trap lines of the study area.

O'Farrell (1960) found that the Webb strip-census technique was not feasible for estimating the number of hares on the study area. I concur. The hare's pelage provides good camouflage in summer and winter. This, plus their habit of "freezing" when alarmed, makes hares difficult to see during either season. Although hare sign was abundant on the study area, I seldom saw more than two or three hares (and often none) while running the trap lines in winter. Even fewer hares were seen during summer, because of dense foliage. This method might be feasible during the autumn pelage change when many hares possess a large amount of white fur before any snow has fallen, and in the spring when the snow has melted and some hares are still partly white.

Hartman's (1960) toe-clip ratio.-- This method can be used only when there is snow on the ground. It consists of capturing a large number of hares, clipping one toe from the hind foot of each hare, and then releasing the hares. At a subsequent time the proportion of "clipped" tracks crossing a predetermined line is noted. This method is based on the same principle as the Petersen ratio described above.

In Ontario, Hartman (1960) clipped one hind toe from each of several hares, released the hares, and at a subsequent time noted the proportion of "clipped" tracks on his study area. According to him, this method was satisfactory. I clipped toes from the right hind feet of 25 hares on 29 October 1960, and from the left hind feet of 13 hares on 28 December 1960. I could not distinguish "clipped" tracks from normal tracks. The snow was always too dry and powdery or too grainy to show sharp impressions. Hares leave only indistinct, rounded tracks. Hartman must have worked with moist snow in which hares left distinct tracks. This snow condition is not common in Interior Alaska.

Indices.-- A change in population size can often be detected by comparing counts of related phenomena (e.g., runways) taken at different times. Two indices were used on the Ballaine study area; the number of hare runways crossing trap lines, and counts of hare pellets in twenty 1/10,000-acre plots.

Runways crossing the trap lines on the Ballaine study area were counted several times during the winter of 1960-61 (Table 4). Since my censuses yielded such unreliable estimates, I cannot relate the number of runways to a known population.

From 30 December 1960 to 7 January 1961 Rex Thomas operated twenty 1/10,000-acre plots for pellet counts on the study area. Few pellets were deposited in the plots, yielding unsatisfactory results, chiefly because the sampling intensity was too low.

A low point in the hare population fluctuation in the Fairbanks area occurred in 1955-56 (Dean, *viva voce*). As the hares began to increase again, O'Farrell (1960) used a Petersen ratio to obtain an estimate for April 1960 of 42 to 94 hares on the Ballaine study area. I have cited this estimate because it has the narrowest confidence band of any of O'Farrell's estimates, and so may be regarded as his best

TABLE 14. NUMBER OF RUNWAYS AND INDIVIDUAL HARE TRACKS CROSSING TWO ONE-HALF MILE TRANSECTS ON THE BALLAINE STUDY AREA, COLLEGE, ALASKA

Date	Snow depth, inches	Snow Surface hardness g/cm^2	Transect	No. runways	No. individual tracks
21 Nov. 1960	5.0		B, D	abundant	abundant
29 Nov.	8.6		B	41	171
10 Dec.	6.0	6	B	61	abundant
10 Dec.	6.0	6	D	69	abundant
13 Dec.	8.0	4	B	81	67
13 Dec.	8.0	4	D	62	80
30 Dec.	7.7	9	B	34	118
30 Dec.	7.7	9	D	34	113
3 Jan. 1961	12.0		B	40	42
3 Jan.	12.0		D	50	22
6 Jan.	12.0	7	B	35	10
6 Jan.	12.0	7	D	50	12

indication of the population size at that time. The population size in November 1961 was probably near the estimate I obtained using the Petersen ratio, i.e., between 200 and 500 hares. In relative terms, the number of hares present on the study area in November 1961 may have been two to five times as large as it was in April 1960.

Trap response and response to weather.-- The nature of a hare's response to a trap is an important factor to be considered when censuses are made. In many census techniques it is assumed that there is a uniform probability of capture in the population. This assumption is relatively invalid, especially in the case of Snowshoe Hares. Some hares are attracted to a trap after having been caught in it once. Perhaps it is the bait which attracts them. Some extreme examples are as follows: (i) a juvenile male was caught in trap B-1 on the reconnaissance study area on 16, 20, 22, 24 August and 6, 9, 10 September 1960 (dead and mutilated); and (ii) a juvenile female was caught in trap B-4 on the reconnaissance study area on 24 August and 7, 8, 10, 11, 12, 13, 14, 15, 16 September 1960. She died on 16 September after losing considerable weight and becoming weaker each day.

Some hares may be caught several times in the same trap at intervals which are not quite so frequent. Again, the reason may be because of attraction to the trap, or perhaps because the trap occupies a runway which the hare uses more frequently than other runways.

Many hares were caught only once, or were caught once and recaptured only after a long interval. Many of these probably avoided traps. On the Ballaine plot 271 hares were tagged between 1 April and 31 December 1960. One hundred thirty-two of these (49%) were not caught again, and 65 (24%) were caught only once more. Most of the hares (110 or 83.3%)

caught only once were juveniles, which probably emigrated from the area. Evidence which seems to support the idea that hares avoid traps is shown in Table 2. The table shows that eight hares were not recaptured until more than a year after the first capture, even though trapping was carried out many times in the interval. Almost two years elapsed between successive captures of two of these hares. Seven of the hares listed in Table 2 were recaptured at the same trap, ten were recaptured within 500 ft. and three farther than 500 ft. This indicates that although these hares were not captured for periods ranging from ten months to almost two years, they had remained in the same vicinity, no doubt avoiding the traps.

Other workers have found bias in live-trap samples. Young, et al (1952), studying the heterogeneity of trap response in a population of House Mice, _Mus musculus_, stated that "live-trap samples of the sort used are likely to be strongly biased, and unlikely, therefore, to provide a secure basis on which to construct estimates of population size." Geis (1955) found Eastern Cottontails, _Sylvilagus floridanus_, to have much variability in trap response. He gave three reasons why rabbits may enter traps more often than expected: some rabbits have a small home range within which the trap is located so as to be encountered frequently; rabbits vary in their innate tendency to enter traps; and once a rabbit has had experience with a trap, its behavior is altered so that it is more likely to be recaptured. My interpretation of the Ballaine plot data, as discussed above, is that once a hare has had experience with a trap, it is quite as likely to become shy of that trap as to become attracted to it.

In Table 5 the trap success and recapture success are listed by

TABLE 5. MONTHLY TRAP SUCCESS AND RECAPTURE SUCCESS, MAY 1960 - NOVEMBER 1961

Year	Month	Cum. no. tagged*	A No. captures	B No. re-captures	C No. trap-nights	D Trap success, A/C x 100	E Recapture success, B/A x 100
1960	April	166					
	May	181	44	29	744	6%	66%
	June	207	42	16	720	6	38
	July	273	102	36	840	12	35
	Aug.	335	108	46	728	15	43
	Sept.	359	45	21	288	16	47
	Oct.	384	54	29	87	62	54
	Nov.	396	26	14	44	59	54
	Dec.	420	88	64	202	44	73
1961	Jan.	420	7	7	178	4	100
	Feb.	422	10	8	24	42	80
	March	424	3	1	15	20	33
	April	424	2	2	10	20	100
	May	442	53	35	335	16	66
	June	455	25	12	178	14	48
	July	464	13	4	80	16	31
	Aug.	501	41	4	223	18	10
	Sept.	512	12	1	95	13	9
	Oct.	536	42	18	288	15	43
	Nov.	542	23	17	96	24	74
TOTALS		542	740	364	5175		
AVERAGES						14%	49%

*Cumulative number of hares captured since beginning of O'Farrell's (1960) project, July 1958.

month for the entire study period. Trap success is expressed as a percentage. This percentage represents the ratio of total captures to units of effort, viz. trap nights. During the study, 740 hares were caught (including recaptures), resulting in a trapping success of 14%. The number of hares had increased since O'Farrell's (1960) study. O'Farrell caught 348 hares in 1959 and 1960 (including recaptures), for a trapping success of 8.4%. In 1960 the trapping success was lowest in May and June, being only 6%. The reasons for this probably were (i) the adults present on the study area had become somewhat "trap-educated"; (ii) the hay bait in the traps was less desirable as green plants became available; (iii) as Grange (1932a) suggests, females move around very little during late pregnancy; and (iv) the young born during the latter part of May were not yet active. Trapping success increased to 12%, 15%, and 16% in July, August, and September, respectively, and the young born during the summer became more active and were caught in the traps. In the fall, as snow covered the vegetation, more hares were probably attracted to the hay bait; trapping success increased to 62%, 59%, and 44% in October, November, and December, respectively. In January 1961 trapping success dropped to 4%, perhaps in part because of low temperatures (-25° to -35° F.). A trapping success of 42% was obtained for February. The number of trap nights and number of hares caught during March and April were too small to yield any reliable information. During May and June 1961 trapping success was 16% and 14%, respectively, higher than the success during the same period in 1960, probably because I had not trapped very often during the late winter and early spring. Also, the population was greater at this time than it was in the spring of 1960. Trapping success figures for July, August, and September 1961 were 16%, 18%, and

13%, respectively, which was unexpectedly lower than the figures for the same months in 1960. Low success may have been due in part to avoidance of traps, and in part to the weather. In October hares probably moved little, as frequent thaws alternated with low temperatures and heavy snowfalls occurred. The efficiency of the traps was lowered considerably by alternate thawing and freezing; the traps were often frozen open, and therefore were impossible for a hare to spring.

Recapture success can be defined as the proportion of recaptured hares in a sample, expressed as a percentage. In Table 5 the recapture success for each month of the study is listed. In May 1960 recapture success was 66%, which is relatively high. At that time a large proportion of the hares living on the study area had been tagged by O'Farrell (1960) and by Peter Dzikiewicz. As young hares were added to the population, the recapture success was lowered in June and July to 38% and 35%, respectively. Recapture success began to rise as a larger proportion of the young was tagged. The figure was 43% in August, and rose to 73% in December. Since so few hares were captured in January, February, March, and April 1961, little of significance can be obtained from the figures for these months. In May 1961 recapture success was 66%, as high as in May 1960. It decreased again in June and July 1961, and then increased in the fall as it had in 1960.

I cannot detect a significant difference in trap response between males and females (Table 6), since the ratios varied so widely. O'Farrell (1960) stated that more males than females were captured during April 1960 because males were more active than females during the breeding season. This trend appeared to carry over into May 1960. However, I doubt its significance, since in May 1961 the ratio was 21 males to 32 females.

TABLE 6. SEX AND AGE RATIOS OF HARES CAUGHT AT COLLEGE, ALASKA, FROM MAY 1960 TO NOVEMBER 1961

Year	Month	Adult males	Adult females	Juvenile males	Juvenile females
1960	May	31	13	0	0
	June	10	12	9	11
	July	6	3	50	43
	August	2	3	41	62
	September	0	3	17	25
	October	6	3	21	24
	November	1	0	13	11
	December	7	7	31	40
1961	January	2	5	0	0
	February	6	4	0	0
	March	0	3	0	0
	April	1	1	0	0
	May	21	32	0	0
	June	3	15	1	5
	July	0	3	3	7
	August	0	5	19	15
	September	0	0	4	8
	October	9	4	19	10
	November	4	4	8	7
TOTALS		109	120	236	268

Inclement weather seemed to restrict the movement of hares. In Table 7 catches are listed for days which followed nights of inclement weather. The mean trap success for 35 days preceded by rain or snow in the evening or night was 7.5%. The mean trap success for 53 days preceded by nights of clear weather was 14.5%.

Hares are usually active in the evening, night, and early morning. During this study, inclement weather such as rain, snowfall, or thawing (creating wet conditions) at these times tended to reduce hare activity. During long rainy periods hare activity seemed low at first, then as rain continued day after day the hares again began to move about, getting caught in the traps again. The evening preceding 26 August 1961 was rainless, but heavy rain fell during the night. Four hares were caught, presumably in the evening, and died from overwetting. Hares weemed relatively inactive during snowfalls, but soon after a snowfall ended many fresh tracks appeared.

Censuses in which live-traps are employed can easily be affected by any hare behavior which affects trapability. The biologist should consider these types of behavior before embarking on a census whose results may not justify the time and effort expended in obtaining them.

IHterior Alaska Population Level

The number of hares seen per mile along a road has been suggested by some biologists as a possible means of determining the relative abundance of hares. Paul E. Tovey (data on file at the Cooperative Wildlife Research Unit, College, Alaska) conducted four highway surveys in June 1955, 1956, 1957, and 1958, respectively, on a route which included the Steese Highway and the Fairbanks-Gulkana-Tok Junction highway triangèe. His surveys were conducted between 1900 and 0700 hours. He

TABLE 7. RESPONSE TO WEATHER: NUMBER OF HARES CAPTURED FOLLOWING NIGHTS OF INCLEMENT WEATHER, BALLAINE STUDY AREA, COLLEGE, ALASKA

Date	No. captures	No. trap-nights	Weather condition preceding night	Date	No. captures	No. trap-nights	Weather condition preceding night
12 June 1960	2	24	raining	8 Sept. 1960	2	24	raining
15 June	0	"	"	12 Sept	0	"	"
16 June	0	"	"	13 Sept.	5	"	"
30 June	0	"	"	13 Nov.	3	10	snowing
6 July	1	"	"	2 Jan. 1961	2	24	"
7 July	0	"	"	3 Jan.	0	"	"
20 July	4	40	"	6 Jan.	0	"	"
29 July	2	"	"	7 Jan.	0	"	"
2 Aug.	6	"	"	11 May	7	"	raining
5 Aug.	3	"	"	6 Aug.	2	"	"
16 Aug.	1	24	"	11 Aug.	6	"	"
18 Aug.	4	"	"	26 Aug.	4	"	"
20 Aug.	3	"	"	9 Sept.	1	"	"
21 Aug.	2	"	"	21 Oct.	0	"	"
25 Aug.	3	"	"	23 Oct.	1	"	snowing
27 Aug.	0	"	"	24 Oct.	0	"	"
5 Sept.	1	"	"	28 Oct.	1	"	"
				30 Oct.	1	"	"

counted 661 hares in June 1955 and 95 hares in June 1956, in each of two 536-mile surveys. Again in June 1957 he made a 536-mile survey, and saw two live hares and one dead one. In June 1958 he drove 1,000 miles on the same route and saw only two hares on the Steese Highway.

Apparently the hare population did not "crash" in all areas of Interior Alaska in the winter of 1954-55. The population in the College area did crash at that time, but Tovey's highway survey of June 1955 indicated that the hares were still abundant, at least on the highways, in other parts of the Interior.

In July and August 1960, I drove 464 miles in eight evenings on five different roads. Twenty-seven hares were seen. Nineteen of these were on the Steese Highway in a local area of high hare density north of the Tanana Hills, near Central. These drives were mainly exploratory. I was attempting to find a road on which a sufficient number of hares could be seen to allow me to obtain data on hare activity. No satisfactory roads were found in the vicinity of Fairbanks, although I knew from collecting that hares were abundant in many of the areas concerned. Centering driving time around sunrise, 106 miles were driven in six days on a circuit including Farmer's Loop Road, Yankovich Road, and Sheep Creek Road, all north or west of College. No hares were seen, although hares were known to be abundant throughout the area. Driving time was then centered around sunset, and the above circuit driven twice and the Chena Hot Springs Road once. No hares were seen. A constant speed of 30-35 mph. was maintained on all morning and evening drives.

On 15 July 1961 hares were counted along the Elliot Highway between Fox and Livengood, a distance of 68 miles. Sixty-two hares were seen. Of these, 14 were seen between 1800 and 2010 hours on the way to Livengood, and 48 were seen between 2115 and 2325 hours on the way back to Fox. On the same date, in a short exploratory drive north of Livengood on the "Reservoir Road," approximately 70 hares were seen in 3.5 miles, between 2010 and 2025 hours. This local area apparently had a very dense population that was, perhaps, near a cyclic peak. The onyy other area where hares were commonly seen along a road was in the vicinity of Central, between the Tanana Hills and Circle City. On 5 September 1961 John Burns, a fellow graduate student, and I drove from the base of the Tanana Hills to Central, then to Circle Hot Springs and about eight miles along Deadwood Road. We saw 38 hares between 1650 and 2030 hours.

Only in areas of very dense hare populations does one see even a few hares along roads. Heavy traffic is an important factor in the vicinity of Fairbanks. I believe that any of the local roads which are potentially suitable for road surveys are too heavily traveled, and so repel hares. In driving to and from the study area hares were seldom seen, although they were known to be abundant.

Many variables affect a road survey: weather, sexual activity of hares, traffic, and attractive salts and minerals on the roads. Extensive highway surveys such as Tovey's made over a period of years, under the same conditions each year, may show gross changes in the Interior Alaska hare population. This seems an impractical procedure, because the questionable validity and gross nature of the results probably would not justify the expense of the survey.

REPRODUCTION AND DYNAMICS OF THE POPULATION

Data on reproduction were gathered by live-trapping on the Ballaine study area and by collecting hares in other areas, using snares, live-traps, and a .410-gauge shotgun. Snares and live-traps proved most effective. These were placed in runways in various areas of good hare habitat near College.

Sex Ratio

From April 1959 to February 1960, when the Ballaine hare population was low, O'Farrell (notes on file at Cooperative Wildlife Research Unit, College, Alaska) captured 207 hares of which 109 (53%) were males and 98 females. This does not differ from a 1:1 ratio at the .05 level when subjected to a chi-square test. From 7 to 30 April 1960 O'Farrell captured 114 hares of which 85 (75%) were males and 29 females. He attributed this difference in ratio to the greater activity of males during the breeding season. During April 1961 I did not capture enough hares to determine any difference in sex ratio.

From May 1960 to November 1961 I captured 229 adult hares. The sex ratio was 109 males (48%) to 120 females. Of 504 juveniles captured during this period, 236 (48%) were males and 268 females, (Table 6). Neither ratio differed from a 1:1 ratio at the .05 level, when subjected to a chi-square test. All hares were considered to be adults between December and June.

Other biologists have found similar ratios. The following sex ratios have been reported for high hare populations. Unfortunately, the term "high" is subjective. It would be interesting to know exactly when peaks occurred in the following populations. Webb (1937) in Minnesota found 53.6% males in 3,930 hares. Aldous (1937) in Minnesota found

54% males in 1,625 hares. Severaid (1942) in Maine found 49% males in 219 live-trapped adult hares, and 54% males in 119 young born in captivity.

Rowan and Keith (1956) in Alberta found 30.3% males in a sample of 109 adult and juvenile hares taken from a population which was near the peak of its cycle. This ratio differed significantly from a 1:1 ratio. A shift in sex ratio occurred at the peak, which restored a 1:1 ratio. This shift in sex ratio was believed by Rowan and Keith to be positively correlated with the peak of the cycle. Philip (1939) collected 151 hares in the Fairbanks area during June and July 1937. Of these, 19.2% were males. This obviously differs from a 1:1 ratio. 1937 was a peak or near-peak year.

Dodds (1960a) in Newfoundland found 52% males in the 642 hares caught between 1955 and early 1959. These hares were collected from several areas with differing population densities.

<u>Natality Factors</u>

O'Farrell (1960) found that the breeding season for Ballaine study area hares began in mid-March with the descent of the testes. He noted courting behavior in early April and the first litters were born during the last week in May. After 18 July no males with scrotal testes were captured. O'Farrell stated, "After July 9 all adult female hares were lactating but none appeared pregnant. Probably no litters are conceived after mid-July and the last litters were born at that time." Combining data from the summers of 1960 and 1961, I found that the earliest litter was born on about 17 May and the latest litter on about 5 August. Two litters were known tohave been born on about 23 July. The first pregnancy observed was on 5 May, and the last on 28 July. The first lactating female hare was noted on 27 May and the last (two hares) on 30 August.

The Snowshoe Hare's breeding season appears to begin at about the same time across the continent, in mid- and late March (Severaid, 1945; Aldous, 1937; Green and Evans, 1940c; Adams,1959; Criddle, 1938; Dodds, 1960a). Rowan and Keith (1956) said that more southerly hares often bear young slightly earlier than hares farther north, but that the northern hares seem to extend their breeding season later into the fall. In Alberta, Rowan and Keith found that 13.4% of the recorded pregnancies occurred in August. Green and Evans (1940c), in Minnesota, found a negligible number of births in August. Criddle (1938) believed that some Manitoba hares breed as late as September and occasionally October. Adams (1959) found lactating hares in Montana in mid-September. Dodds (1960a) found that the testes ascend in early August in Newfoundland; hares could therefore be born in August and early September. Hensel (1960, notes on file at Cooperative Wildlife Research Unit, College, Alaska), in an experimental study of hares planted on some small islands near Kodiak Island, Alaska, found the breeding season to extend from mid-March to August. No doubt some Interior Alaska hares are born in August, but they probably constitute a small proportion of the season's young.

Table 8 shows litter sizes found by biologists in North America. It appears that litters, as Rowan and Keith (1956) suggested, are somewhat larger in northern latitudes. It also appears that litter size may fluctuate somewhat with population density. Dodds (1960a) found the litter size to be 2.3 young in a high, decreasing population. From two populations which were low and increasing he calculated a mean of 4 young per litter. His grand average for both wild and captive hares was 3.2

TABLE 8. SNOWSHOE HARE LITTER SIZE AND FREQUENCY IN NORTH AMERICA

Authority	Region	Approx. N latitude	No. F in sample	$\bar{x}$ no. yg/ litter	$\bar{x}$ no. litters/ F season	Potential no. yg/ F season
Severaid (1945)	Maine	44°	161	2.9	2.8[a]	8.2
Aldous (1937)	Minn.	46°	266	2.8		
Green and Evans (1940c)	Minn.	46°	140	2.9	2.4[b]	6.8
Adams (1959)	Mont.	48°	41	2.7 - 3.0	2.9[c]	
MacLulich (1937)	Ontario	46°- 49°	33	2.8		
Criddle (1938)	Manitoba	50°	149	3.4		
MacLulich (1937)	Manitoba	51°	26	4.1		
Dodds (1960a)	Newf.	46°-52°		3.2	2.6[d]	
" "	"	"	18	4[e]		
" "	"	"		2.3[f]		
Rowan and Keith (1956)	Alberta	56°	82	3.8	2.8[b]	10.5
Hensel (1960)	Kodiak, Alaska	58°	44	4.9	2.2[c]	10.8
Philip (1939)	Fairbanks, Alaska	65°	46	4.9[g]		
Tovey and Bishop	Interior, Alaska	65°	114	4.2[b,g]		
Trapp (this study)	College, Alaska	65°	12	4.6[b]	1.7[c]	7.8

*Notes on file at Cooperative Wildlife Research Unit, College, Alaska

[a]From captive hares.
[b]From embryo counts.
[c]From palpations.
[d]From captive and wild hares.
[e]From two small, increasing populations.
[f]From a large, decreasing population.

young per litter. Two biologists in Alaska, Philip (1937) and Hensel (1960, notes on file at Cooperative Wildlife Research Unit, College, Alaska), each obtained a mean of 4.9 young per litter. Philip studied a near-peak population, and Hensel studied a rapidly increasing island population. A mean number of 4.2 embryos per female was found in 114 female hares collected in several areas in Interior Alaska, where populations were high, in June and July of 1955 and 1956 (Tovey and Bishop, notes on file at Cooperative Wildlife Research Unit, College, Alaska). In 12 pregnant hares examined during the summers of 1960 and 1961, I found a mean of 4.2 fetuses per female.

Green and Evans (1940c) believed that litter size was not an important factor in cycles, but the important factor was varying mortality rate in juveniles. They reported a constant reproductive rate for their seven-year study period.

Using the method employed by Green and Evans (1940c), I calculated the average number of litters per female per season. Table 9 shows the calculation and the result, 1.7 litters per female per season. This is unexpectedly low, in view of the increasing population. Most biologists (Table 8) have obtained higher figures, from 2.2 to 2.9 litters. My sporadic trapping, and differential trap response between pregnant and non-pregnant females, may have been responsible for the low figure. Pregnant hares may not move around as much as non-pregnant females, and hence may be less susceptible to capture. Of 59 pregnant hares trapped, 41 or 69% were captured during the first two periods shown in Table 9 (5 May to 3 June). This seems to indicate that the majority of females participate in the first breeding activities of the season. Probably fewer females have second and third litters. Severaid (1942) said that

TABLE 9. AVERAGE NUMBER OF LITTERS/FEMALE HARE SEASON, CALCULATED BY GREEN AND EVANS (1940c) FORMULA, FOR COLLEGE, ALASKA

Period	No. days in period		Percent females pregnant		No. days recognizable pregnancy
5 May - 19 May	15	x	94%	=	14.1
20 May - 3 June	15	x	82%	=	12.3
4 June - 18 June	15	x	11%	=	1.7
19 June - 3 July	15	x	86%	=	12.9
4 July - 18 July	15	x	50%	=	7.5
19 July - 28 July	10	x	20%	-	2.0
TOTAL					50.5

$$\frac{\text{Total number of days of recognizable pregnancy}}{\text{Number of days embryos can be distinguished } \underline{\textit{in utero}}} =$$

Average number of litters/female season

$$\text{Ex.} \quad \frac{50.5}{30} = 1.7$$

of 17 captive female hares in Maine, 100% conceived once, 94.1% twice, 64.7% three times, and 23.5% four times. It seems quite likely that some Ballaine study area hares conceive a third time, but unlikely that fourth litters occur. Since the hare's gestation period is approximately 36 days (Grange, 1932a), and since a female may breed again on the day of parturition (Severaid, 1942), it is possible for a Ballaine study area hare to bear a first litter on 17 May, a second on 22 June, and a third on 28 July.

Mortality and Longevity

Snowshoe Hares are short-lived in the wild. Their environmental longevity seems to be considerably shorter than their physiological longevity. Of 55 known-age hares born in the summer of 1959, at least 20 or 36% survived at least one year, and at least 3 or 5% survived at least two years. Trapping has not continued into the third year for this cohort. Differential trap response and emmigration were partly responsible for the apparently high mortality. I captured three hares in 1961 which were at least three years old, probably born in the summer of 1958. Further trapping on the study area should reveal what proportion of the 1959 cohort survived for three years.

Aldous (1937) said that hares survive and average of two years. Green and Evans (1940b) made one of the longest and most detailed studies of the population dynamics of Snowshoe Hares. They studied a Minnesota population the adult segment of which consisted of 44% yearlings, 39% two-year-olds, 7% three-year-olds, 8% four-year-olds, and 2% five-year-olds. The annual mortality of adults was about 70% throughout the study. The rate was constant regardless of cyclic phase. However, the juvenile mortality varied greatly, and the variations in population size seemed to be due chiefly to this factor. In 1938, the low point in the cycle, only 8% of the young born survived until February. The following year 91% survived until February.

Some decimating factors which affect hare mortality to varying degrees are predatory mammals and birds, parasites, diseases, and hunting by man. The nomenclature of the mammals discussed below is that of Hall and Kelson (1959).

Predators.-- O'Farrell (1960) reported seeing Lynx, *Lynx canadensis*, on the study area. No signs of this predator were seen during my study. I saw one small Black Bear, *Ursus americanus*, and frequently observed fresh bear scats on the study area in the summer of 1960. It is doubtful that Black Bears commonly prey on Snowshoe Hares, except perhaps small leverets. O'Farrell (1960) reported seeing signs of Mink, *Mustela vison*, Short-tail Weasels, *Mustela erminea*, and Least Weasels, *Mustela rixosa*, but I did not see much evidence of their presence. Although I saw no hares killed by Red Foxes, *Vulpes fulva*, I often saw fox tracks on all parts of the study area. Peter Dzikiewicz reported seeing a Red Fox on the study area in April 1960. Foxes are known to den in the Fairbanks area, and the remains of many hares were found at one den.

Mammalian predators were not necessarily important factors in hare mortality, at least under natural aonditions. Several dogs owned by nearby residents commonly ranged over the study area and surrounding woods. Quite frequently they distrubed traps, killing and mutilating the imprisoned hares. On 6 November 1960 dogs killed and mutilated all of the 18 hares caught in live-traps that day.

Common Ravens, *Corvus corax*, and Gray Jays, *Perisoreus canadensis*, acted as scavengers rather than predators. I saw two Sharp-shinned Hawks, Accipeter striatus, one Marsh Hawk, Circus cyaneus, and a Hawk Owl, Surnia ulula, in the vicinity of the study area during the summer of 1960. These three species no doubt preyed only on leverets, if they preyed on hares at all. More important predators were the Great Horned Owl, Bubo virginianus, the Goshawk, Accipiter gentilis, and the Red-tailed Hawk, Buteo jamaicensis, all of which were seen occasionally on or near the area. Great Horned Owls were reported in the vicinity by nearby residents. I saw Goshawks several different times on and near the study area. Rex Thomas operated the trap lines on 1 January 1961 and reported that a large hawk attacked (and missed) a hare released at trap A-4. This was probably a Goshawk. During the summers of 1960 and 1961 I often saw one or two Red-tailed Hawks soaring over the study area; on 11 September 1960 I flushed one from a freshly killed hare.

The nomenclature used for the preceding birds is from the A. O. U. Checklist of North American Birds (1957).

Parasites.-- Twenty-seven hares collected on the study area and near the University were examined for parasites by parasitology students at the University during the fall and winter of 1961-62. These hares were autopsied in detail, except for the intestines of two. No trematodes were found. Both adult and larval tapeworms were common. Mosgovoyia pectinata was recovered from the small intestines of all (eight) young hares killed during the summer. Taenioid larvae were found in the coeloms of five hares and in the musculature of one hare. Three species of nematodes were found in the hares: Dirofilaria scapiceps adults were found in the hind feet, and larvae were found in the blood of five hares; stomach worms, Obeliscoides cuniculi, were found in the stomachs of 12 hares; and lungworms, Protostrongylus boughtoni, were found in the lungs of 14 hares.

Since most of the hares had been frozen for varying lengths of time before autopsy, the incidence of arthropod ectoparasites could not be determined. I often found ticks, Haemaphysalis leporis-palustris Packard (Cooley, 1946), on hares in the summer of 1960. I found them much less frequently during the summer of 1961. Fleas described by Hopkins and Rothschild (1953) as Hoplopsyllus glacialis Lynx (Baker) were abundant, especially on the hind feet of many hares collected in the fall and early winter of 1960.

Dodds and Mackiewicz (1961), in Newfoundland, reported parasites in hares. They did not find Dirofilaria or Protostrongylus, but did find liver flukes, Dicrocoelium denderiticum, larval tapeworms, Hydatigera taeniaformis and Multiceps sp., and the nematode, Trichostrongylus axei.

The rather high incidence of Protostrongylus in hares of the Ballaine study area may have important implications in population crashes. These nematodes may weaken hares and cause secondary infections. Helminen (1959) collected 433 Lepus timidus pellet samples in 1957, and 303 in 1958, from different areas in Finland. He found that the occurrence of lungworm larvae, Protostrongylus commulatus, was 78.3% in 1957 and 83.8% in 1958. He implied that this parasite was important in epizootics which have at least twice coincided with the decline of hare populations in Finland, during the 1930's and 1940's.

Philips (1939) found that hare ticks taken in the Fairbanks area in 1937, a year of high hare density, were harboring Bacterium tularense. Hopla (1960) reported that all of the B. tularense specimens he found in the Fairbanks area came from ticks, and that the Fairbanks area supports the largest populations of ticks in Alaska. He said that Alaskan tularemia is less virulent than is tularemia farther south. Snowshoe Hares in this area seem to be resistant to it. However, the Alaska Department of Public Health reported at least two cases of tularemia in humans who had handled hares near Fairbanks in the fall of 1961.

Other decimating factors.-- Other than occasional hares killed by dogs, 15 hares were found dead or in a weak condition in the live-traps of the study area. Hares taken from traps while in a weak condition usually died during or soon after the tagging procedure. "Shock-disease" may have caused this, and possibly was responsible for deaths of those hares found already dead in traps. Those which died while being handled showed typical shock symptoms. The head would be held stiffly back with chin high, and the body would stretch out in a rigid manner. Riger mortis would set in within one or two minutes after convulsions had ceased.

The Ballaine study area was posted with "no hunting" signs, so hunting as a decimating factor was probably negligible. The woods across Ballaine Road from the study area were hunted occasionally. In other parts of the Fairbanks vicinity, hunting and snaring of hares may be more important.

HOME RANGE AND MOVEMENTS

Home range data were obtained by trapping, tagging, and releasing hares on the 160-acre live-trap grid. For comparative purposes it was necessary to recalculate home ranges of the hares which O'Farrell caught in 1959 and 1960. Data were obtained on other hare movements while collecting hares for autopsy specimens, outside the study area.

Home Range

The home range of an animal is that area traversed by the individual in its normal activities of food gathering, mating, and caring for its young (Burt, 1943). Occasional trips outside this area are excluded from the definition, as such trips may be the result of disturbance, exploring, or visiting (Dice, 1952). The animal is "at home" in its home range. It knows the escape routes, the refuges, and where food and resting places may be found. In a strange area outside its home range, an animal is at a disadvantage until it can become acquainted with the features of the new area.

The use-patterns of a home range may change with conditions such as population density or availability of food. The boundaries may vary from time to time (Stickel, 1954). Logically, home range boundaries are considered diffuse. However, when calculating the area, arbitrary boundaries must be drawn. The chief method for determining home range area is by live-trapping, marking, and recapturing animals. Hayne (1949) defined trap-revealed home range as an area in which the animal enters traps with greater or less frequency, according to the location of the traps. The interference introduced by trapping adds to the difficulty of deciding on home range boundaries (Stickel, 1954). Hence, the trap-revealed home range may not entirely coincide with the true home range of an animal.

New methods for tracking animals are being developed, some of which may prove useful in determining home range size. One such method consists of tagging animals with radioactive isotopes (Griffin, 1952; and Kaye, 1961). Another involves attaching small radio transmitters to animals (Dr. Rexford D. Lord, Jr., viva voce).

To calculate home range size for Snowshoe Hares, I used the exclusive-boundary-strip method described by Stickel (1954). This method is derived from Blair's (1942) inclusive-boundary-strip method. The inclusive-boundary-strip method consists of constructing squares, whose sides are equal to the distance between two adjacent traps, around successful trap sites. The external points of these squares are connected so as to enclose the maximum possible area, regardless of what is thereby included (Fig. 5). This amounts to adding a boundary-strip around the connected points of capture equal to one-half the distance to the next trap beyond each peripheral capture site. A particular animal's home range obviously will not correspond exactly to this configuration.

The exclusive-boundary-strip method for calculating home range also involves constructing squares around capture sites, but in this case the squares are so connected as to enclose the least area (Fig. 5), and to exclude as far as possible traps where the animal was not caught. Stickel (1954) experimentally compared various methods of calculating home range size. She made circular and oval discs of clear plastic and tossed these known-area "home ranges" randomly upon a grid of "traps" on paper. She noted the traps included in the area covered by each disc, then calculated areas of the home ranges by different methods. She compared each of the calculated home range figures with the true home range size, i.e., the area of the disc used, and found that the exclusive-

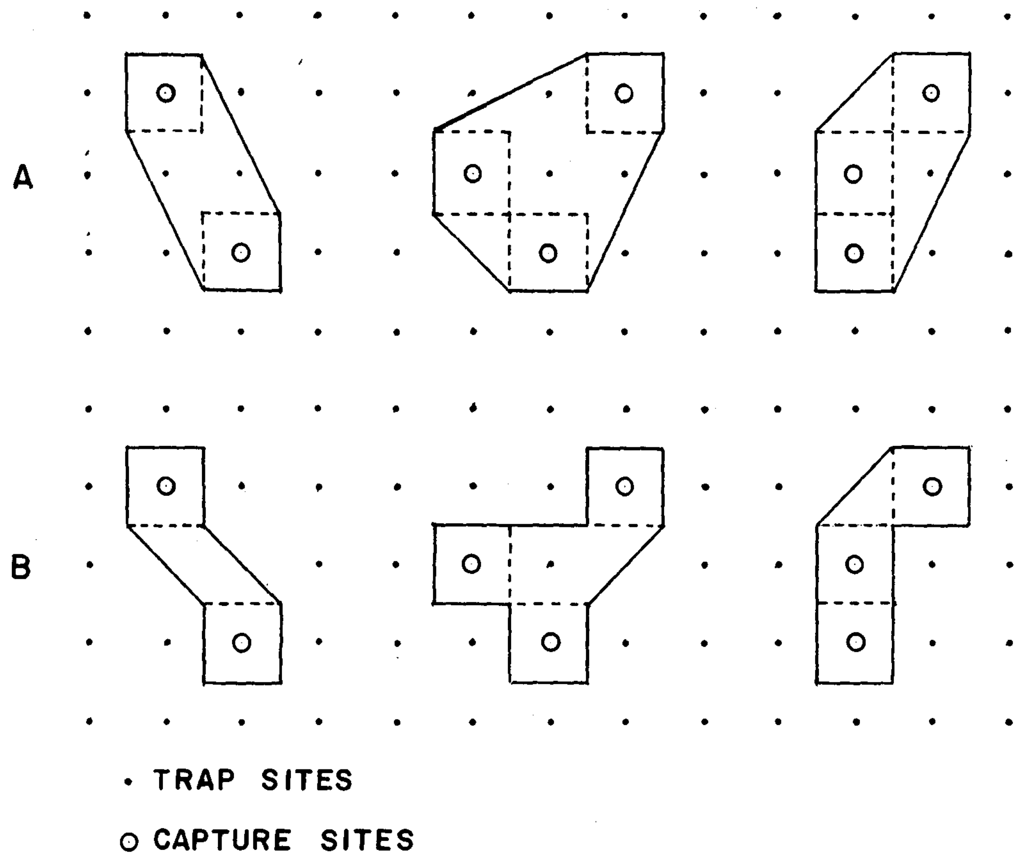


Fig. 5. Two methods of outlining home ranges for size measurement. (A) Inclusive-boundary-strip method. (B) Exclusive-boundary-strip method. From Stickel (1954), p. 3.

boundary-strip method was the most accurate. Range sizes by this method averaged 2% too large. Calculated ranges based on the inclusive-boundary-strip method averaged 17% too large. In this experiment, traps were close enough together so that at least two were located in each range.

I calculated home range size by the exclusive-boundary-strip method for my own data (Table 10) and for part of O'Farrell's (Table 11), the object being to compare size of home range at different population densities. I used hares caught four or more times. Since O'Farrell calculated home range size for hares by a different method and included hares caught less than four times, I could not directly compare his figures with mine.

The mean home range size for 26 hares caught by O'Farrell 144 times between June 1959 and April 1960, inclusive, was 14.5 acres. The means for males and females were not significantly different, being 14.5 and 14.4 acres, respectively. The mean home range size for 31 hares caught by me 1[illegible]3 times between May 1960 and November 1961, inclusive, was 13.1 acres. The mean for males was 12.1 acres, for females 14.1 acres. Applying a t-test, these last two figures are not significantly different at the .05 level. The mean home range sizes of O'Farrell's hares and mine differ significantly at the .01 level when subjected to a t-test.

Stickel (1960) showed that <u>Peromyscus</u> ranges decrease in size as the population increases. Snowshoe Hare density in the 1959-1960 study period was still comparatively low, and the mean home range size was 14.5 acres. The density of hares in the 1960-1961 period was higher (quantitative differences could not be determined accurately), and the mean home range size had decreased to 13.1 acres. The biological sig-

TABLE 10. RECAPTURE DATA COLLECTED FROM MAY 1960 TO NOVEMBER 1961 ON THE BALLAINE STUDY AREA, COLLEGE, ALASKA

Tag no.	Sex	Date of capture	Trap no.
1607	F	25-XII-1960	E3
		28-XII	E3
		12-V-1961	E3
		18-V	E3
1778	M	11-VIII-1961	D3
		26-X	E3
		27-X	E3
		31-X	E3
		2-XI	E3
1800	M	25-X-1961	C5
		2-XI	C5
		3-XI	C5
		4-XI	C5
2213	F	25-VI-1960	B2
		4-VIII	B2
		19-VIII	B2
		30-XII	B2
		29-I-1961	B2
		20-X	B2
2227	M	8-VIII-1960	C3
		20-VII	C4
		11-V-1961	B3
		8-XI	C5
2241	M	13-VIII-1960	C3
		13-IX	C3
		13-V-1961	C3
		24-V	C4
2247	F	15-VII-1960	A3
		6-IX	A3
		27-XII	A2
		5-I-1961	A2
		22-VII	A2
		30-VIII	A3
2276	F	3-VIII-1960	A1
		8-VIII	C5
		15-IX	A3
		19-II-1961	A1
2294	M	20-VII-1960	D2
		8-IX	D2
		22-XI	D2
		11-XII	D2
		3-XI-1961	D2
2557*	F	7-V-1960	D3
		10-V	E5
		11-XII	D3
		24-XII	D3
		28-XII	C2
		18-V-1961	D3
		26-X	D4
		27-X	D3
2611*	M	10-V-1960	B4
		16-V	C4
		19-II-1961	B4
		2-XI	C4
2677	M	21-IV-1960	E1
		2-V	D2
		6-VI	E2
		9-VI	D1
2709	M	21-V-1960	B4
		29-X	B4
		25-XII	B4
		20-X-1961	B4
2724	F	1-VII-1960	C3
		24-XII	D4
		27-XII	D4
		30-XII	D4
		22-VII-1961	D4
2780	M	11-VI-1960	B4
		7-VII	B4
		4-VIII	B3
		24-XII	C5
		26-XII	B3
		19-II-1961	B3
3495	F	3-VIII-1960	B3
		10-VIII	C4
		18-VIII	E4
		13-IX	C4
		29-X	C4
		22-XI	C4
		26-XII	C4

TABLE 10. (continued)

Tag no.	Sex	Date of capture	Trap no.
3497	F	28-VII-1960	D1
		1-VIII	D1
		9-VIII	E2
		15-IX	D1
		26-XII	D1
		12-V-1961	D1
3711	F	27-VII-1960	A4
		8-IX	B4
		27-XII	B4
		23-IV-1961	B4
		13-V	
3723	F	28-VII-1960	A5
		4-VIII	B4
		23-VIII	A5
		6-IX	A5
3769	M	9-X-1960	D5
		22-XI	D5
		11-XII	D5
		24-XII	D5
		26-XII	D5
		27-XII	D5
		28-XII	D4
		26-II-1961	D5
3803	F	9-VIII-1960	E4
		11-VIII	E4
		29-X	E4
		24-XII	E4
		28-XII	E4
		29-XII	E4
		30-XII	E4
3821	M	17-VIII-1960	B1
		25-VIII	B1
		18-X	B1
		25-XII	B1
3852	M	23-VIII-1960	A1
		9-X	A1
		18-X	A1
		29-X	A1
		25-XII	A1
		23-IV-1961	A2
		20-X	A1

Tag no.	Sex	Date of capture	Trap no.
3873	F	25-VIII-1960	E3
		13-IX	E3
		11-XII	E4
		11-V-1961	E3
		16-V	E3
		11-VIII	E3
3883	M	7-IX-1960	A4
		25-XII	A4
		11-V-1961	A4
		25-X	A3
		30-X	A3
3899	F	10-IX-1960	A4
		18-X	A4
		29-X	A4
		24-XII	A3
		26-XII	A4
		27-XII	A4
		28-XII	A4
		2-I-1961	A4
3915	F	15-IX-1960	C3
		16-IX	C3
		14-V-1961	C2
		15-V	C2
		20-V	C3
		5-VIII	C3
3923	M	13-V-1961	B2
		16-V	B2
		19-V	B2
		20-V	B2
		8-VI	A1
		30-VI	A1
		22-X	B2
3951	M	29-X-1960	B3
		17-V-1961	B3
		8-VI	B'
		9-VI	B1
3965	F	29-X-1960	D2
		25-XI	C2
		26-II-1961	D2
		12-III	D1
		11-V	C2
		1-XI	D2
		12-XI	D2

TABLE 10. (continued)

Tag no.	Sex	Date of capture	Trap no.
3975	M	22-XI-1960	D3
		25-XII	D3
		27-XII	D3
		29-XII	D3

* See Table 11.

TABLE 11. RECAPTURE DATA COLLECTED FROM APRIL 1959 TO APRIL 1960 ON THE BALLAINE STUDY AREA, COLLEGE, ALASKA

Tag no.	Sex	Date of capture	Trap no.
2157	M	20-VI-1959	C2
		10-IV-1960	D2
		12-IV	C2
		15-IV	C3
2159	M	20-VI-1959	C5
		9-XI	C5
		10-IV-1960	D5
		15-IV	C4
		20-IV	D5
		21-IV	C4
		25-IV	C4
		28-IV	C4
2189	F	29-VI-1959	D4
		7-VII	A1
		16-VII	B2
		19-VII	B2
		22-VII	B2
		31-VII	A1
		21-X	A1
		30-X	A1
2507	M	17-VII-1959	B3
		1-VIII	B3
		13-IV-1960	B2
		17-IV	C2
		21-IV	B2
		26-IV	B2
2519	F	19-VII-1959	E1
		30-X	E2
		6-XI	E1
		12-XI	E2
2525	F	25-VII-1959	D4
		30-VII	D4
		23-IX	D4
		30-IX	D4
		19-IV-1960	D4
		1-V	D5
2533	M	31-VII-1959	D4
		3-XI	D4
		10-XI	D4
		26-XI	D4
		27-XI	
2545	M	7-VIII-1959	B2
		16-XII	A1
		16-IV-1960	A2
		19-IV	A2
		22-IV	B2
2557*	F	9-VIII-1959	D4
		22-X	D3
		16-IV-1960	D3
		19-IV	D3
		23-IV	E5
2587	M	17-VIII-1959	D1
		12-IV-1960	D2
		16-IV	E3
		23-IV	E4
2607	F	23-IX-1959	B4
		30-XII	A1
		3-I-1960	B4
		6-I	A4
2611*	M	30-IX-1959	C4
		14-IV-1960	B4
		20-IV	C5
		22-IV	C5
		23-IV	B4
2613	F	30-IX-1959	E3
		24-XII	E3
		29-XII	E3
		1-I-1960	E3
		4-I	E3
		7-I	E3
2645	M	27-X-1959	B3
		10-XII	B3
		14-XII	B3
		9-IV-1960	C3
		12-IV	B3
		13-IV	C3
		19-IV	B3
		20-IV	C2
		23-IV	C3
		26-IV	B3

TABLE 11. (continued).

Tag no.	Sex	Date of capture	Trap no.
2655	M	30-X-1959	A4
		3-XI	A4
		23-XI	A4
		27-XI	A4
		9-IV-1960	A4
		14-IV	A4
		15-IV	A2
		16-IV	A4
		19-IV	A4
2663	M	4-XI-1959	B3
		9-XI	C3
		13-XII	C2
		26-XII	C2
		30-XII	C2
		31-XII	C3
2669	M	5-XI-1959	D1
		13-IV-1960	D1
		15-IV	D2
		25-IV	D2
2671	M	6-XI-1959	B5
		13-IV-1960	A5
		17-IV	B4
		21-IV	A5
2693	M	16-XII-1959	A4
		28-XII	A2
		30-XII	A4
		12-IV-1960	A4
		13-IV	A2
		18-IV	A3
		22-IV	A3
2695	F	24-XII-1959	A2
		31-XII	A1
		2-I-1960	A1
		18-IV	A2
2697	M	24-XII-1959	A5
		27-XII	A5
		31-XII	A5
		9-IV-1960	A5
2699	M	25-XII-1959	A3
		29-XII	A3
		11-IV-1960	A3
		21-IV	A2
		23-IV	A2
2711	F	18-IV-1960	C3
		19-IV	C2
		20-IV	C3
		22-IV	C3
		24-IV	C3
		29-IV	C3
2718	M	13-IV-1960	E3
		14-IV	D3
		17-IV	E3
		18-IV	D3
		20-IV	E3
		23-IV	E3
2720	M	13-IV-1960	C5
		18-IV	C5
		24-IV	C5
		25-IV	C5
2722	M	13-IV-1960	C4
		17-IV	C3
		18-IV	C4
		21-IV	C3
		24-IV	C4

* See Table 10.

nificance of the ± 10% decrease in range size with increase in population density is probably slight. Continued study of the same population may reveal the trend more clearly.

Range Length

Range length is a linear expression often used by biologists. It can be described in two ways: the observed range length and the adjusted range length. The observed range length is the distance between the most widely separated capture sites. The adjusted range length is similar, with the addition of a distance equaling one-half the distance to the next trap beyond each of the two capture sites. In Stickel's (1954) experiment described above, observed range lengths averaged 25% smaller than the true range length, and adjusted range lengths averaged 3% larger.

Ranges used for determining home range size were also used for calculating adjusted range length. The mean adjusted range length for 26 hares caught by O'Farrell in 1959 and 1960 was 1,150 ft. The mean adjusted range length for 31 hares caught by me in 1960 and 1961 was 1,073 ft. Applying a t-test, these means do not differ significantly at the .05 level. I believe that in determining the adjusted range length of O'Farrell's hares and that of mine can be attributed to this method's minimizing effect on differences in range size.

Movements

Aldous (1937) believed one-eighth mile to be the usual distance traveled by hares, but 18 hares returned to their home ranges after he had moved them one mile or more away. Green and Evans (1940a) also believed that Snowshoe Hares seldom travel more than one-eighth mile from the point of first capture. MacLulich (1937) stated that the greatest distance traveled by the hares with which he worked was 250 yards (750 ft.), which is well within the mean adjusted range length of the Ballaine study area hares.

Movements greater than one-eighth mile are probably common among dispersing juvenile hares. At times during this study, hares were collected by snaring beyond the boundary of the study area. Three tagged juvenile hares were snared which probably had dispersed or were in the act of dispersing. These hares are as follows: (i) a juvenile male was tagged on 30 June 1959 at trap B-3 and was snared approximately 2,000 ft. south on 4 July 1960; (ii) a juvenile female was tagged on 14 July 1960 at trap A-1 and was snared approximately 2,500 ft. south on 14 January 1961; and (iii) a juvenile male was tagged on 24 August 1960 at trap B-3 and was snared approximately 2,500 ft. south on 14 December 1960. Another juvenile female moved a greater distance; she was captured and tagged on 26 August 1960 one-half mile north of the University and was recaptured on 9 September 1960 in the Ballaine study area at trap B-1. She had moved approximately 8,500 ft., or 1.6 miles, in 14 days. This distance and rate of travel seems unusual, but probably is not difficult for a hare. Keith and Waring (1956), who studied orientation and homing of Snowshoe Hares in Alberts, recorded the homing movement of a hare which traveled three miles in three days. O'Farrell (1960) recorded a surprisingly long hare movement. He tagged a juvenile female on 24 August 1958 on the Ballaine study area and recaptured it once that year in the same area. A local sportsman shot it on 27 September 1959 at Mile 6 on the Elliot Highway, 12.5 miles north of the study area.

BEHAVIOR

Opportunities were found for observing hare behavior chiefly in the following situations: on the live-trap grid while tagging and releasing hares; while collecting; while on road surveys; and while watching hares in an enclosure.

Two adjacent 40 x 40 ft. pens were constructed about one-half mile north of College, in an upland situation. On 30 June 1961 a pregnant hare was placed in each enclosure. Each female gave birth to six young. One or two leverets were collected at regular intervals for lenses. An animal, probably a dog, broke into the pens during the night of 18-19 July. The following day I found the two adult hares and one remaining leveret dead.

Use of Forms and Burrows

A form usually consists of a simple, slightly oval depression in the grond litter, under good cover. Forms are used the year around. Many notes on the use of forms by hares can be found in the literature. Seton (1909) mentioned that a hare may have more than one of these resting places. Grange (1932a) said that hares remain in their forms during inclement weather. He noted that winter forms are often found with hairs frozen to them. As a result, when the form thaws it appears that hair was used to make this "nest". Adams (1959) noted that a hare may use a form once, or repeatedly, and that two or more hares may use the same form, but never at the same time. Gould (1938) noted that hares do not use the same form day after day, but seem to have several located about their ranges. Severaid (1942) said that forms are found in places where hares can derive protection from predators and from the elements, i.e., under bushes, among clumps of small trees, under logs or fallen trees, or under trees bent over by snow. O'Farrell (1960) mentioned hares utilizing the protection of vegetation bent over by the snow that collects on it (qali).

The bending over of vegetation in this area by qali provides in winter many more places suitable for forms than would otherwise be available (Fig. 6 and 7). Qali becomes so deep at times that a bent-over shrub or tree top may provide excellent protection from all sides, functioning slmost as a small cave or burrow. The hare's heat loss by radiation when sitting in such a place would probably be considerably retarded. Irving, et al. (1957) found that hares conserve heat during cold periods in winter by obtaining shelter in thick cover, which acts to supplement the insulation of their thick fur.

Another snow feature used by hares is the bowl-shaped depression about the base of a spruce tree. Pruitt (1957) used the Kobuk Valley Eskimo term "qamaniq" to describe this snow feature. The snow depth at the base of a spruce tree is usually slight, increasing outward beyond the tree's "snow shadow" to the depth found on the less protected forest floor (Fig. 8). The temperature in a qamaniq is probably several degrees higher than the air temperature over the snow beyond it because the branches retard radiation. This makes the qamaniq a good resting place for hares, and forms are found here occasionally. Hare sign is not found here as often as under bent-over shrubs, etc., which are covered more completely by qali.

In the southern part of the study area there were three empty five-gallon gasoline cans (without tops) lying on their sides, which were used as "forms" by hares.

Fig. 6. Many willows and small spruces are bent to the ground by qali, providing covered forms for hares.

Fig. 7. A bent-over alder completely covered by qali. Hare sign was found in the large space underneath.

Fig. 8. A qamaniq under a black spruce. Hares occasionally use such depressions in the snow as forms.

It is generally believed that Snowshoe Hares are not ordinarily burrow-inhabiting animals like <u>Sylvilagus</u> or <u>Oryctolagus</u>. However, evidence seems to indicate that if unused burrows of foxes, Woodchucks, etc., are available, hares may use them. Although Richardson in 1829 (<u>fide</u> MacLulich, 1937) and Audubon and Bachman in 1[illegible]4 (<u>fide</u> Grange, 1932a) did not believe that Snowshoe Hares use burrows, MacLulich (1937), Grange (1932a), and Adams (1959) presented evidence that they do so on occasion. O'Farrell (1960) reported a rather large snow burrow used by a hare or hares. Dr. Brina Kessel and Dr. Frederick C. Dean have reported one and two burrows, respectively, used by hares. I have seen two old Red Fox or Porcupine burrows in the Ballaine study area, on a small knoll north of the E-line, which had definitely been used by hares. A third burrow near these two was probably used also, but since its entrance was protected from above by an overhanging bank, no snow fell immediately in front of it, and no tracks could be seen definitely entering it. As previously mentioned, some vegetation becomes bent over by the weight of snow and is so completely covered that the open space underneath could in many cases be regarded as a temporary burrow.

<u>Voice and Thumping</u>

I have heard hares omit three types of vocal sounds. Adults or young utter a sort of grunt or growl indicating anger or fear. Young hares often uttered this sound when picked up or when attempting to fend off my hand with a quick, charging bluff. Adults often "grunted" when behaving defensively in live-traps. This sound became much like a low growl when they bit and scratched the burlap sack in which they were placed.

Hares scream in a piercing manner when taken from a live-trap.

This scream may attract predators or other hares. On 8 September 1960 a large, immature Goshawk (Accipiter gentilis) landed on a white spruce near which I was tagging a hare. It was probably attracted by the screaming. Once on the Ballaine study area, in the summer of 1960, a large dog was attracted to the screaming of a hare during a tagging operation. When screaming young hares were being handled, adults would come bounding up close, often thumping loudly with their hind feet. When one of the two-day-old leverets in a 40 x 40 ft. pen was picked up it squealed, and the others in the nest immediately scattered in all directions. On 5 September 1961 I was collecting in the vicinity of Central, Alaska, and shot a hare which screamed, attracting another hare to within a few yards of the scene. In the study area on 7 September 1961 I tried to imitate a hare scream by producing a squealing sound with pursed lips. One hare appeared and sat watching me several yards away. A second dashed to within ten feet of me, looking around and turning its ears this way and that in an alert manner. A third dashed through the trees nearby. Often when I made such a noise on seeing a hare or releasing one, the sound would send it away faster.

These sounds, grunting (or growling) and screaming, have been reported in the literature, e.g., Severaid (1942). A third sound, a click resembling the sound commonly written "tch", is uttered by hares and has not to my knowledge been described in the literature. I was not able to determine the significance of the sound, although I have heard it several times. On three occasions, 8 July, 30 July, and 11 August 1960, hares made these low clicking shounds before being removed from traps. They appeared nervous. On 20 July two hares were released at different trap sites, and each made the sound. One nibbled some Vaccinium a few feet from me, uttering a click every few seconds. After a minute or so it hopped away. In each of these cases I released the hare gently and then remained very still. A similar case took place on 11 September 1960. I released a hare, it ran about three yards, uttered two clicks, and hopped away. In all three of these cases the hares seemed to be nervous, probably as a result of the tagging operation. I have heard this sound on two other occasions. On 4 July 1961 my wife and I were sitting on an eight-foot-high observation platform, watching the behavior of two female hares in two enclosures below us. One female hopped nervously back and forth near the far side of her enclosure. The other hare hopped about her enclosure, occasionally coming directly beneath our platform. We could hear her uttering c licks at various locations in the enclosure. On 14 July 1961 I placed an adult male hare in the enclosure with the latter female. For almost 20 minutes the two hares remained at opposite sides of the enclosure. Then they approached to within two feet of each other, both alert and looking in all directions. The female, who had been uttering clicks while watching the male, chased him three or four times. I could not see that the male reacted to the clicking sounds at any time during this observation. The female behaved nervously the entire time.

The hare's habit of "thumping" consists of hitting the ground forcefully with the hind feet while hopping. This behavior seems to alert other hares in the vicinity. I often heard other hares thumping when one I was handling screamed. Hares occasionally thumped when frightened or flushed from a form. Once I observed a Red-tailed Hawk, <u>Buteo jamaicensis</u>, in a small clearing in the woods and heard a hare thumping nearby. I do not know whether the hare was frightened by the hawk or me. Occasionally after being released, a hare would thump a few times as it hurried away.

<u>Agonistic and Investigative Behavior</u>

Scott's (1958) definition of agonistic behavior includes escape behavior as well as fighting and hostile behavior. Agonistic behavior was observed closely in two types of situations: on removing a hare from a trap and releasing it, and on placing an adult male hare in an enclosure with an adult female.

Adults seemed to be more aggressive than younger hares. When I approached a live-trap which held a hare, the hare often crouched low with ears back, apparently trying to hide. When I opened the trap, I reached in and grasped the hare by its hind legs to avoid being scratched or bitten. Occasionally when I reached into a trap containing an adult, the hare would utter a sort of grunt or growl, scratching with its front feet, biting, or both. When placed in a burlap sack for weighing, such an angry adult usually seized a piece of burlap in its mouth and proceeded to pull, raking the burlap with both front and hind claws. Hares attacking the sack in this manner usually did so with ears laid back and eyes closed, and often grunting or growling. One hare when the sack was turned inside out lay on the ground kicking and biting the sack with its eyes closed, not realizing it was free to escape.

An adult male hare was placed in a 40 x 40 ft. enclosure containing an adult female, in hopes that coition would occur. The female avoided the strange male at first. She frequently uttered clicking sounds. After watching him intently for about 20 minutes, she approached him, then chased him three or four times. In each chase the female, with ears laid back, dashed after the male four or five feet. The male always ran away, seeming to fear the female. One such encounter occurred when the male was in a corner of the enclosure. He jumped into the air and over the female to escape her. The male was left in the enclosure overnight and was found dead the next day with superficial scratches on his body, probably inflicted by the female. Dr. William O. Pruitt, Jr., had described to me several similar encounters of hares at his home two miles west of the University, where he had placed out feed to attract wild animals. The hares' aggressiveness was probably due in these instances to competition for the food, and since the hares were free-living probably no deaths resulted.

O'Farrell (1960) adequately discussed escape behavior in the hares of the study area. I have a few notes to add. When I remained still after releasing a hare, the hare often remained within a few yards, perhaps nibbling vegetation. In most cases when I dropped the hare to the ground, it dashed two or three yards away (sometimes only two or three feet) and immediately began to eat some leaves or grass. This may have been due either to a voracious appetite or to displacement behavior. Many hares probably had remained in the traps 12 hours or more, and no doubt were very hungry after consuming the hay bait. Still, I do not think their hunger was so strong that it would have dominated the impulse to escape. Certainly the hares were in a dangerous situation, since a predator had just released them. To run only a few feet away and begin eating seems odd in such a situation. There may have been a conflict between two motivations: curiosity, and the drive to escape. A hare, on being dropped from a dark burlap sack and seeing no movement around it, could have been bewildered as to the source of its discomfort. The conflict between escape and curiosity drives may have resulted in displacement activity. Displacement activity occurs when two incompatible drives conflict, and a third unrelated drive is expressed instead. Tinbergen (1952) said displacement activity is "...an activity belonging to the executive motor pattern of an instinct other than the instinct(s) activated." He also said that there must be a surplus of drive. A hare which has just been tagged may be excited enough to have such a surplus. Tinbergen said that displacement activities are common in hostile situations, and that foraging is a common form of displacement activity; it is an outlet through which the thwarted or conflicting drives may find expression.

Hares exhibit investigative behavior (Scott, 1958) when examining new territory or looking for the source of a noise. Occasionally I have seen hares sit up on their haunches to look at something, with torso straight and forelegs held up in front. A female in an enclosure did this in order to look over the low vegetation at a male I had place in the enclosure. In many instances I have seen hares sit up this way when surprised.

When examining objects, a hare often bobs its head up and down. When I looked into a trap that contained a hare, and then remained still, the hare usually approached my end of the trap, bobbing its head and apparently sniffing the air. Some captive leverets cautiously investigated their surroundings in this manner.

Use of Runways

Hare runways in the winter have some characteristics worth noting. O'Farrell (1960) suggested that runways are rarely so deep that a hare cannot see the surrounding snow surface. This may be important in preventing surprise attacks by predators. I have noted that a hare runway does not always consist of a continuous path, but sometimes is a series of "landing spots," with short patches of untrodden but somewhat leveled-off snow in between. Runways often become very hard under certain cold weather conditions, and easily support the weight of a man. On 29 January 1961 I measured the hardness of 17 runways on the study area. These measurements were taken with a pressure gauge which was pushed against the snow surface. I recorded the pressure at which the snow surface collapsed. The mean hardness was 717 g/cm^2, or about 10.6 lb/in.^{2}. With all four feet resting on the snow surface, a hare exerts a pressure of about 9 g/cm^2. I obtained this figure by determining the area of a hare's footprints in the thawing snow of April 1962. The four footprints covered a total of 168 cm^2. The mean weight of 31 young-of-the-year hares weighed in the winter of 1960-61 was 1,489 g. Dividing 1,489 g. by 168 cm^2 yields 9 g/cm^2. This figure is a slight underestimate of the pressure applied to the snow surface. The area of a hare's track in the snow is a little larger than the actual area of the foot, due to snow caving in on the edges of the track.

Hare "Nests" and Behavior of Young

On 30 May 1961 Dr. William O. Pruitt, Jr., reported finding a hare form at 2030 hours containing five recently born leverets. The form was located near his home, in a white spruce stand with an alder and willow understory. It was situated partly within a small brush pile under a leaning willow (Fig. 9). The form was oblong, 28 cm long and 18 cm wide. At one end was an entrance. The other end was partly beneath the brush pile, which was about 16 cm high. The sides of the form were 10 to 11 cm high and consisted of dead twigs and grass (Fig. 10). This particular form could just as well have been called a nest. However, there were no hairs lining it, and my observations lead me to believe that its

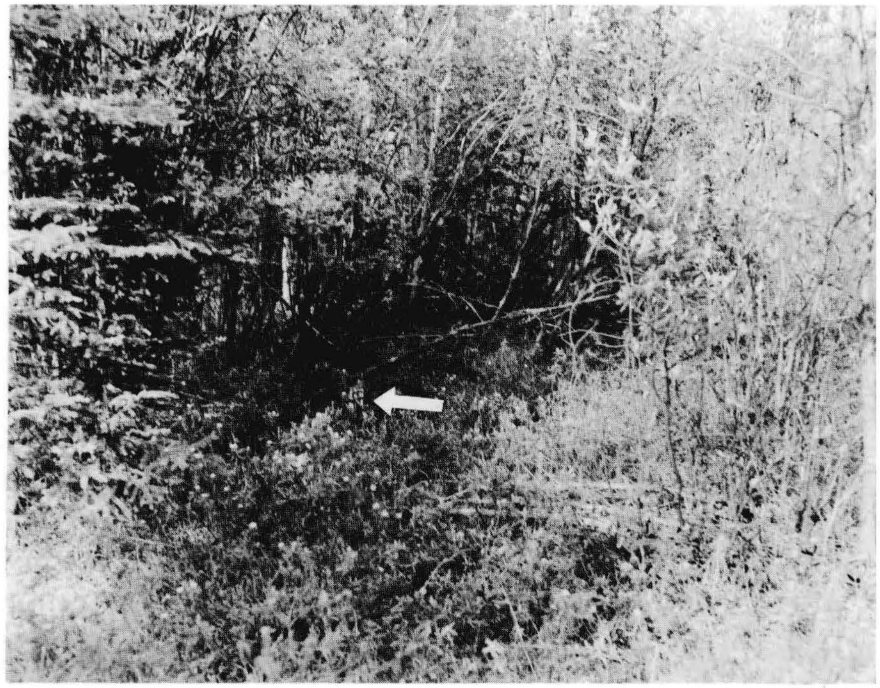


Fig. 9. White spruce-willow-alder stand where a hare "nest" with young was found in June 1961. Arrow indicates location of form.

Fig. 10. Knife placed in the form (Fig. 9), blade pointing to the hollow under a brush pile where leverets were found.

nest-like appearance was an exception to the usual appearance (a simple depression in leaves) of forms where litters are born. When I investigated the form at 2330 hours on 30 May 1961, only one leveret remained, hiding under the brush pile. The others may have moved off by themselves, may have been carried away by the mother or may have remained well hidden nearby. Dr. Pruitt noted that when he made a sharp noise by breaking a stick, one leveret in the above nest awkwardly moved 15 to 20 ft. away. He replaced it in the form. The measurements of the remaining leveret were as follows: body length 155 mm, tail 8 mm, hind foot 40 mm, ear from notch 26 mm, ear from base 30 mm, sex undetermined, age about three or four days. The leveret remained still while I watched it except once when it came slowly toward me for about a foot.

On 30 June 1961 two pregnant hares were placed in two 40 x 40 ft. outdoor enclosures located in an upland situation one-half mile north of College. One female gave birth to six young on 3 July. She was discovered crouching over them in a circular depression in the leaves about 24 cm in diameter. The form was partly protected from above by a balsam poplar and a Shepherdia shrub (Fig. 11). The mother hopped back and forth nervously on the far side of the enclosure while her young were examined. The leverets, which were probably not more than 24 hours old, did not "freeze" at my approach, nor did they make any sign of noticing me. Each leveret was tagged. On 4 July one leveret was dead. This one had seemed weak during the tagging operation the previous day. Recent droppings indicated that the mother had visited the form during the night, which had been cold and rainy. On 5 July the young had moved out of the form and were huddled at the base of a Shepherdia bush nearby. It had been raining a short time previously and the leverets were slightly

Fig. 11. Form under a Shepherdia shrub, where six young were born on 3 July 1961. Steel rule marks diameter of the form.

Fig. 12. Form under a small white spruce, where six young were born on 5 July 1961. Steel rule marks diameter of the form.

wet on their backs. After being weighed, one of the two-day-old leverets walked away, using its hind feet alternately. It was replaced with the others and immediately escaped in another direction. When replaced again it squealed, whereupon the other four leverets scattered.

During the night of 4-5 July the other adult female gave birth to at least six young. In the afternoon of 5 July three of the leverets were found in a leafy depression 29 cm in diameter. The form was under the branches of a small white spruce and was surrounded by dead willow twigs (Fig. 12). The leverets were weighed and tagged. Three more were found in the next few days, in different parts of the enclosure. Apparently they had moved from the nest when less than a day old, or were moved elsewhere by the mother. When the first three were tagged one squealed, and the other two scattered at once. Natural camouflage made the leverets difficult to see on the littered ground (Fig. 13 and 14). The mother showed concern when I handled her young, but she would not come within 20 ft. of me. All the penned hares were annoyed by mosquitoes, which were abundant. The adults were constantly flicking their ears, and mosquitoes were seen biting the young around their eyes.

It seems that leverets less than a day old can move away from the form in which they were born. Severaid (1942) observed that "Leverets are fully precocial and, if disturbed, will walk by the time their hair dries." He went on to say, "Even when undisturbed they leave the form in a week or less, and in captivity can generally be found scattered about the pen after the third or fourth day."

One two-day-old leveret had green stains on its front feet. It may have been eating plant material already. A six-day-old leveret which was collected had green material in its stomach, along with some white

Fig. 13. Leverets less than 24 hr old, in the form where they were born.

Fig. 14. A leveret's small size and protective coloration make it difficult to see among the leaves.

material which was probably partly digested milk. Nice et al. (1956) observed a three-day-old leveret chewing and swallowing grass. Severaid (1942) said that leverets are normally weaned between the fourth and fifth weeks.

Food Habits

In summer, hares seem to feed on any green plant food available. Hares rapidly ate all the *Equisetum arvense* from two outdoor enclosures (Fig. 15). The winter diet consists mainly of small twigs and tips of *Vaccinium uliginosum*, *Ledum groenlandicum*, *Rosa acicularis*, and *Salix*, spp. *Betula papyrifera* bark and twigs also seem to be an important winter food of hares in Alaska. Bark of *Salix* spp., *Alnus fruticosa*, *Populus tremuloides*, *P. balsamifera*, *Picea mariana*, and *P. glauca* is resorted to mainly in the latter part of the winter when other food has become scarce. Barked trees were most frequently observed in early spring. Many stands of small birch and poplars were conspicuously barked and girdled at this time. No doubt many of the damaged trees died. Hares may be an important factor in forest succession, due to the extensive damage they do by barking and girdling trees when populations are high.

Seiskari (1954) noted that the five most-preferred winter foods of *Lepus timidus* are, in order of decreasing usage: *Vaccinium myrtillus*, *Populus tremula*, *Salix* sp., *Betula* sp., and *Vaccinium vitis-idaea*. Dodds (1960b) stated that birch is the most important hardwood food source for Moose, *Alces americana*, and the most important of all tree species for hares, in Newfoundland. He said that both hares and Moose browse plants less than 6 ft. high very heavily.

Seiskari (1956) stated that Finnish Moose, Snow Hares and Willow

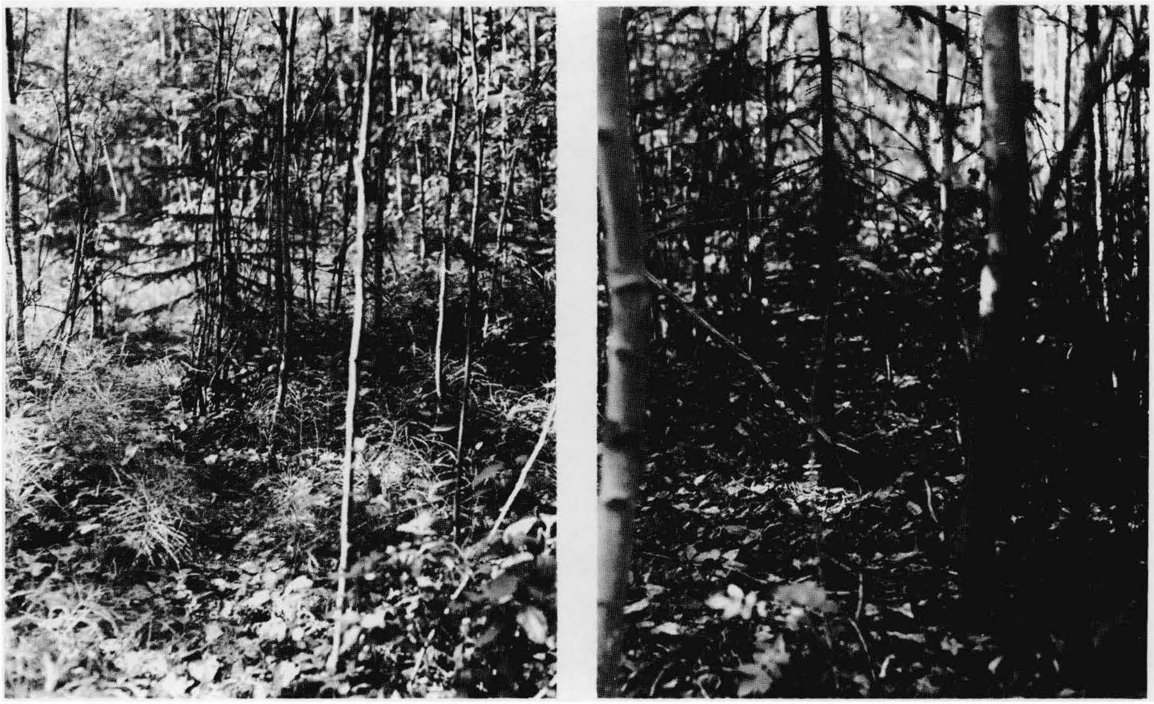


Fig. 15. Comparison of vegetation inside and outside hare pen. Left, outside. Note the abundant Equisetum. Right, inside. Hares have consumed all Equisetum.

Fig. 16. Brush pile, mostly willows, debarked by hares.

Ptarmigan each favor certain species of willow, and therefore do not compete with each other for this food. He said that Moose are less selective than the other two. They eat equal quantities of Salix aurita, S. caprea, and S. cinerea. Hares favor S. cinerea and S. caprea, and the Willow Ptarmigan prefers S. phylicifolia. Feeding height is similar for all three animals. The genus Salix is ubiquitous in Alaska and is represented by many species. Research on the species used by hares and other animals might yield similar findings.

Windfalls, brush piles, and fresh spruce, poplar, birch, and willow branches on the ground seem to receive attention from hares at any time during the winter. Often I left a fresh branch of Picea glauca or Populus tremuloides on a trail in the study area. In a few days all bark and part of the outer wood were usually gone. Dr. Brina Kessel reported that hares had been feeding on several freshly cut slash piles near her home north of the study area in February 1961. Some of the willow piles were almost completely debarked, including the small top branches, some of which were at least three feet above the snow surface. The photograph (Fig. 16) was taken in May after the snow was gone. How a hare could have climbed on top of the brush pile and reached the uppermost branches is an interesting question. Perhaps hares have unsuspected climbing abilities.

While on road surveys, on several occasions I noticed hares which appeared to be eating gravel from the road. I was not able to obtain concrete evidence of this. It has been observed that many animals crave certain minerals, and will eat soil to obtain them. I noticed a hole about 10 cm in diameter and 10 cm deep in the ground of a black spruce muskeg stand on the study area. Hares kept the hole open and free from snow throughout the winter of 1960-61. Apparently it contained a mineral or salt which attracted the hares. MacLulich (1937) said that hares eat sand. Adams (1959) reported finding sand in the fecal pellets of hares in Montana.

Hares will be carnivorous, as will many rodents, when given the opportunity. Seton (1928) mentioned a report about hares feeding on frozen, skinned carcasses of other Snowshoe Hares, foxes and weasels. Hares seem to prefer their meat frozen, but will not feed on the carcass of a clean unskinned animal (Soper, 1921). Soper said that only when a wound is present to provide a starting point will hares eat a frozen carcass. In November 1961 six frozen hares which had died in live-traps were left in the study area. Four of these remained untouched. The other two, which were somewhat blood-spattered and from which patches of hair had been removed, were eaten. Eventually they were reduced to scattered bits of bone and fur by other hares, Gray Jays (*Perisoreus canadensis*), and perhaps other animals.

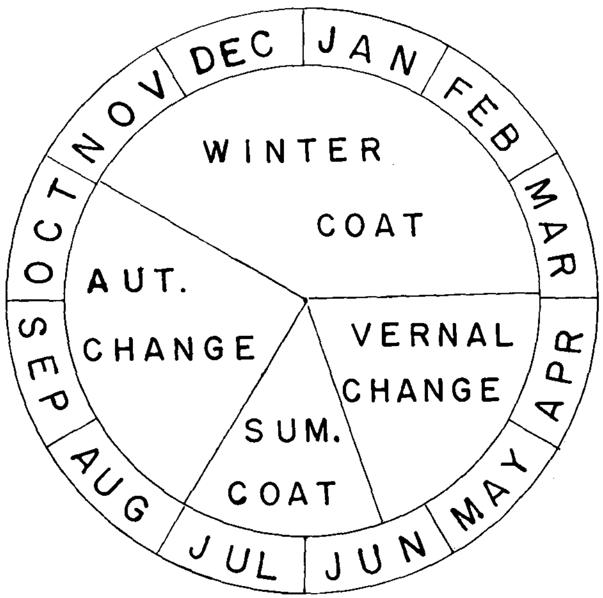
PELAGE CHANGE

I obtained data on pelage change by observation of hares which were live-trapped, collected, or observed in the woods.

Snowshoe Hare pelage and pelage change have been described thoroughly by Grange (1932b) in Wisconsin and Severaid (1942, 1945) in Maine. My observations on pelage change in the hares of the Fairbanks area substantiate O'Farrell's (1960) findings. During the first week in August hares begin to change from their short, grayish-brown summer pelage to the longer white winter coat. The change is completed by the first of November. Vernal molt begins in late March, and the hares have obtained their dark summer coat by mid-June (Fig. 17). According to Grange (1932b) and Severaid (1942) Snowshoe Hares in Wisconsin and Maine begin their autumn pelage change in late September and finish in December (Fig. 17). In the spring, in Wisconsin and Maine, the change begins in early March and is completed by early June. While the Alaskan hare retains its winter coat for nearly five months, the hares of Maine and Wisconsin keep theirs for less than three months. The long Alaskan winter is reflected in the thickness and duration of the white coat. Northern hares have richer and fuller winter coats than do hares in more southerly latitudes. In Wisconsin and Maine, Snowshoe Hares are in summer pelage for nearly four months, whereas in Alaska hares keep their summer coats for less than two months.

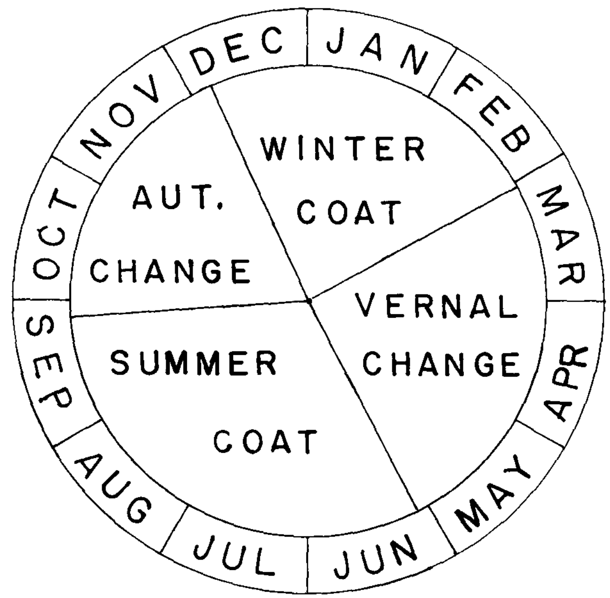
The periods of molt occupy a large part of the year. Severaid (1942) described seven arbitrary stages in Vernal and Autumnal pelage change. He designated the vernal stages V-1 through V-7, and the autumnal changes A-1 through A-7.

It is well known that pelage characteristics in hares vary from one



A. PELAGE CHANGE IN ALASKA

65° N. LAT.



B. PELAGE CHANGE IN MAINE AND WISCONSIN

CA. 45° N, LAT.

Fig. 17. Pelage phenology of hares in (A) Interior Alaska, and (B) Wisconsin and Maine.

region to another. Hares in the State of Washington (*Lepus americanus washingtoni*) never turn white in winter, but remain in brown pelage the year around. Adams (1959), in Montana, was able to distinguish adults, which had white feet, from immature hares, which had brown feet. This criterion does not hold for hares in Alaska. All the adult hares O'Farrell (1960) captured in this area during July 1959 had brown feet, which seems to negate Nelson's (1909) statement that in summer Interior Alaska hares have white hind feet. I collected six adults in the summer of 1960 which had completely brown feet. Nelson was not entirely wrong, since some adult hares do retain white hind feet in summer. On 4 July 1960 I captured an adult hare, age 1 year 1.5 months, which had completely white feet. Some adult hares have hind feet which are mottled brown and white.

AGE DETERMINATION

Several age-determination criteria were tested: hind-foot color, epiphyseal groove closure, genital morphology, hind-foot length, body weight, and lens weight. Collected hares provided most of the data, since dissection was necessary to obtain lenses and long bones. Genital morphology and body weight were also recorded from hares live-trapped and released on the study area. Known-age hares for body-weight and lens-weight studies were obtained from two sources; hares live-trapped on the Ballaine study area, and hares collected outside its boundaries. When very small (under 600 g.) hares were captured, their ages were estimated according to O'Farrell's (1960) body-weight curve. Many young hares were collected outside the study area. Many adult hares captured on the study area had been caught first when very young, and so their ages could be determined. The young born in the hare pens were weighed every other day from birth. At the same intervals one or two leverets were collected for their lenses.

Hind-Foot Color

The use of hind-foot color to distinguish adult hares from juveniles has been discussed above under pelage change. Adult hares cannot be separated from juveniles in Interior Alaska on the basis of foot color, because adults may have white, completely brown, or mottled hind feet in summer. Brown and mottled feet have been observed more frequently than white.

Epiphyseal Groove Closure

In many studies, the presence or absence of an epiphyseal carilage plate on one of the long bones has been used as a criterion for separating immature from adult animals. In lagomorphs the epiphyseal groove seems to become indiscernable during the animal's first winter. The date of closure may vary with species, nutrition, land fertility, growth rate, day length, sex, and time of birth (Hale, 1949). Martinson, et al. (1961) reported that the epiphyseal groove in the Swamp Rabbit, Sylvilagus aquaticus, closes at about ten months and that in Eastern Cottontails, Sylvilagus floridanus, it closes at seven months in males and eight months in females. Dodds (1960a) noted that in Snowshoe Hares in Newfoundland the epiphyseal groove is indiscernable at about seven months. Closing of the epiphyseal groove in Interior Alaska hares seems to occur at approximately seven months, but due to the paucity of data (Table 12) a reliable conclusion cannot be drawn.

Genital Morphology

In most cases, the sex of a Snowshoe Hare is easily determined. Newborn leverets are an exception; their genitals are so tiny that it is easy to err in sexing them. A juvenile male can be recognized by his short, stubby penis (Fig. 18), and an adult by his larger, posteriorly curved, pointed penis (Fig. 19). Juvenile and adult females can be recognized by a ramp-shaped vulva with a slit completely down the posterior surface (Fig. 20 and 21). Höglund and viklund (1953) are the only other biologists who have, to my knowledge, published a description of the difference between young male and female hare genitals (in their case Lepus timidus of Finland).

O'Farrell (1960) noted the difference between juvenile and adult hare penises and suggested that this difference might be useful in separating the two age classes in the field. This criterion was especially useful to me in separating young-of-the-year from males a year or older,

TABLE 12. CLOSURE OF THE EPIPHYSEAL GROOVE IN INTERIOR ALASKA SNOWSHOE HARES

Age in months	No. hares in sample	Condition of epiphyseal groove
0.5 - 3.5	43	open
4.0	1	closed
4.0	1	nearly closed
5.5	1	nearly closed
5.5	2	closed
6.5	1	nearly closed
7.5	1	closed
13.5	1	closed
17.5	1	closed

Fig. 18. Juvenile hare penis. A, anterior. P, posterior.

Fig. 19. Adult hare penis. A, anterior. P, posterior.

Fig. 20. Juvenile hare vulva. A, anterior. P, posterior.

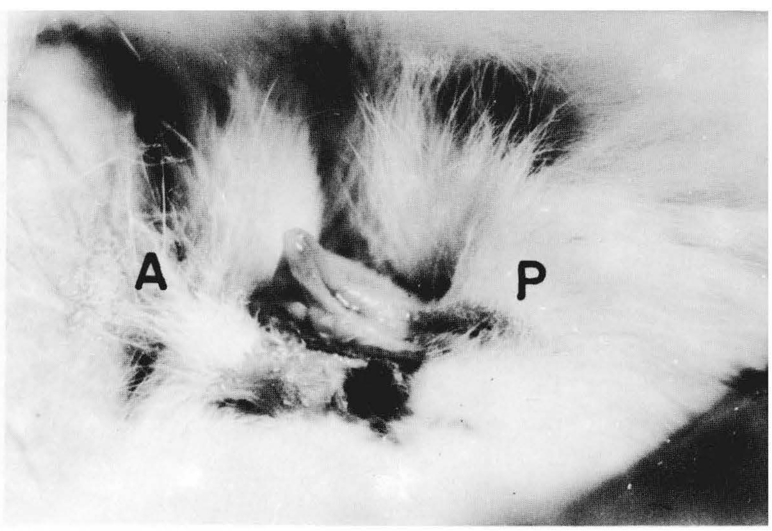


Fig. 21. Adult hare vulva. A, anterior. P, posterior.

in the fall and early winter. It is at this time that the adult and juvenile age classes are difficult to separate by body weight and general appearance alone. I have attempted to determine the date at which the first young-of-the-year obtains an adult-type penis.

A hare's genitals can be seen by pressing back the skin just anterior and posterior to the genital region. The penis can be recognized with little difficulty, even in leverets as young as two days old. The short juvenile penis undergoes morphological changes to reach the adult form. During most of the change period it still remains rather stubby, but develops a small projection which points anteriorly (Fig. 22).

I recorded penis shapes of several known-age hares. Hare No. 3769 was captured at the ages of 146, 166, 179 and 243 days. Through 179 days the penis was stubby, but possessed an anteriorly projecting process. At 243 days it was nearing adult form, but still pointed anteriorly. Two hares, No. 3821 and No. 2294, captured at 155 days and 169 days respectively, both had short, stubby penises. Hare No. 2264, 180 days old, had a short, stubby penis with a small projection from the center. The adult penis is usually much longer than the juvenile; it points posteriorly when unsheathed, and is quite pointed (Fig. 19). Hare No. 2780, caught at age 214 days, had a penis which apparently had recently attained the adult form. It was pointed posteriorly, but was unusually thin.

Other data which may indicate when the juvenile penis changes to the posteriorly pointed penis of the adult is as follows. Of 11 male hares captured in November 1960, ten had stubby penises and one an adult penis. Of 39 males captured in December 1960, 29 had stubby penises, 3 had penises of a transitional shape, and 7 had adult penises. Only two male hares, both with adult penises, were captured in January 1961. Of

Fig. 22. Transitional hare penis. A, anterior. P, posterior.

six males captured in February 1961, four had transition-type penises, and two had adult penises. The first transition-type penises appeared in December, indicating that it was possible for some young-of-the-year hares to have adult penises by the end of that month.

It seems that the hare penis attains adult form at approximately 200 days (or 6.5 months), perhaps later. If the first young are born in late May, they would be 6.5 months old in the middle of December. I believe this criterion can be used with confidence until the end of November.

O'Farrell (1960) also noted the difference between vulvas of juvenile and adult hares. When the skin around an adult female's genitals is stretched, the vulva spreads easily and appears thick and fleshy. The vulva of a juvenile has the characteristic ramp-like shape, but is not so fleshy and does not spread open easily. O'Farrell's description of female hare genitals seems adequate. I have found similar characteristics. Fig. 20 shows a juvenile vulva spread open. It is rather blunt, and may be mistaken for a penis by an inexperienced observer. Note the ramp-like shape and the posterior slit. An adult female can often be distinguished from a juvenile in the summer and early fall by a more easily spread, longer, and more pointed vulva (Fig. 21). She may also be identified by palpable teats, which juveniles lack. I do not know at what age the criterion of vulva shape becomes untrustworth in distinguishing young-of-the-year from adult females. The difference is slight at any time, and is certainly unreliable after November.

Body Weight

O'Farrell discussed the growth of Interior Alaska hares and compared his results with those of Severaid (1942) and Adams (1959). He found that Alaska hares grow faster than the Montana hares of Adams' study. They grow at a rate similar to Severaid's Maine hares until 60 days, after which Alaska hares grow at a greater rate. This is to be expected at Alaskan latitudes, where the growing season is short, and the winter long and severe.

O'Farrell weighed three leverets at birth, obtaining a mean weight of 52 g. The mean weight of nine leverets less than 24 hours old born in my hare pens was 64 g. Lacking any better standard, I used O'Farrell's growth curve to determine the ages of all leverets captured in the field. Ages of hares whose weights exceeded 1,000 g could not be determined with confidence, since O'Farrell's growth curve begins to level off at this weight. Fig. 23 shows the growth data obtained from 38 known-age weights derived from pen-raised leverets, and weights of 86 hares whose ages were determined by interpolation on O'Farrell's growth curve. These 86 weights represent hares which were first captured as leverets (under 600 g), their ages determined by interpolation, and then released. These hares were subsequently recaptured and weighed again. Weights of adults during the breeding season were not used.

If I were to construct a curve to fit the growth data in Fig. 23, it would be as misleading as I believe O'Farrell's curve to be; perhaps more so, since it would be based on O'Farrell's. After 70 days the adult weights of hares in my study vary between 992 g and 1,790 g. O'Farrell's curve, based on a small sample, is deceptively smooth; the points show little variation, even in adult weights.

Age determination of this sort, especially using wild leverets weighing 300 g or more, can be misleading, as Severaid (1942) has shown. He raised many hares in outdoor enclosures, and found that weight alone

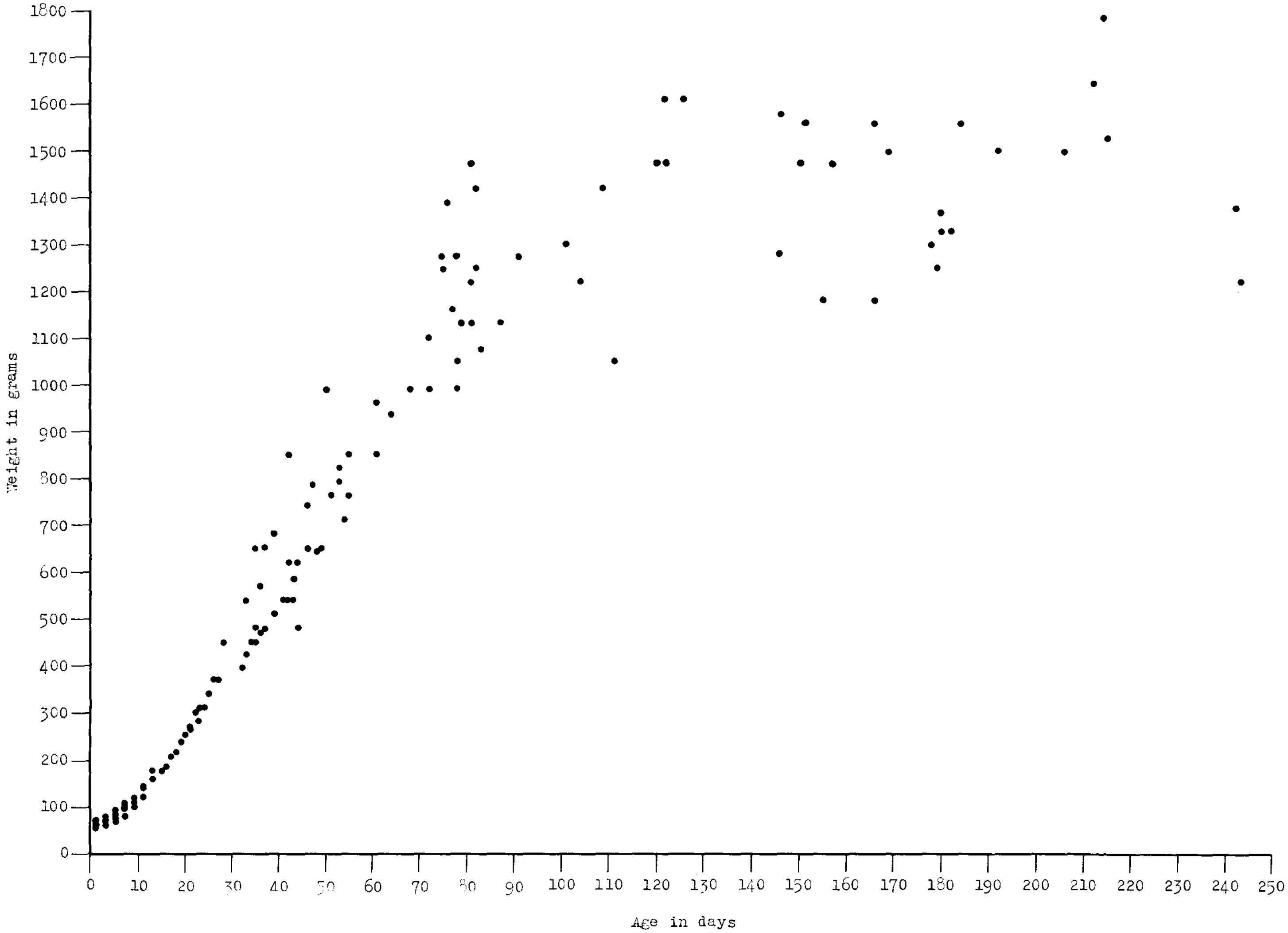


Fig. 23. Increase in body weight in Interior Alaska hares.

is not satisfactory for age determination. He believed that any one measurement is not sufficiently stable to determine the exact age of a growing hare, but by matching weight and appendage measurements with averages and variations of known-age hares, the age may be estimated with a fair degree of accuracy.

Hind-Foot Length

Hind-foot growth data were obtained from 38 measurements of pen-raised leverets and 30 hind-foot measurements of hares collected and recaptured in the field. Hind-foot measurements taken in the field seemed subject to considerable error. Those which showed inconsistencies (e.g., successive measurements of 138 mm, 123 mm, 130 mm, 123 mm, and 142 mm on one adult hare) were not used.

The plot of the points (Fig. 24) appears to level off at the adult hind-foot length of 139 ± 8 mm, at about 80 days (11.5 weeks). Severaid's (1942) hind-foot growth curve for Maine hares began to level off at about 16 weeks, and showed no further increase after 24 weeks, when the adult hind-foot length averaged 136 - 138 mm.

Several attempts were made to fit curves to the hind-foot data with the aid of an IBM 1620 Computer, but none of the results were satisfactory. A polynomial of the form $y = a + b_2x^2 + b_3x^3$ resulted in a curve which appeared to fit the data nicely up to 81 days from birth; after that it went 6 - 7 mm too high, and subsequently fell below the data at about 160 days. Brody's (1945) exponential growth equation of the form $W = A - Be^{-Kt}$ was also tried. A is a constant with an assumed maximum value; B and K are also constants, but with values calculated to give a fit. W is hind-foot length in millimeters, and t is time. This formula with an assumed maximum value of 145 mm resulted in a curve which

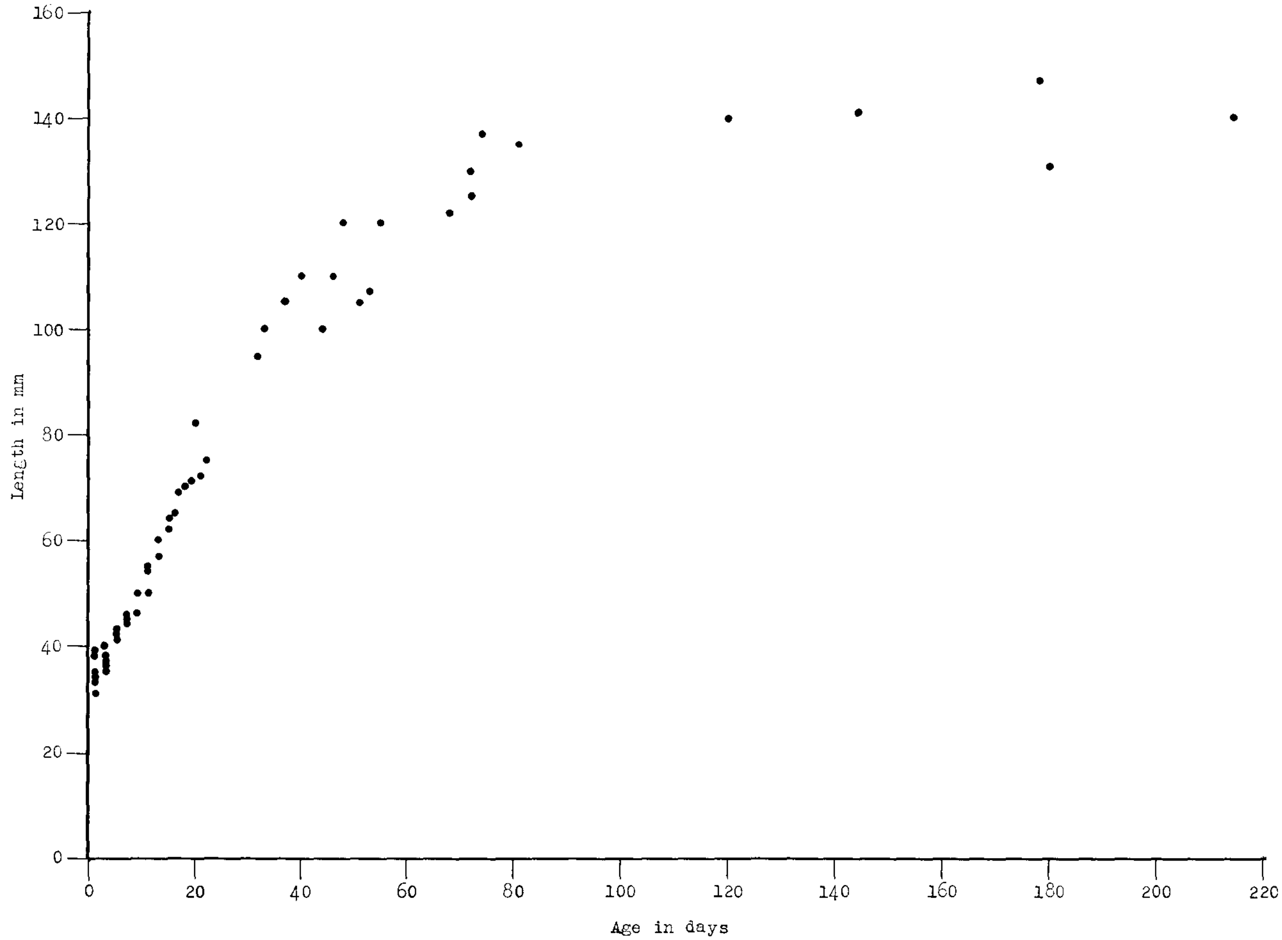


Fig. 24. Increase in hind-foot length in Interior Alaska hares.

started 10 mm below the data at zero days, crossed that data at six days, and thereafter remaind 3 - 5 mm above the data. A sigmoid type of differential growth equation of the form $\frac{dW}{dt} = KW(A - W)$ was used. In this case W is hind-foot length, K is a constant, A is the maximum assumed hind-foot length, and t is time. This equation yielded a curve which started 20 mm too high at zero days, crossed that data at 15 days, was 20 mm below the data at 35-40 days, and eventually approached the data at about 200 days. This was the general form of the curve for the different assumed values of A (140, 142, 145, 147.5, and 150 mm).

Lens Weight

Generally, my procedure for handling lenses was similar to Lord's (1959). One eye was dissected from each hare and was placed in 10% formalin to harden the lens. All lenses remained in formalin at least two weeks, although Lord said that one week is sufficient. After fixing, the lens was removed from each eye, rinsed in tap water, rolled on a paper towel to remove excess moisture, and placed with an identifying tag in a small crucible. Crucibles were then placed in a Bench-Top Laboratory Oven (Planchets, Chelsea, Mich.) and allowed to dry for 36 hours at 80 C. One lens at a time was removed from the warm oven and weighed immediately on a Roller-Smith precision balance (Roller-Smith Co., Bethlehem, Pa.). Results are shown in Table 13.

Lord (1959) found the lens weight of the Eastern Cottontail, *Sylvilagus floridanus*, to be a potential tool for age determination; in 1961 he published a lens growth curve for the Florida Gray Fox, *Urocyon cinereoargenteus*. Other lens growth studies have been conducted on Blacktail Jackrabbits, *Lepus californicus*, by Fineman and Detman (1960); on Raccoons, *Procyon lotor*, by Sanderson (1961); on Swamp Rabbits,

TABLE 13. LENS GROWTH IN SNOWSHOE HARES

Age in months	Lens wt in mg	Age in months	Lens wt. in mg	Age in months	Lens wt in mg
	12.2		52.2		85.4
	14.1		54.9		85.6
	15.7		55.2		87.6
	15.9		57.4		90.8
	16.8		63.9		92.0
	19.9		64.0	2 - 3	93.0
	20.9		64.5		93.1
0 - 1	22.1		65.6		94.2
	22.5		66.4		94.4
	22.8	1 - 2	66.5		119.3
	25.4		67.0		127.3
	26.1		67.3		86.0
	35.7		68.6		91.7
	41.9		68.6	3 - 4	97.7
	56.6		72.0		109.9
	19.1		73.6		114.2
	22.5		74.8		93.8
	23.5		77.6	4 - 5	107.2
	24.2		78.2		113.4
	35.2		64.0		84.6
1 - 2	39.4		73.4		95.5
	43.9	2 - 3	76.8	5 - 6	97.8
	49.3		82.3		98.4
	50.6		84.7		137.0
	50.7				

TABLE 13. (continued)

Age in months	Lens wt in mg
5 - 6	143.5
6 - 7	133.4
7 - 8	144.6
9 - 10	120.5
10 - 11	187.4
11 - 12	154.6
13 - 14	162.6
	186.2
16 - 17	187.2
	194.8
	196.4
17 - 18	189.2
	200.7
27 - 28	190.8
29 - 30	198.3
	201.5

Sylvilagus palustris, by Martinson, *et al.* (1961); on the wild rabbit, *Oryctolagus cuniculus*, by Dudzinski and Mykytowycz (1961); and on Pronghorn Antelope, *Antilocarpa americana*, by Kolensky and Miller (1962). Fineman and Detman; and Martinson, *et al.*, did not present curves, but simply separated their data into juvenile and adult groups. Sanderson's lens growth curve for the Raccoon flattens out at approximately one year and is useful only for telling the month of birth of the Raccoons less than a year old. The lens weights of cottontails, wild rabbits, Gray Fox, and Pronghorn Antelope increase rapidly in the first part of growth, then the rate decreases. Growth does not stop, but appears to continue increasing slowly.

I weighed lenses from 89 hares (Table 13). Nine of these were from known-age, pen-raised leverets; the remainder from hares captured in the field, whose approximate ages had been determined by using O'Farrell's body-weight growth curve. The lens weights range from 12.2 mg in a leveret less than 24 hours old to 201.5 mg in an adult 2.5 years old. The plot of the points (Fig. 25) appears to level off at 15-17 months, at approximately 194 mg. Whether or not the lens really does stop growing cannot be determined from the few data in the older age classes. Lens-weight data can be used to separate juvenile hares from hares one year or older at 160 mg.

Attempts to fit curves to the lens-weight data, using an IBM 1620 Computer, yielded unsatisfactory results. The same polynomial as that used for the hind-foot growth data was tried. It resulted in a curve which appeared to fit the data well, except at ages less than two months, where the curve was 10 - 15 mg above the data. An exponential fit was attempted, using the equation $W = A - Be^{-Kt}$, as described in the dis-

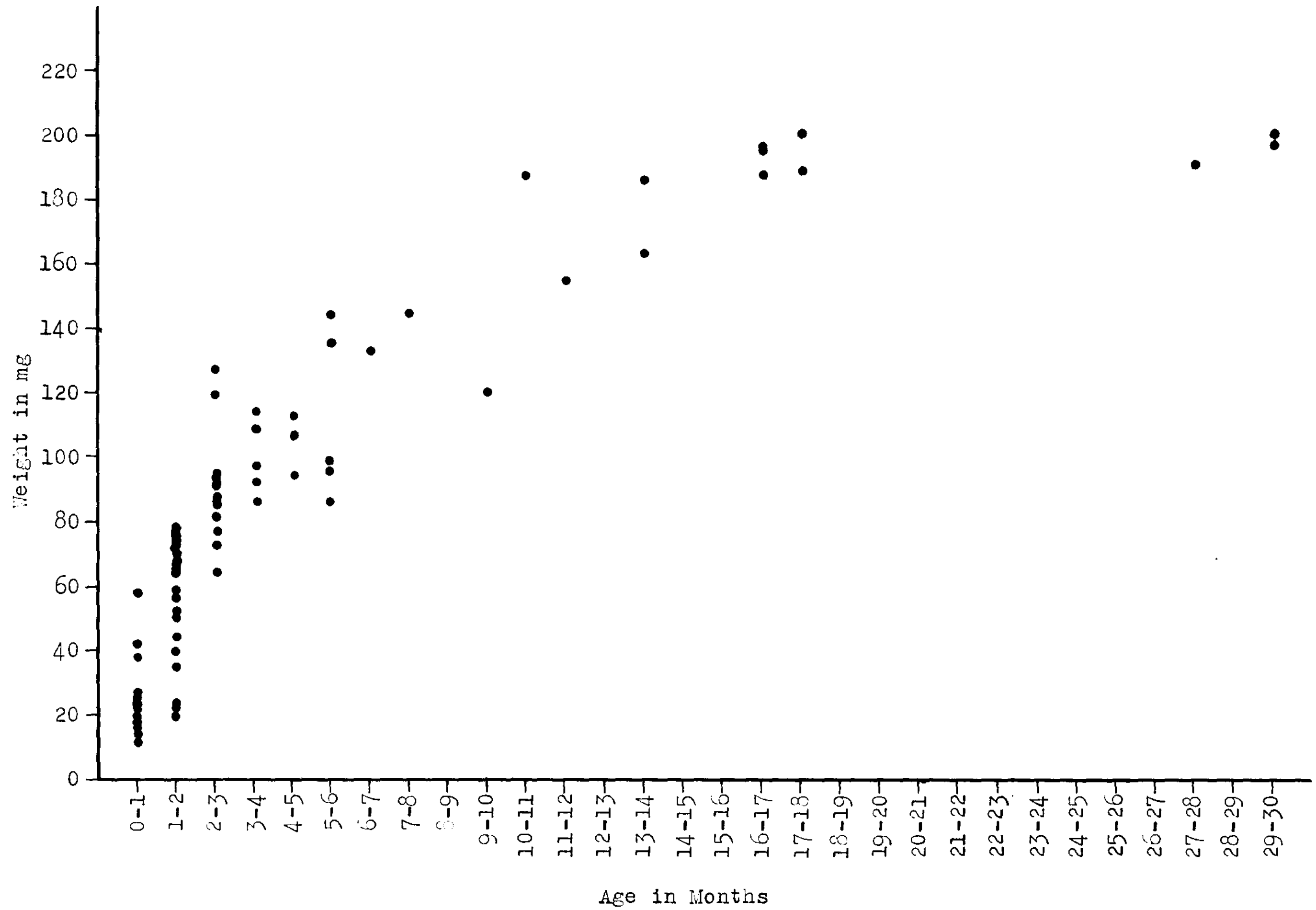


Fig. 25. Lens growth in Interior Alaska hares.

cussion of hind-foot growth. This also appeared to fit the data except at ages less than two months, where it also was about 10 - 15 mg above the data. Huxley's differential growth equation of the form $y = bx^K$, as used by Kolensky and Miller (1962), resulted in a curve which started about 17 - 18 mg above the data at one month, then crossed the data and paralleled the lower part of it until 10 months, where it went and thereafter remained far above the data. A futile attempt was made to decipher an equation used by Dudzinski and Mykytowycz (1961) on the growth of the lens in Oryctolagus. They were able to construct a curve and calculate 95% confidence limits, but they found that lens weight was a reliable indicator of a rabbit's age only until about 150 days.

Probably the most practical way to determine ages of juvenile hares is to use a combination of body weight and hind-foot length. For greatest accuracy, only ages of hares weighing less than 1,000 g should be determined from the body-weight data, i.e., hares less than 70 days old. Using the hind-foot data, approximate ages can be determined only for hares whose hind feet are less than 100 mm long, i.e., hares less than 40 days old. When using body-weight and hind-foot-length data together, the latter will be the limiting factor. Body-weight-determined age can be matched with hind-foot-determined age, and the mean used as the hare's age. Since this method can be applied only to a small segment of the population (hares less than 1.5 months old), its usefulness is limited.

SUMMARY

From May 1960 to November 1961 a field study was conducted on an increasing population of Snowshoe Hares on a 160-acre study area on Ballaine Road near College, Alaska. The objectives of the study were (i) to determine the effect of population density on home range size; (ii) to study reproduction, behavior, and age-determination criteria; (iii) to continue compilation of data on this population as part of a long-term study; and (iv) to test census methods. Data were obtained chiefly by live-trapping and snaring.

An increase in hare sign in marginal habitat indicated that the hare population had increased between 1958 and 1961. No reliable method has been found for measuring this increase. The Schnabel (Krumholz) formula and the Petersen ratio were tested, but were invalidated by differential trap response. The calendar graph, Webb strip-census, and Hartman toe-clip ratio all proved poor or useless under Interior Alaska conditions. Indices tested were the number of hare runways crossing lines on the study area, and counts of hare pellets. Neither method, as tried, yielded reliable results.

Some hares acquired a "trap habit" and became caught in the same trap several times in succession. A larger number appeared to avoid traps after being caught once, some for periods up to two years. Most of these appeared to have remained close to the point of first capture.

Total trapping success was 14%. It increased from a low of 6% in May and June 1960 to 62% in October, and diminished again during the winter. The summer of 1961 showed a success similar to that of 1960. During the entire study recapture success was highest in May, decreased during the summer as young were added to the population, and increased

again in the fall as the young were marked. Inclement weather restricted movements of hares, as shown by low trapping success on days following nights of rain or snow.

Counts of hares along roads were useless for determining the relative abundance of hares in the Fairbanks area because very few hares were seen, even where they were known to be abundant.

The earliest litters in 1961 were born in mid-May and the latest in early August. Lactation in some females appeared to be continuous from late May until late August. Dissection of 12 pregnant hares showed a mean of 4.6 fetuses per female per pregnancy.

In a cohort of 55 known-age hares at least 20 (36%) survived at least one year, and at least 3 (5%) survived at least two years. Differential trap response and emmigration apparently contributed to this apparent high mortality.

Foxes, Goshawks, and Red-tailed Hawks were probably the most important natural predators on hares.

The following internal parasites were found in hares: *Mosgovoyia pectinata*, *Taenia pisiformis*, *Dirofilaria scapiceps*, *Obeliscoides cuniculi*, and *Protostrongylus boughtoni*. Ticks were frequently found on hares in the summer of 1960, but were rare in the summer of 1961. Fleas seemed especially abundant on the hind feet of hares collected in the fall and early winter of 1960.

Home range size as calculated by the exclusive-boundary-strip method decreased significantly at the .01 level from 14.5 acres in a period of low population density (June 1959 - April 1960) to 13.1 acres in a period of higher density (May 1960 - November 1961). The mean adjusted home range length figures minimized differences in range area, and so were unsatisfactory for determining relative home range size.

The greatest dispersal movement noted, 1.6 miles in 14 days, was achieved by a juvenile female hare.

Qali covers shrubs and trees in winter in Interior Alaska, bending them to the snow surface and thus providing good cover for hares.

Evidence was found that hares occasionally use burrows.

Hares make a sound resembling a low click ("tch"), apparently when nervous.

Some agonistic, investigative, and possible displacement behavior was observed in hares.

Seventeen hare runways had a mean hardness of 717 g/cm^2 in January 1961. A hare, when standing, exerts about 9 g/cm^2 on the snow surface.

Two litters were found in simple depressions in the leaves, and one in a nest-like form. Leverets could move from their place of birth when less than 24 hours old. A six-day-old leveret had green plant material in its stomach.

Hares seemed to eat almost any green plant food available. Winter food consisted of small twings and tips of most deciduous plants and heaths. In late winter hares turned to the bark of willows, poplars, birch, and alders. Hares sometimes appeared to eat sand or gravel on roads. Hares ate frozen carcasses of other hares when a wound was present as a starting point.

The autumnal pelage change extended from the first week in August to the first of November, and the vernal change from late March to mid-June. Hares retained their winter coats for nearly five months and summer pelage for less than two months.

The color of a hare's hind feet cannot be used as an age criterion in summer, since adults may have brown, white, or mottled feet at this time. Epiphyseal groove closure in the humeri appears to occur at about seven months. Juvenile males have short, stubby penises until December. An adult male has a larger, posteriorly pointed penis. Juvenile females have short, blunt, hard-to-spread vulvas in summer and fall, and lack palpable teats. Adult females have palpable teats, and their vulvas, which spread easily, are longer and more pointed.

Body weight, hind-foot length, and lens weight were considered as age-determination criteria. None proved suitable, because of excessive variability. Matching body weight and hind-foot length may be an accurate method when used on juvenile hares with hind feet less than 100 mm long. The year of birth of an adult hare cannot be determined by these criteria. A lens weight of 160 mg can be used to separate hares less than a year old from older hares.

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APPENDIX

The nine vegetation stands of the Ballaine study area are depicted in Fig. 27 through 44. Each pictorial graph represents one 100-ft. line transect placed subjectively in the approximate center of a stand. Coverage was determined by the line-intercept technique. Heights of trees were either estimated or determined with an Abney level. The nomenclature used is that of Anderson's (1959) Flora of Alaska.

A description and photograph of each stand supplement the pictorial graphs. Following each graph is a table in which coverages are listed. Some classes of vegetation are excluded from some of the graphs in cases where the ground layer was so dense that it was impossible to depict all of its components. Species or classes with a trace coverage are not shown on the graphs. Symbols used to depict plants or plant types are shown in Fig. 26. Table 14 shows a complete list of the species in each class.

Stand A occupies the SW corner of the plot (Fig. 3). It is characterized by tall Betula papyrifera (ca. 50 ft.), Picea glauca, and Salix app. (Fig. 27 and 28, Table 15). There is an abundance of Equisetum arvense in the summer, but little other ground cover. Bryoids are present but sparse. In a limited area immediately around trap A-1 there is a dense stand of Alnus fruticosa which has a thick ground cover of Ledum groenlandicum and Vaccinium uliginosum. This was not treated as a separate stand, since it occupies only a very small area next to the road. Stand A, and all other areas above the 600-ft. contour line, are better drained than those areas below this level.

Stand B occupies that part of the SW corner of the plot bordering Stand A, and is also present in the SE corner (Fig. 3). Picea glauca

FIG. 26. SYMBOLS USED TO DEPICT VEGETATION.

TABLE 14. SPECIES OF PLANTS COMPRISING THE PHYSIOGNOMIC CATEGORIES IN VEGETATION STANDS ON THE BALLAINE STUDY AREA, COLLEGE, ALASKA

Those species marked with an asterisk are the commonest and and most conspicuous members of their category. The nomenclature is from Anderson's (1959) Flora of Alaska.

Bryoids:

*Sphagnum spp.

*lichens (several unidentified species)

Heaths:

*Ledum groenlandicum Oeder

*Vaccinium uliginosum L.

*Vaccinium vitis-idaea L.

*Empetrum nigrum L.

Shepherdia canadensis (L.) Nutt.

Chamaedaphne calyculata (L.) Moench.

Forbs:

*Cornus canadensis L.

*Mertensia paniculata (Ait.) Don.

*Linnaea borealis L.

*Epilobium angustifolium L.

*Rubus arcticus L.

*Petasites frigidus (L.) Fries

*Pyrola secunda L.

*Rubus chamaemorus L.

Achillea millefolium L.

Saussurea angustifolia (Willd.) DC

TABLE 14. (continued)

Epilobium palustre L.

Aconitum delphinifolium DC.

Solidago multiradiata Ait.

Arenaria lateriflora L.

Geocaulon lividum (Rich.) Fern.

Polemonium acutiflorum Willd.

Actaea arguta Nutt.

Moneses uniflora (L.) Gray

Chenopodium capitatum (L.) Achers

Lysiella obtusata (Pursh.) Rydb.

Equisetum:

*_Equisetum arvense_ L.

Graminoids:

*_Calamagrostis_ (inexpansa A. Gray?)

Carex spp.

Shrubs:

*_Rosa acicularis_ Lindl.

*_Viburnum edule_ (Michx.) Raf.

Ribes triste Pall.

Trees:

*_Betula papyrifera_ Marsh

*_Populus tremuloides_ Michx.

*_Picea mariana_ (Mill.) B. S. P.

*_Picea glauca_ (Moench) Voss.

TABLE 14. (continued)

*_Salix_ spp.

*_Alnus fruticosa_ Rupr.

Populus balsamifera And.

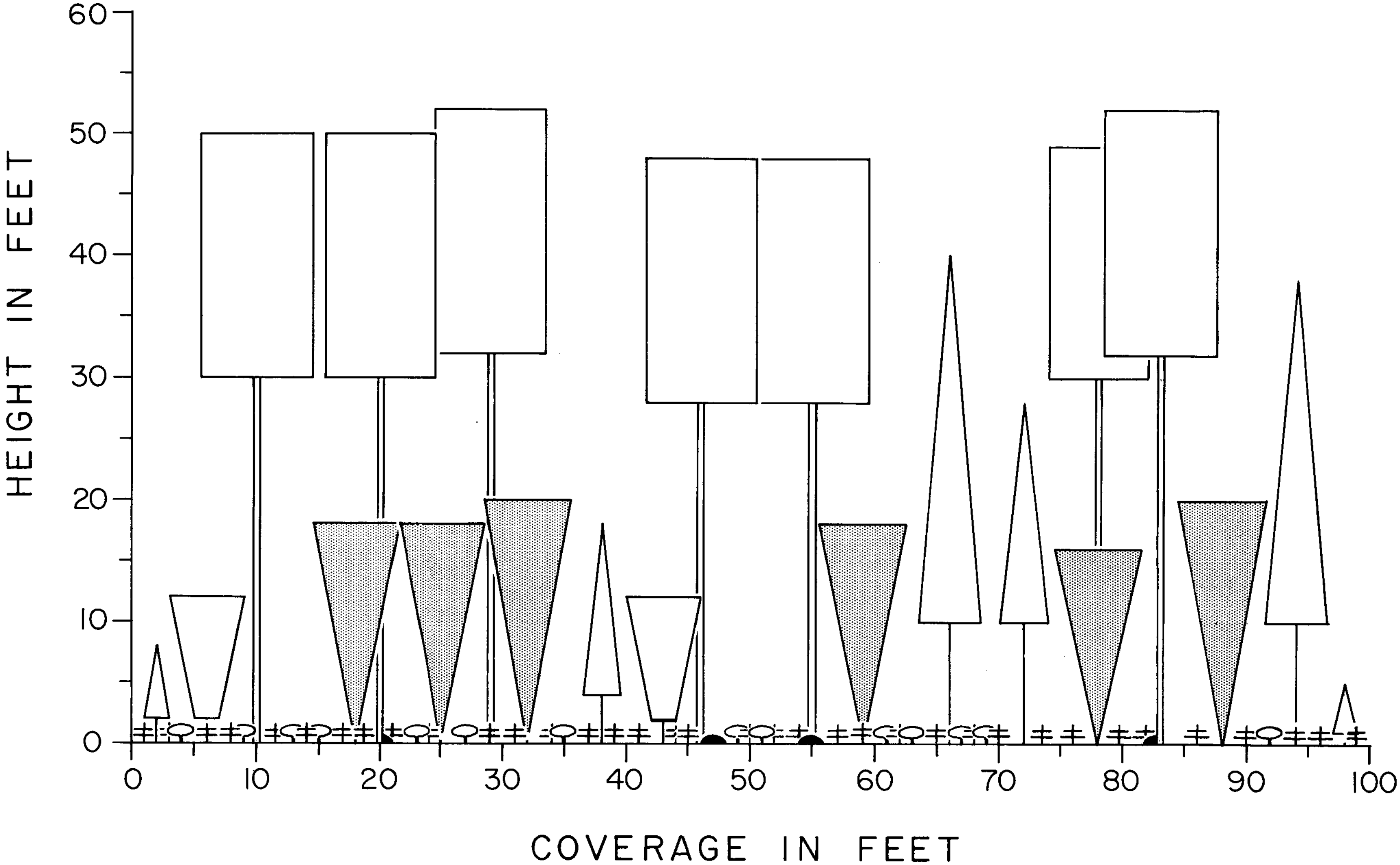

FIG. 27. VEGETATION STAND A.

TABLE 15. VEGETATION COVERAGE IN STAND A (FIG. 27), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	6%
Heaths	0
Forbs	28
Equisetum	71
Graminoids	0
Shrubs	0
Trees	
Betula papyrifera	58
Picea glauca	21
Salix spp.	42
Alnus fruticosa	12

Fig. 28. Vegetation stand A.

is the predominant tree here (Fig. 29 and 30, Table 16). Some *Salix* spp. and *Picea mariana* are present also. This stand is distinguishable from Stand A by its lack of large *Betula papyrifera*, and by the presence of a dense ground cover of *Ledum groenlandicum*, *Vaccinium uliginosum*, *Equisetum arvense*, and bryoids. In the SE corner of the plot *Picea glauca* are slightly more dense, but not as tall as in the SW corner. The SW corner has a denser growth of *Salix* spp. and *Alnus fruticosa*.

Stand C, located in the NW corner of the plot (Fig. 3), has a dense tree layer of *Betula papyrifera* and *Salix* spp. (Fig. 31 and 32, Table 17). *Equisetum arvense* and *Ledum groenlandicum* form a dense ground cover. Bryoids are fairly abundant. *Picea glauca* and *Alnus fruticosa* are abundant in some parts of the stand. The area is well drained.

Stand D is a small, well-drained stand occupying a small hill in the south-central part of the plot (Fig. 3). It is surrounded by lower, more poorly drained muskeg. Tall *Picea glauca* and *Populus tremuloides* are conspicuous in the tree layer (Fig. 33 and 34, Table 18). Shorter *Picea mariana* are also common. There is essentially no shrub or ground layer, except for a covering of bryoids.

Stand E is located on the south border of the plot (Fig. 3), and is slightly wetter than the other upland stands. North of the A-line, where the transect was made, the tree layer consists of a very dense mixture of *Betula papyrifera* and *Salix* spp. (Fig. 35 and 36, Table 19). There are no shrubs, and the ground cover is sparse. South of the A-line this situation changes abruptly to an open stand of increasingly taller *Populus tremuloides* and some *Picea glauca*. There are more forbs and bryoids in the southern part. In the northern section, trees become shorter and *Betula papyrifera* fewer as the stand merges with muskeg to the north.

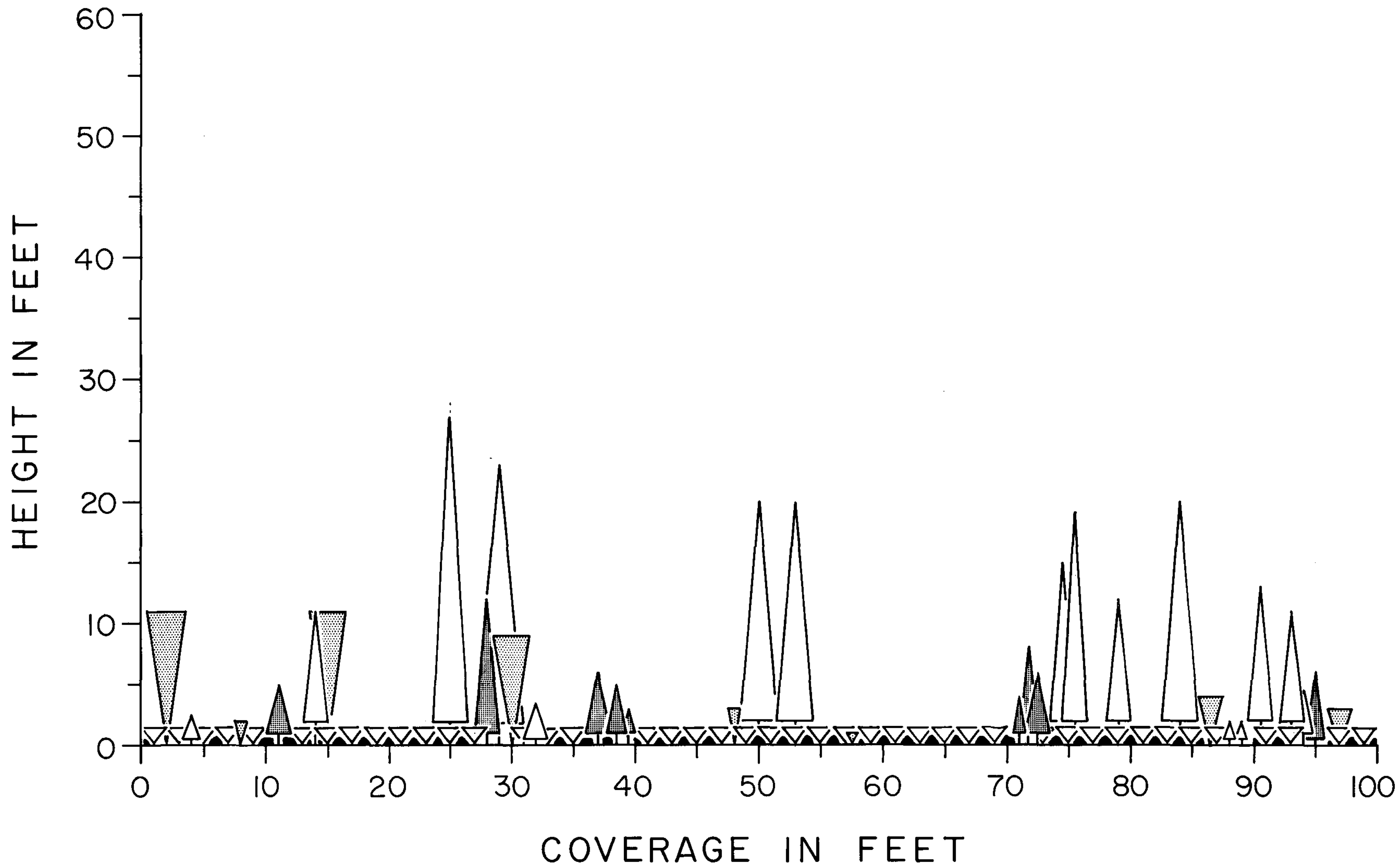

FIG. 29. VEGETATION STAND B.

TABLE 16. VEGETATION COVERAGE IN STAND B (FIG. 29), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	98%
Heaths	86
Forbs	Trace
Equisetum (not shown)	30
Graminoids	Trace
Shrubs	Trace
Trees	
Betula papyrifera seedlings	trace
Picea glauca	34
Picea mariana	13
Salix spp.	16

Fig. 30. Vegetation stand B.

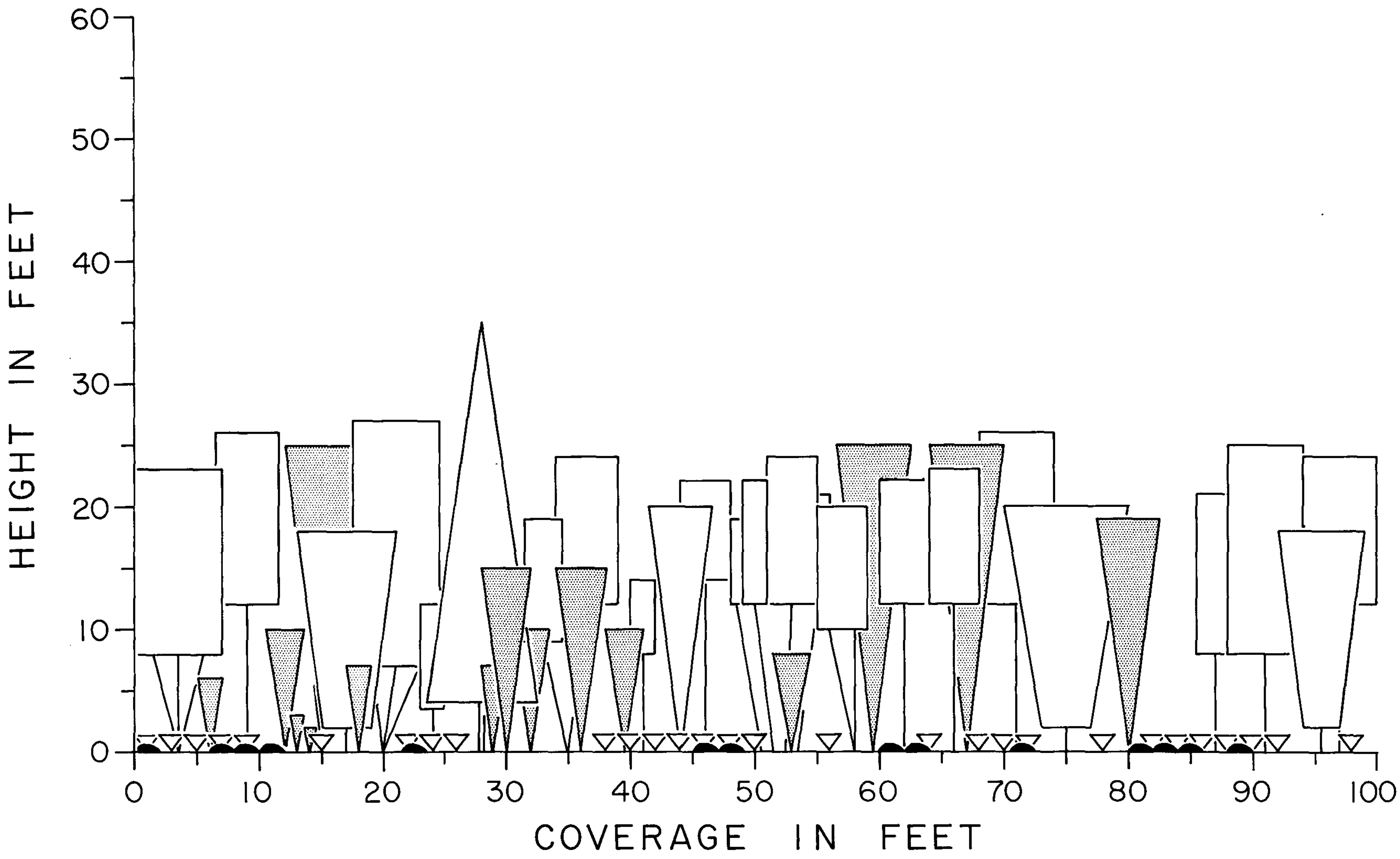

FIG. 31. VEGETATION STAND C.

TABLE 17. VEGETATION COVERAGE IN STAND C (FIG. 31), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	28%
Heaths	58
Forbs (not shown)	36
Equisetum (not shown)	89
Graminoids	0
Shrubs	trace
Trees	
Betula papyrifera	71
Picea glauca	9
Salix spp.	48
Alnus fruticosa	25

Fig. 32. Vegetation stand C.

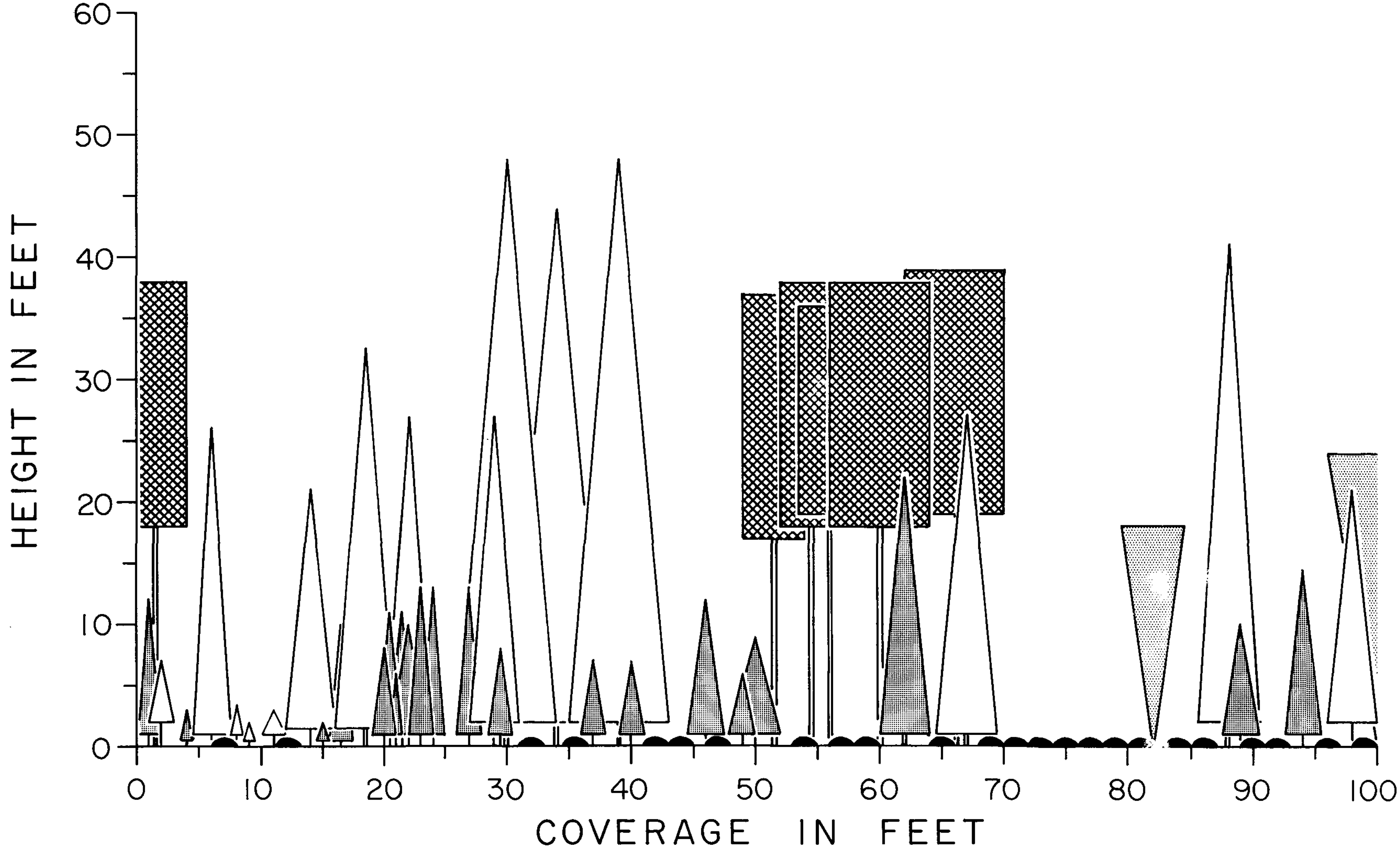

FIG. 33. VEGETATION STAND D.

TABLE 18. VEGETATION COVERAGE IN STAND D (FIG. 33), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	48%
Heaths	trace
Forbs	trace
Equisetum	trace
Graminoids	0
Shrubs	trace
Trees	
Populus balsamifera	trace
Populus tremuloides	25
Picea glauca	52
Picea mariana	37
Salix spp.	9

Fig. 34. Vegetation stand D.

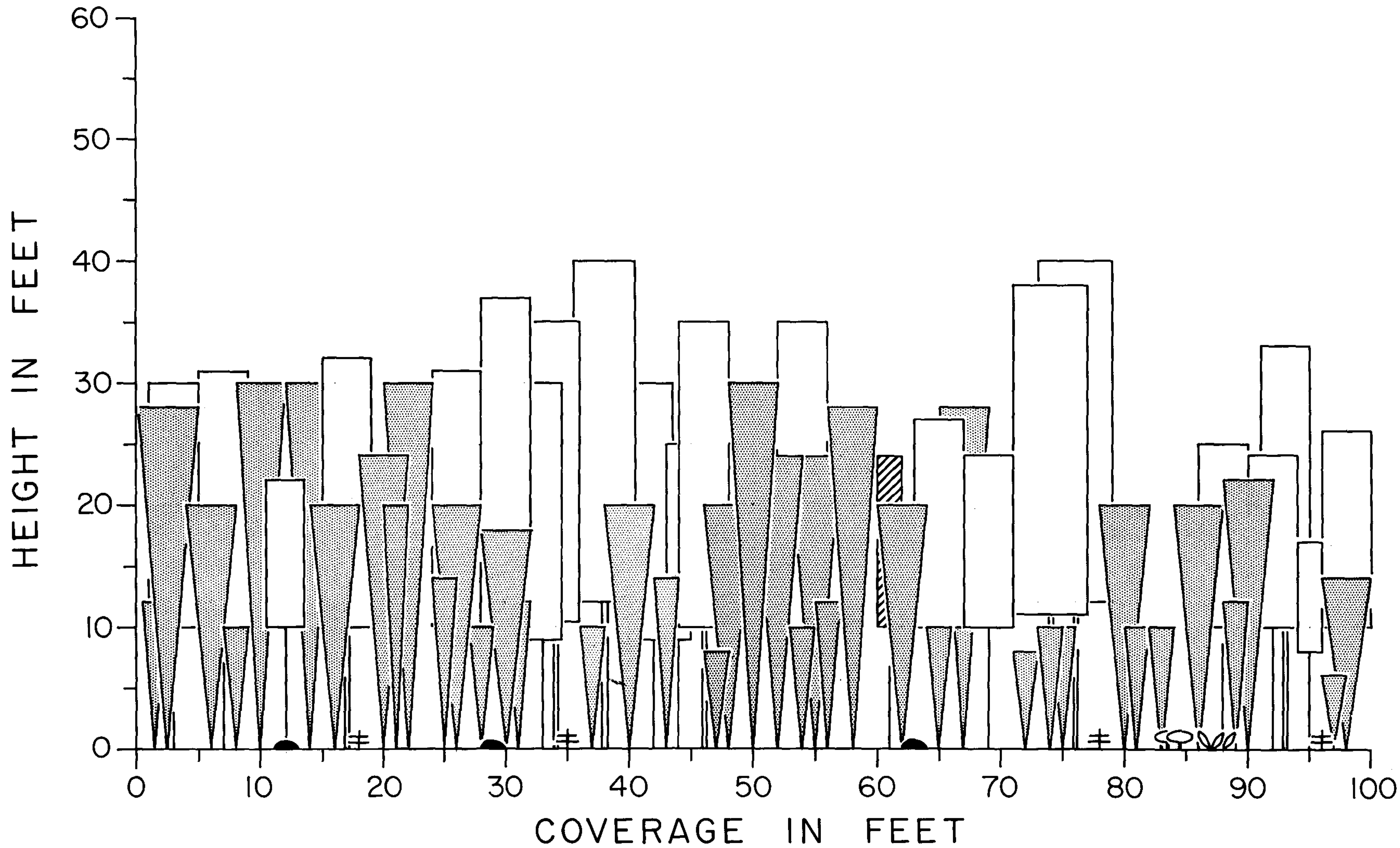

FIG. 35. VEGETATION STAND E.

TABLE 19. VEGETATION COVERAGE IN STAND E (FIG. 35), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	6%
Heaths	0
Forbs	3
Equisetum	8
Graminoids	3
Shrubs	0
Trees	
Betula papyrifera	73
Populus balsamifera	2
Salix spp.	86

Fig. 36. Vegetation stand E.

Stand F occupies the drainages of Pearl Creek, and intermittant stream crossing the plot from the north-central boundary to the SE corner (Fig. 3). Pearl Creek is flooded in the spring by melting snow, and often contains running water in summer during prolonged rainy periods. There is a dense canopy of Salix spp. interspersed with Alnus fruticosa (Fig. 37, 38, Table 20). There is a lush ground layer of Equisetum arvense. There are few shrubs. Bryoids are common, and graminoids are present. The latter are found in greater numbers here than in any other stand, except Stand H. There are a few forbs and a very few heaths in the ground layer.

Stand G occupies the highest portion of the plot, the NE corner (Fig. 3). The canopy consists of a dense layer of Salix spp. of varying heights interspersed with taller Betula papyrifera (Fig. 39 and 40, Table 21). There is a sparse shrub layer consisting almost entirely of Rosa acicularis. There is a dense ground layer of Equisetum arvense. Forbs and bryoids are common, but heaths are almost entirely lacking.

Black spruce muskeg is the most extensive stand on the plot (Stand H, Fig. 3). The tree layer consists of clumps of Picea mariana of relatively low height, plus a few Salix spp. and occasional Betula papyrifera and Picea glauca (Fig. 41 and 42, Table 22). Heaths are abundant in the ground layer. Below these is an almost continuous blanket of bryoids, mostly Sphagnum. There are few shrubs, forbs, or Equisetum arvense. Graminoids are relatively common. This stand is underlain largely by undifferentiated silt impregnated with permafrost. It is less well-drained than those stands underlain by frost-free loess on higher ground.

Stand I is located in the north-central portion of the plot (Fig. 3). It is muskeg similar to Stand H, with fewer Picea mariana and with a larger number of Salix spp. and Betula papyrifera (Fig. 43 and 44, Table 23).

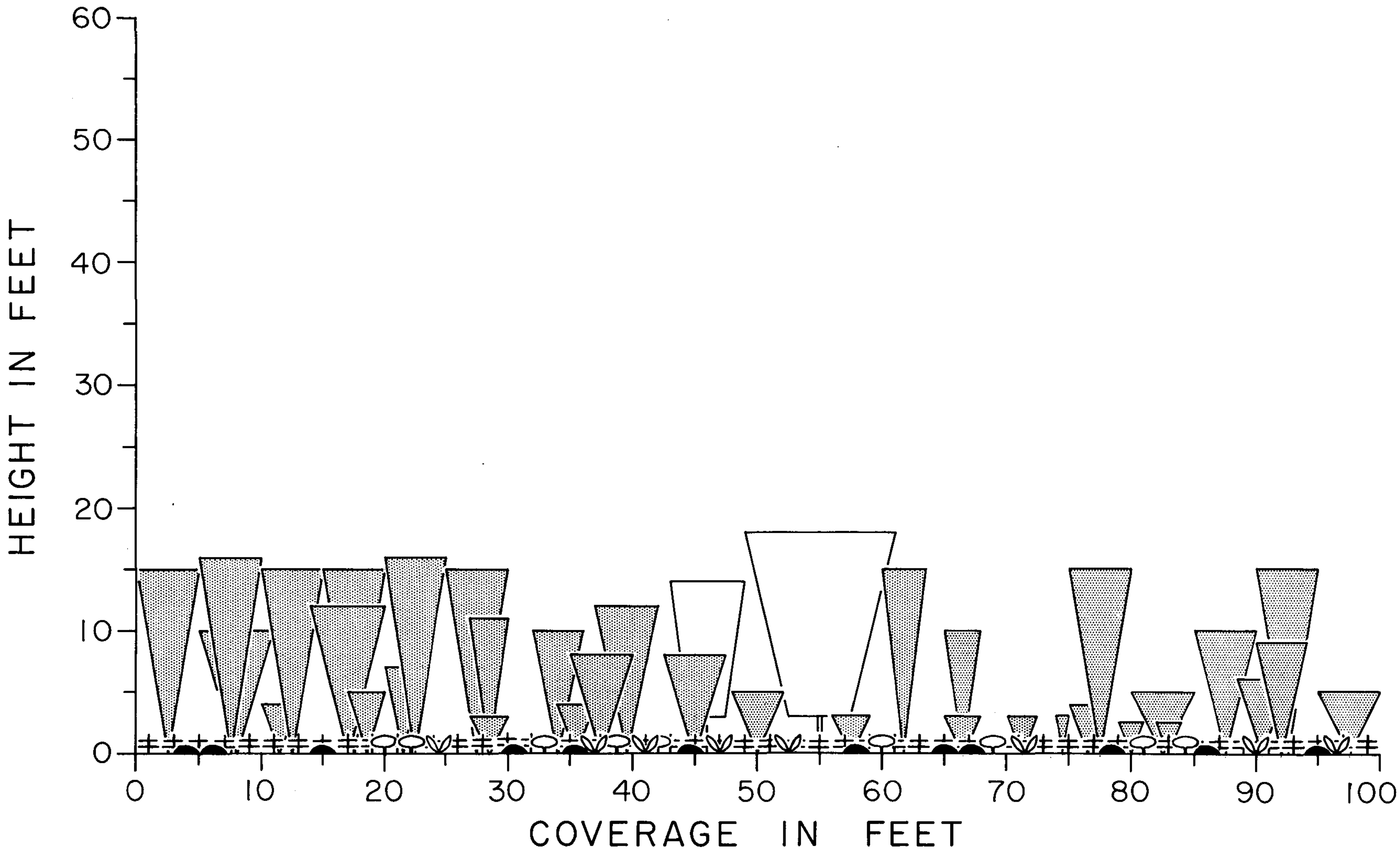

FIG. 37. VEGETATION STAND F.

TABLE 20. VEGETATION COVERAGE IN STAND F (FIG. 37), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	24%
Heaths (not shown)	2
Forbs	17
Equisetum	98
Graminoids	16
Shrubs (not shown)	4
Trees	
Picea glauca	trace
Salix spp.	88
Alnus fruticosa	18

Fig. 38. Vegetation stand F (foreground).

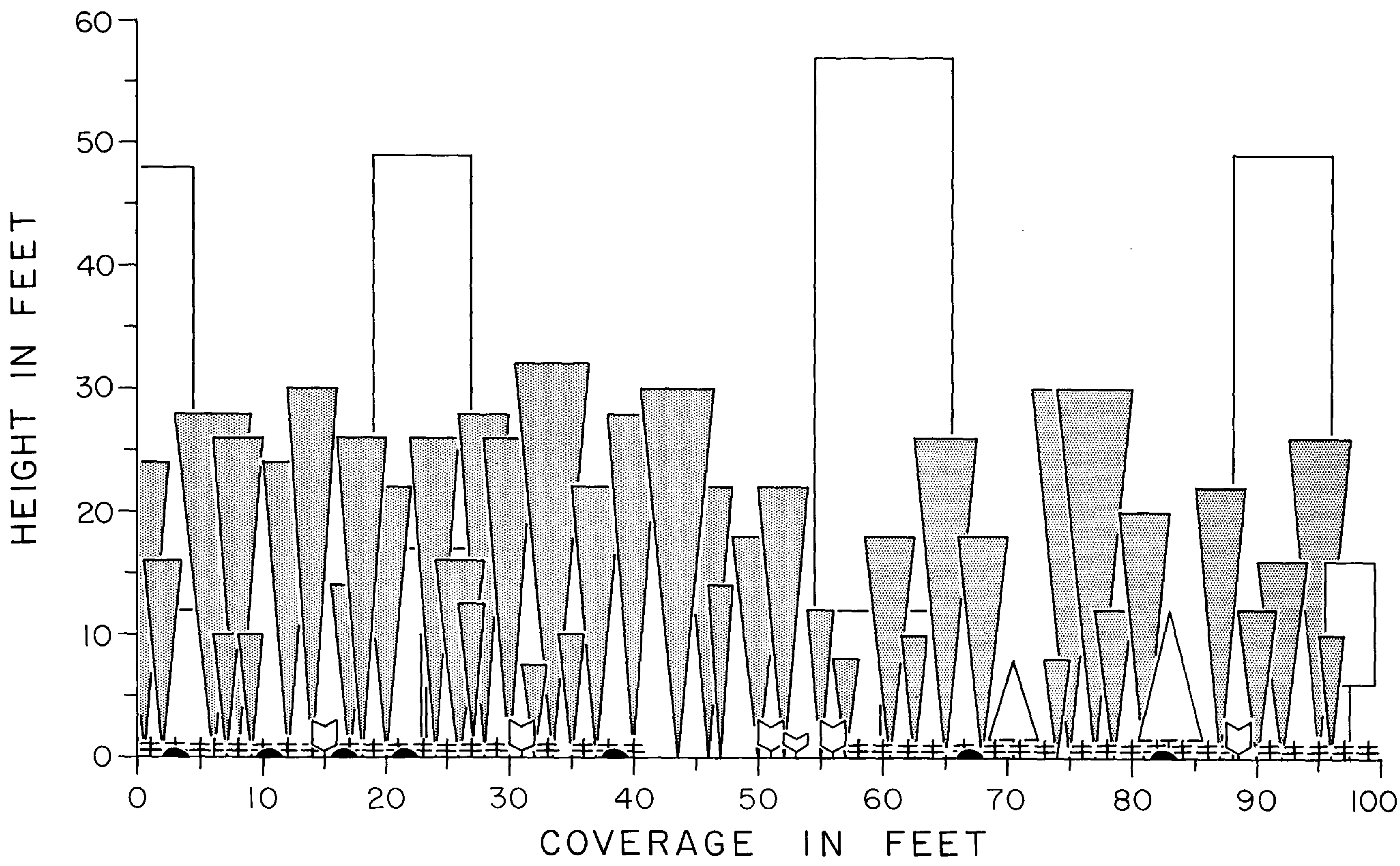

FIG. 39. VEGETATION STAND G.

TABLE 21. VEGETATION COVERAGE IN STAND G (FIG. 39), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	14%
Heaths	trace
Forbs (not shown)	20
Equisetum	77
Graminoids	trace
Shrubs	12
Trees	
Betula papyrifera	35
Picea glauca	9
Salix spp.	93
Alnus fruticosa	trace

Fig. 40. Vegetation stand G.

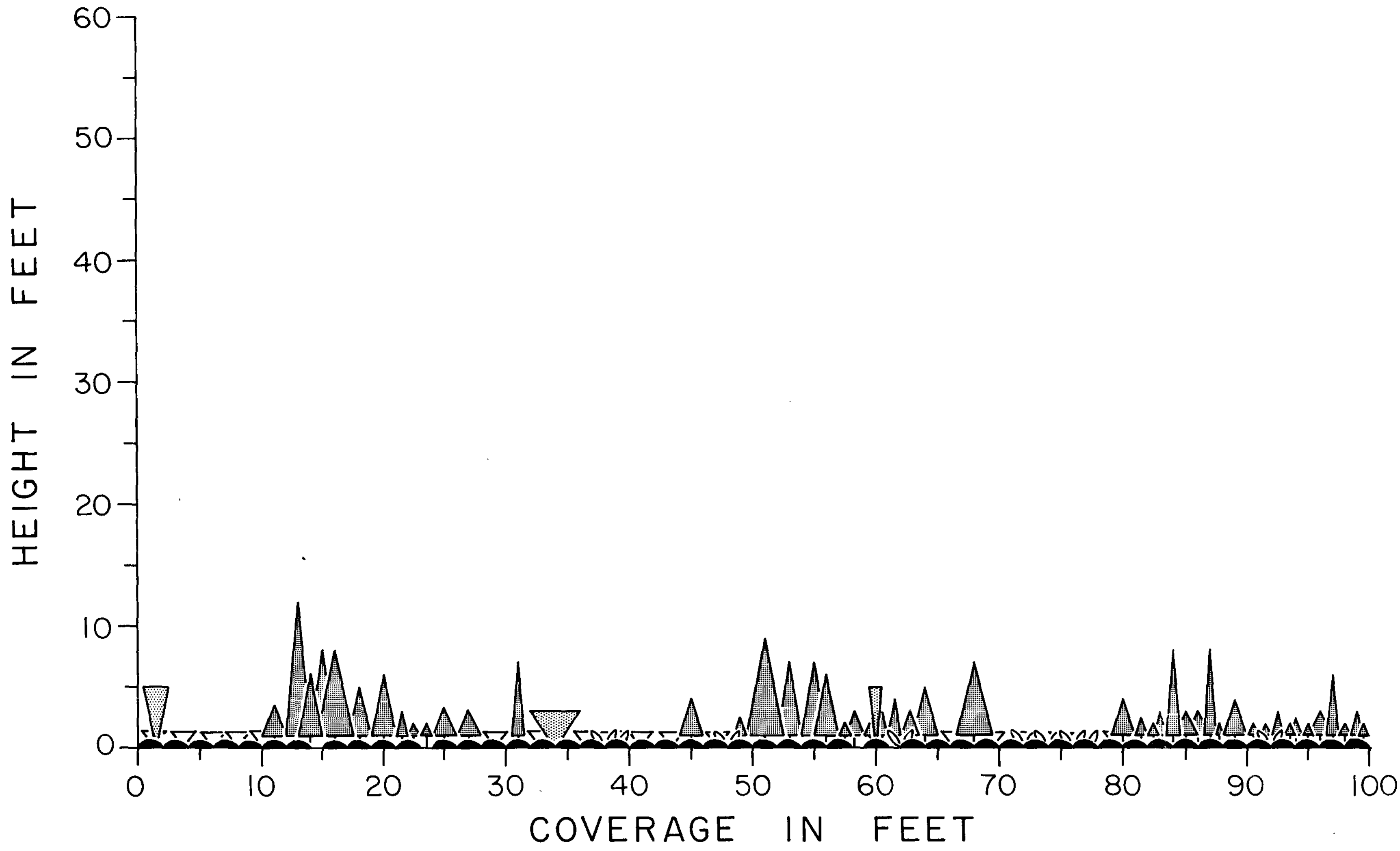

FIG. 41. VEGETATION STAND H.

TABLE 22. VEGETATION COVERAGE IN STAND H (FIG. 41), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	96%
Heaths	86
Forbs	8
Equisetum	trace
Graminoids	16
Shrubs	trace
Trees	
Betula papyrifera	trace
Picea glauca	trace
Picea mariana	64
Salix spp.	7

Fig. 42. Vegetation stand H (foreground).

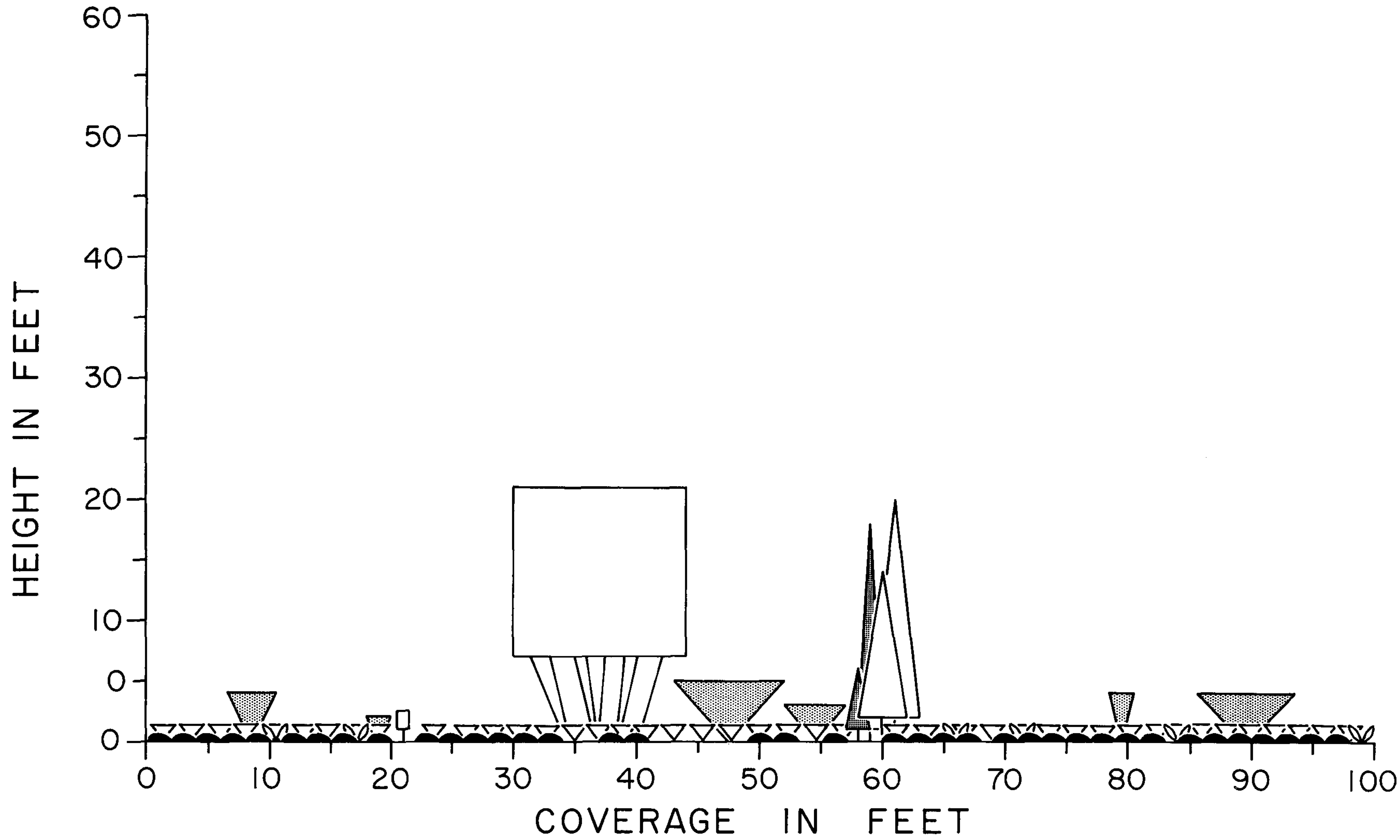

FIG. 43. VEGETATION STAND I.

TABLE 23. VEGETATION COVERAGE IN STAND I (FIG. 43), BALLAINE STUDY AREA, COLLEGE, ALASKA

Vegetation form	Percent coverage
Bryoids	76%
Heaths	96
Forbs (not shown)	8
Equisetum (not shown)	1
Graminoids	12
Shrubs	trace
Trees	
Betula papyrifera	15
Picea glauca	5
Picea mariana	3
Salix spp.	30

Fig. 44. Vegetation stand I.

This area is very open. A few *Picea glauca* and *P. mariana* are scattered over it. As in Stand H, the ground layer is a dense cover of heaths over an almost continuous blanket of bryoids.