SNOWSHOE HARES IN ALASKA. I

HOME RANGE AND ASPECTS OF POPULATION AND NATURAL HISTORY IN INTERIOR ALASKA

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Not for Publication

PREFACE

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Throughout my study I have received guidance and help from many people, and I would like to acknowledge the parts that they played:

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Mrs. Joan O'Farrell edited, typed and retyped the thesis through many drafts and copies. She also provided the push needed at times to activate a certain potentiality into actuality.

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ABSTRACT

An investigation of the home range, population size and natural history of an Interior Alaska snowshoe hare population was conducted from April, 1959, through April, 1960. Live-trapping and tagging were used to gather the bulk of the data.

The track count method, pellet count method and strip census were not usable under subarctic conditions. The Lincoln Index, Schnabel Method and calendar-graph method gave an indication of the population size. The population was estimated to be between a high of 255 hares in August and a low of 5 in January, 1960.

Home range was calculated using the boundary inclusive method. Males had a home range of 11.8 acres. Females had a home range of 13.0 acres. There was no significant difference between the annual and early breeding season home ranges.

Trapping success was high during the summer and low in the winter. Recapture success was low in the summer, due to recruitment, but rose to 89 per cent in January and April, 1960.

When the snow on the area was not compacted or was thawing, hares used packed runways. Under different snow conditions they used the entire snow cover for movements.

The summer food of hares was most of the green vegetation in the area. Winter food consisted of the bark and twigs of willow, aspen, alder and spruce.

Hares studied did not show a cover preference.

The autumnal molt began in early August and was completed by November 1. The vernal molt began late in March and was

completed by mid-June. At least 68 days were required for a complete molt.

Hares remained inactive during heavy rains or cold weather (-30°F. or below). One hare was shot 12.5 miles from its tagging site. This probably is the longest recorded movement by a snowshoe hare in the literature.

The breeding season extended from mid-March to mid-July. Three juveniles weighed an average of 52 g. at birth. A growth curve was drawn which indicated that Alaska hares grow at a greater rate than Montana or Maine hares.

Predation and shock disease were two mortality factors observed.

Adult and juvenile hares were aged on the basis of the external characteristics of the genitals.

INTRODUCTION

Cyclic fluctuations in populations have become one of the most studied aspects of animal population dynamics since biblical times (Elton, 1924). A great deal of effort has been expended describing those species that fluctuate with regularity and an even greater effort has been directed toward discovering the cause or causes of cycles.

After an initial period in which many fluctuating populations were described, Elton (1942) reviewed the entire field of cycles. His monumental work precipitated several other investigations, and in 1954 the editors of the Journal of Wildlife Management gathered the works of ten authors in the field of cyclic phenomena into a symposium on fluctuations.

Sunspots, predators, fluctuations in quality and quantity of food, random population forces and the adreno-pituitary system have all been cited as possible causes of cycles, but it has not yet been proved conclusively that any one, or several, of the above are the causes of cycles.

Christian (1950) pointed out that the problem in studying cyclic phenomena is not the accelerating phase but rather the phase concerned with the sudden die-off. The accelerating phase tends to be an exponential growth curve common to all growing animal populations. When the cyclic peak is reached, the population may be reduced suddenly and without apparent cause. The cause of this die-off is the unknown of animal fluctuations.

The present study was originated by the staff of the Alaska Cooperative Wildlife Research Unit as part of a long term study of the patterns and causes of snowshoe hare population fluctuations in Alaska. Very little actual field work had been done on fluctuating animal populations in areas of violent cycles, so a continuing program of studies was initiated in 1955. Lack (1945:25) pointed out the need for field research when he stated, "The most astonishing point, to a newcomer, is that despite the enormous number of papers written on cycles, no one, so far as I am aware, has yet studied any cyclic species in the field for even the term of one full cycle. Biology has not normally advanced far by arm-chair methods."

The objectives of this study were as follows:

1.) to determine the size of the home range of snowshoe hares, *Lepus americanus* Erxleben, in Interior Alaska;

2.) to ascertain what census methods could be used under sub-arctic conditions;

3.) to compile natural history about snowshoe hares in their extreme northern range.

Field studies began June 21, 1958, with a four month orientation in hare trapping and tagging procedures. From March to May, 1959, the hare study area described in this paper was selected, surveyed for trapping locations and traps were placed in position. Trapping commenced July 17, 1959, and was halted February 23, 1960. Field assistant Peter Dzikiewicz reopened the traps April 6, 1960, and he is presently collecting data on the breeding season of snowshoe hares.

DESCRIPTION OF THE STUDY AREA

Location

A 160 acre hare study area was established on the east side of Ballaine Road two miles north of the University of Alaska campus. The study area occupies the northeast quarter of section 30 township 1 north, range 1 west of the Fairbanks Meridian and is approximately 64° 50' N. latitude and 147° 50' W. longitude. This particular area was selected because it was known to support a population of hares, human interference was at a minimum, and it was readily accessible for daily observations. Figure 1 shows the location of the hare study area.

Topography

The hare study area is located in the rolling country of Interior Alaska between the Brooks and Alaska Ranges. Uplands rise just north of the Tanana River and separate the drainages of the Yukon and Tanana Rivers with a series of hills known as the Yukon-Tanana uplands. These hills rise between 2,000 and 4,000 feet above sea level and overlook the broad expanses of the two river drainages with their moist muskegs and numerous tributaries.

The hare study area is on a south-facing slope of one of the hills in the Tanana River Drainage. The study area rises an average of two degrees from its lower border which is 550 feet above sea level to the upper boundary which is 700 feet above sea level. Figure 2 shows the elevations of the hare study area.

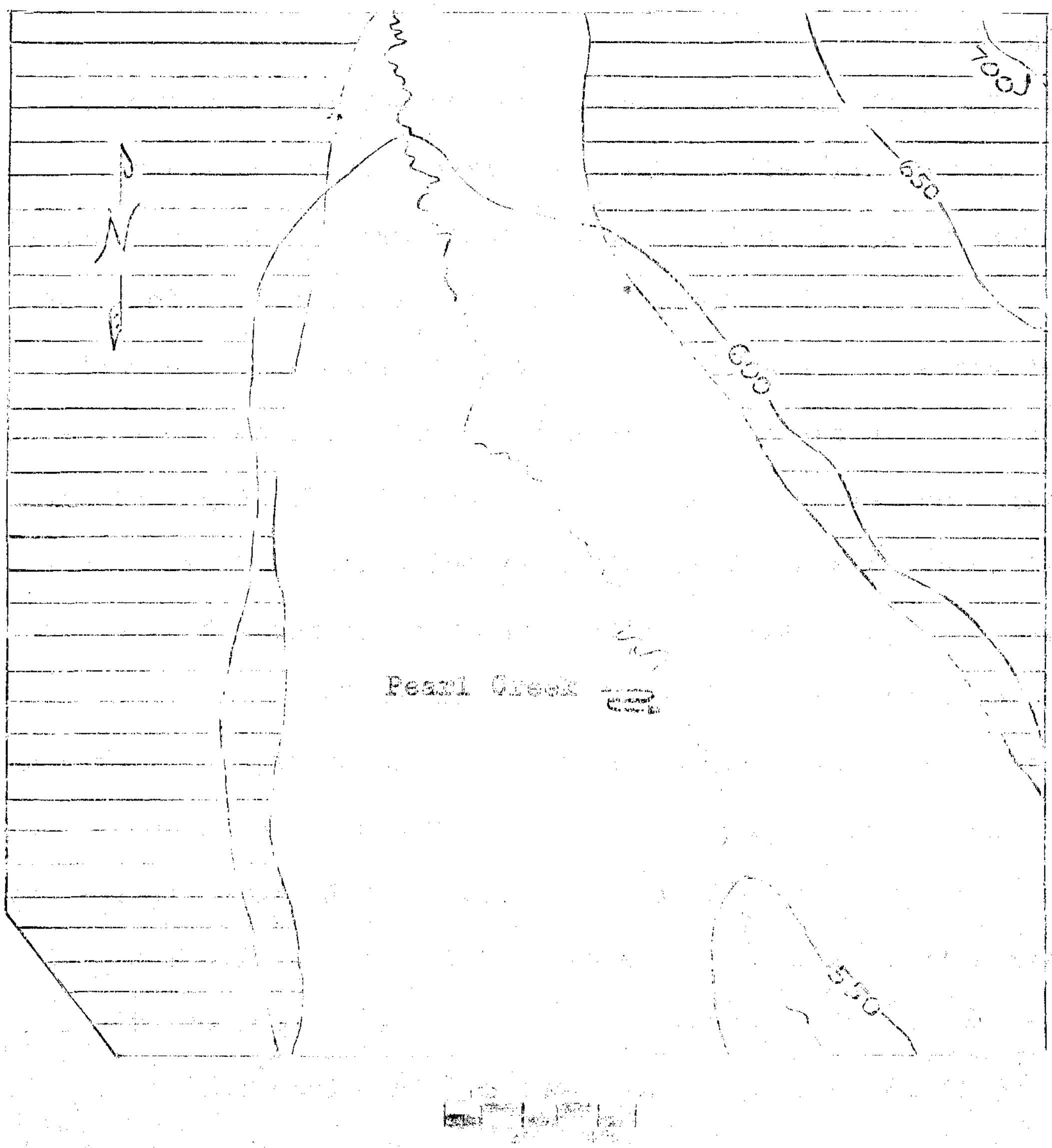
Fig. 1. Location of the Interior Alaska study area. The small map shows the area covered by the large map.

Soil

Péwé (1958) made a detailed study of the geology and soils of the quadrangle in which the hare study area is located, and he found that only two soil types occurred on the study area (Fig. 2.).

The soil from the creek up to the 600 foot contour is undifferentiated silt. This is eolian silt deposited from the higher hills and contains some organic matter and less than 10 per cent clay. Undifferentiated silt is found to a depth of 15 feet where it grades into a layer of organic silt. Organic silt is soil which has been re-worked several times and contains much organic matter, both vegetable and animal. The layer of organic silt occurs between 15 and 169 feet below the surface. Under the layer of organic silt is a horizon of fractured schist which extends from 169 to 176 feet below the surface. Between 176 feet and 245 feet the strata are composed of organic silt and fractured schist. Permafrost occurs where there is undifferentiated silt. The depth to the permafrost on the lower slopes and the creek bottom is one and one-half to four feet below the surface. Near contact with Fairbanks loess (see below) permafrost lies from 5 to 20 feet below the surface. The permafrost is continuous except near the Fairbanks loess and it contains abundant ground ice in sheets, wedges and saucer-shapes.

The soil above the 600 foot contour is Fairbanks loess. This also is an eolian silt, buff to tan gray in color, with less than 10 per cent clay. It is composed mainly of angular grains of quartz, feldspar and mica. The loess extends to a depth of 55 feet and then grades into a substrate of schist.



Scale in Feet
Contour Interval 50 Feet

= Fairbanks Loess = Undifferentiated Silt

Fig. 2. Soil types and elevation of the study area.

There is no permafrost below this soil type.

Climate

Interior Alaska is a region of climatic extremes. The highest temperature on record in Fairbanks is 99°F. and the minimum recorded is -66°F. During the study the highest temperature recorded on the hare study area was 86°F. and the minimum temperature was -47°F. Weather Bureau records show that the mean annual temperature of Fairbanks is 26.1°F., and an average of 233 days per year have temperatures below 32°F. July is the only month in which no freezing temperatures have been recorded, but the temperature did drop to 34°F. on July 18, 1959.

The mean annual precipitation is 11.7 inches. Sixty-three per cent of the annual rainfall occurs between May and September. Snowfall averages 66.6 inches a year.

Table 1 shows the pertinent temperature and precipitation readings for the months in which the study was active as recorded by the U. S. Weather Bureau (1959). The Fairbanks weather is recorded at the Fairbanks International Airport which is located four and one-half miles southwest of the hare study area at an altitude of 436 feet above sea level.

Vegetation

Floral communities were determined by analyzing aerial photographs and by establishing sampling plots. The plots were used to sample the density, frequency and basal area of the trees and shrubs. Trees having a diameter of four inches or larger, two feet above the ground, were sampled with ten by ten

TABLE 1. TEMPERATURE AND PRECIPITATION READING FOR FAIRBANKS, ALASKA, FROM JUNE, 1959, TO FEBRUARY, 1960.

	Temperature (°F.)			Precipitation (In.)		
Month	Maximum	Minimum	Average	Total	Snowfall	Snow on Ground
June	86	34	61.5	1.19	0	0
July	80	35	55.5	2.80	0	0
August	82	33	54.5	1.81	0	0
September	62	26	43.6	0.92	T	0
October	49	-8	24.0	0.68	4.2	3
November	34	-23	6.7	0.55	12.1	10
December	21	-36	-9.5	0.56	12.1	17
January	36	-51	-3.8	0.97	23.6	36
February	31	-29	3.0	0.38	6.5	27

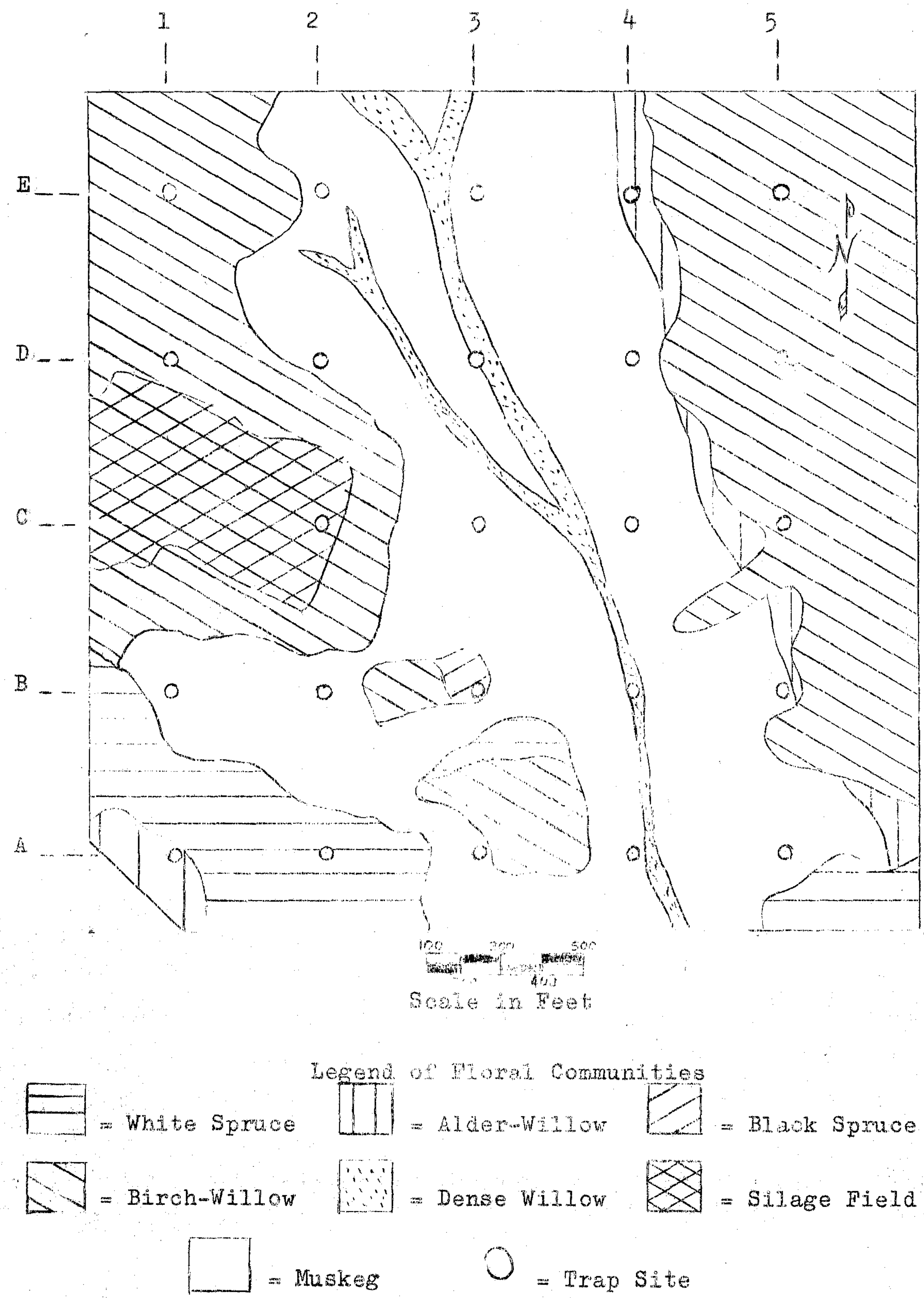


Fig. 3. Map of the trap sites and floral communities of the study area. The letters A to E and the numbers 1 to 5 are the grid lines.

TABLE 2. MAJOR VEGETATION COMMUNITIES OF AN INTERIOR ALASKA HARE STUDY AREA AND THE FREQUENCIES, DENSITIES AND BASAL AREAS OF THE SPECIES FOUND IN EACH COMMUNITY

Community	Mean values on four 10x10 m. plots*			Mean values on four 4x4 m. plots**		
	Frequency Per cent	Density	Basal Area (Sq. in.)	Frequency Per cent	Density	Basal Area (Sq. in.)
BIRCH-WILLOW						
Betula papyrifera	100	1	14.4	100	15	15.5
Salix spp.	100	4	72.0	100	9	12.3
Alnus fruticosa	--	--	--	100	4	6.4
WHITE SPRUCE						
Picea glauca	100	20	489.6	100	5	27.9
Salix spp.	--	--	--	100	1	3.1
ALDER-WILLOW						
Alnus fruticosa	--	--	--	100	22	34.3
Salix spp.	--	--	--	100	20	26.1
Picea glauca	--	--	--	50	1	0.8
Betula papyrifera	--	--	--	25	1	3.1

TABLE 2. (Continued)

Community	Mean values on four 10x10 m. plots* Frequency Per cent	Density	Basal Area (Sq. in.)	Mean values on four 4x4 m. plots** Frequency Per cent	Density	Basal Area (Sq. in.)
DENSE WILLOW						
Salix spp.	--	--	--	100	21	69.2
Picea mariana	--	--	--	100	2	1.4
BLACK SPRUCE						
Picea mariana	--	--	--	100	92	62.1
Salix spp.	--	--	--	100	13	1.9
MUSKEG						
Picea mariana	100	56	1,051.2	100	21	69.2
Salix spp.	--	--	--	100	39	7.1
Alnus fruticosa	--	--	--	100	3	16.1

*Plots of this size were used to sample trees with a diameter of 4 inches or larger.

**Plots of this size were used to sample shrubs with a diameter less than 4 inches.

meter plots. Smaller trees and shrubs were sampled with four by four meter plots. Four sample plots of each size were subjectively located in each of the six major vegetation communities. One four by four meter plot was set up in the northeast corner of each of the larger sampling plots. Herbaceous plants were not quantitatively sampled, but general observations were recorded to determine the relative distribution of certain species. The data gathered on the larger plots has been converted into the same units as the small plot data for the sake of clarity and comparison. Therefore, density figures given are expressed as the number of trees per 16 square meters. Basal area is expressed as the total cross-section area, in square inches per 16 square meters, of all trees measured two feet above the ground. Table 2 lists the densities, frequencies and basal areas of the species found in the six major vegetation communities.

The nomenclature of Hultén (1941-1950) is used in the following descriptions of vegetation.

On the well-drained sites birch-willow communities typical of Interior Alaska are found. Only one species of birch, <u>Betula papyrifera</u> Marsh, was found, but several species of willow, including <u>Salix arbutifolia</u> Pall., <u>S. arbusculoides</u> Ands., <u>S. bebbiana</u> Sargent, <u>S. glauca</u> L., <u>S. pulchra</u> Cham., <u>S. richardsonii</u> Hook. and <u>S. scouleriana</u>, occurred on the area. Most of the trees are less than four inches d.b.h. and few are over 20 feet in height. The birch have a density of 15 and a basal area of 15.5. The willow have a density of nine and a basal area of 12.3 square inches. Alder (<u>Alnus fruiticosa</u> Rupr.) were found in the birch-willow communities but they had

Fig. 4. Birch- willow community near trap E1.

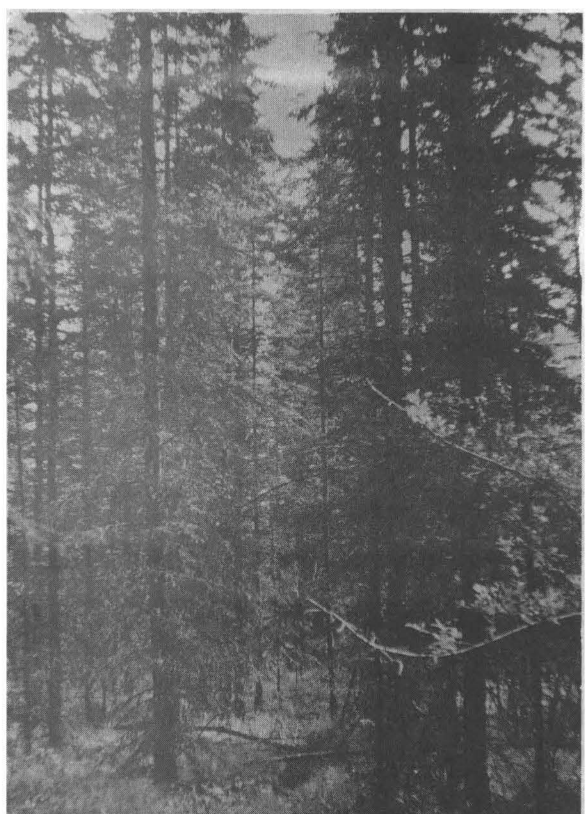


Fig. 5. White spruce community in the vicinity of trap A2.

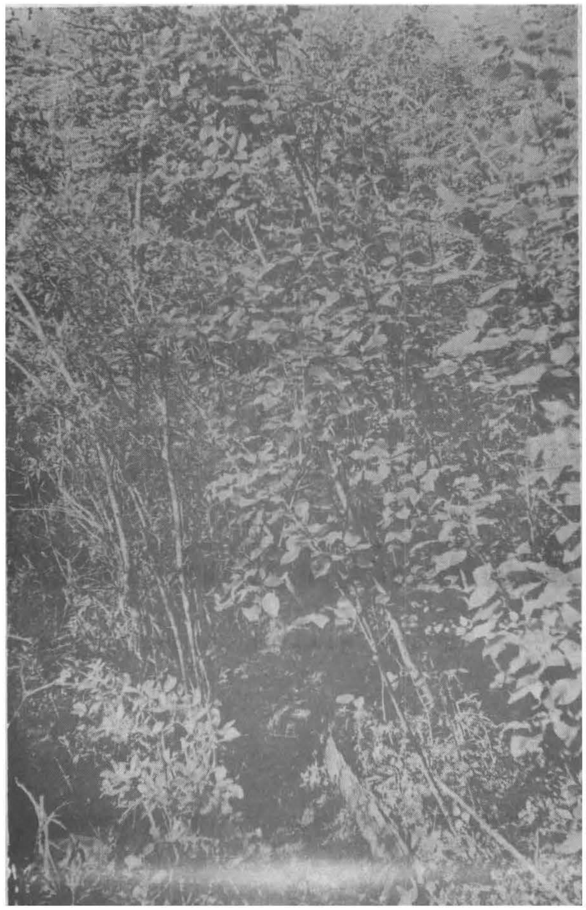


Fig. 6. Alder- willow community surrounding trap Al.

Fig. 7. Dense willow community bordering Pearl Creek.

a density of only four shrubs per 16 square meters and covered 6.4 square inches in basal area. The ground cover, which is the vegetation less than one foot high, consists of decaying leaves and a growth of horsetails (Equisetum arvense L.). The horse-tails had a density of about 25 plants per square foot (Fig. 4.).

On the southwest and southeast corners of the area are tall (40-60 feet) white spruce [Picea glauca (Moendr.) Voss] communities. Spruce with a diameter of four inches and larger have a density of three and a basal area of 489.6. Smaller white spruce have a density of five and a basal area of 27.9. Willow shrubs are rare in the spruce communities and have a density of one shrub per 16 square meters and a basal area of 3.1 square inches. The ground cover is sparse, consisting of a layer of mosses (Sphagnum spp.) and scattered lowbush cranberry (Vaccinium vitis-idaea L.) (Fig. 5.).

Alder-willow communities border the birch - willow and white spruce communities. The alder are seven to ten feet tall and have a density of 22 and a basal area of 34.3. The willow have a density of 20 and a basal area of 34.3 square inches. Small white spruce and birch are found scattered throughout 50 per cent and 25 per cent, respectively, of the community. Both trees have a density of one tree per 16 square meters. Mosses are the dominant ground cover in this community (Fig. 6.).

Bordering Pearl Creek is a community of dense willow. There are 112 willow shrubs per 16 square meters with a basal area of 56.6 square inches. Black spruce occur in the community with a density of 2. The ground cover characteristic of this community consists of mosses, blueberries (Vaccinium uliginosum L.),

Fig. 8. Muskeg community composed mainly of black spruce, willow and alder.

Fig. 9. A view of the silage field on the west border of the study area.

bearberries [Arctostaphylos uva-ursi (L.) Spreng], Labrador tea [Ledum palustre L. ssp. groenlandicum (Oeder) Hult.] and a few grasses and sedges (Fig. 7.).

Surrounding trap B3 is a community of low (3-8 feet) black spruce [Picea mariana (Mill.) B.S.P.]. The spruce have a density of 92 trees per 16 square meters and a basal area of 62.1 square inches. Interspersed among the spruce are 13 willow per 16 square meters. Mosses are the only ground cover in this community.

Almost one-half of the study area is a muskeg community of black spruce, willow and alder. Spruce with diameters of four inches and larger have a density of nine and a basal area of 489.6. The smaller spruce, willow and alder have densities of 21, 39 and 3 trees per 16 square meters respectively. The ground cover is almost entirely composed of mosses and the berries previously mentioned (Fig. 8.).

On the west border of the study area is a 10 acre silage field of grasses (Bromus inermis Leyss), [Agropyron repens (L.) Beauv.], [Calomogrostis canadensis (Michx) Beauv.] and (Hordeum jubatum L.). Figure 9 is a view of the silage field.

Mammals

Fifteen species of mammals were observed at various times throughout the investigation. The following is a list of the mammals on the hare study area that were potentially important in the ecology of snowshoe hares as food competitors or predators.

Moose (Alces alces Peterson). A cow and her two calves were seen three times in the willow along the creek.

Gray wolf (*Canis lupis* Miller). A pack of five wolves was sighted in the Goldstream Valley, less than one mile north of the study area.

Coyote (*Canis latrans* Say). Ludwig J. Rowinski reported seeing a coyote crossing Ballaine Lake, one mile south of the hare study area.

Red fox [*Vulpes fulva* (Desmarest)]. Alan Courtright observed a fox on the hare study area. Fox tracks and droppings were seen on five other occasions.

Dogs (*Canis familiaris* L.). At least four different dogs were known to frequent the study area.

Lynx (*Lynx canadensis* Kerr). Two lynx were live-trapped. One was tagged and released November 28, 1958; the other was collected for the University of Alaska Museum on April 29, 1959. Lynx tracks and scats were two of the most common mammal signs on the hare study area.

Mink (*Mustela vison* Schreber). A male mink was live-trapped at station E1 on September 24, 1959, tagged and released in the area. Mink tracks were seen on three other occasions and on December 16, 1959, a mink tried unsuccessfully to kill a snowshoe hare in live-trap A4.

Shorttail weasel [*Mustela erminea* (Merriam)]. Two weasels were seen during the study, and tracks were quite common.

Least weasel [*Mustela rixosa* (Bangs)]. Only four sets of tracks were seen of this species.

Black bear [*Euarctos americanus* (Pallas)]. A sow with two cubs was seen twice on the hare study area. On May 30, 1959, one of the cubs was live-trapped in a lynx trap and released unharmed. The sow ripped open trap A3 to secure the hare inside.

The hare study area was not visited by humans until three hunters were seen at the beginning of the hunting season. After the hare study area was posted as a research area the local sportsmen were very cooperative and hunted elsewhere. Cross-country skiers traversed the hare study area frequently, but the effect of their activities on the progress of the hare study is unknown.

Birds

There were many different species of birds frequenting the hare study area but only those related to the hare study as potential predators are listed. The nomenclature follows that of the American Ornithologists Union Checklist (1957).

Goshawk [*Accipiter gentilus* (L.)]. An adult and one juvenile were permanent residents of the hare plot and were seen eating rabbits four times.

Rough-legged hawk [*Buteo lagopus* (Pontoppioan)]. This species was seen several times over the area in April and May during their northward migration.

Great horned owl [*Bubo virginianus* (Gmelin)]. This species is a permanent resident in the College area. They are seen and heard regularly by residents of the small community just north of the area.

Great gray owl (*Strix nebulosa* Forster). Dr. William O. Pruitt, Jr. observed one approximately three miles southwest of the study plot.

Red-tailed hawks [*Buteo jamaicensis* (Gmelin)], Swainson's hawks (*Buteo swainsoni* Bonaparte), hawk owls [*Surnia ulula* (L.)], and short-eared owls [*Asio flammeus* (Pontoppidan)] have been observed in the College area and could be considered potential hare predators.

METHODS

Live-Trapping and Tagging

Live-trapping was carried out during the study to collect information on home range, population size and natural history. This technique was chosen because it permitted the gathering of information on all three objectives simultaneously.

Twenty-five trapping stations were laid out in a grid over the 160 acre section of land. Grid lines were 500 feet apart and those running in an east-west direction were lettered from A to E; the north-south lines were numbered from 1 to 5. Each station was labeled according to the grid lines that intersected it (*e.g.* A3, C2, etc.). All trapping locations were accessible by a blazed, lightly cleared trail.

Collapsible, double-door National Live Traps, measuring 9 x 9 x 32 inches were covered with two burlap bags and placed in the most likely looking hare habitat within a 50 foot radius of the grid intersection. All traps were placed in well-used runways and covered with moss (Figs. 10 and 11). Funnels were constructed of logs, sticks, and moss to guide hares toward the traps and to prevent them from avoiding the traps or hopping over them.

Willow leaves and twigs were used for bait during the summer even though it was discovered that unbaited traps were as successful in capturing hares as were baited traps. The willow leaves also provided food for trapped animals. It was necessary to substitute alfalfa hay for *Salix* during the fall and winter. Hay was chosen as bait rather than apples, oatmeal, lettuce, etc., because the hay did not attract rodents capable of debaiting

Fig. 10. Trap D5. Notice the twig funnel and the moss covering the trap.

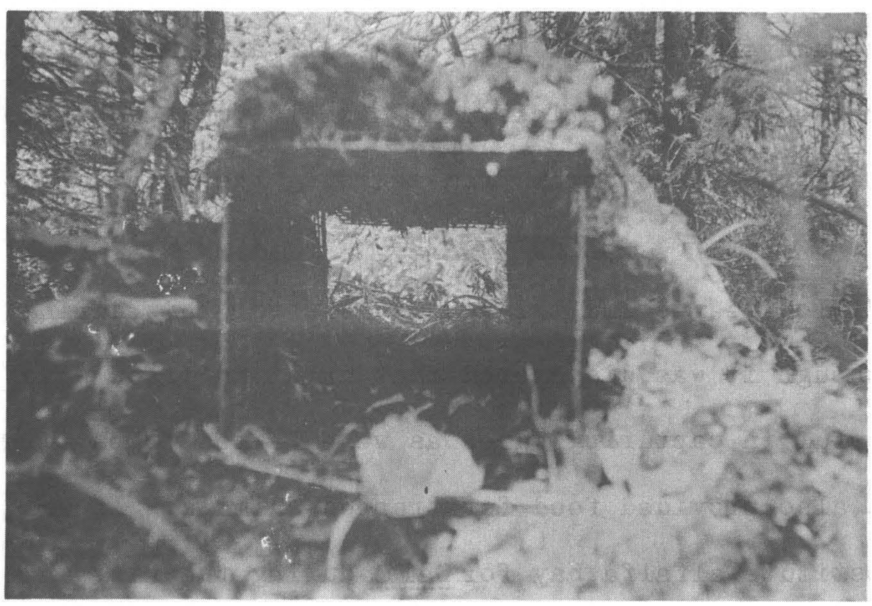


Fig. 11. Hare view of trap C3. The only clear trail is through the trap.

and springing traps.

All traps, except C1 which was in the middle of a silage field and was never frequented by hares, were in daily operation. The traps were checked as early in the morning as possible, usually between 8:00 a.m. and 10:00 a.m. Several trips were made to the area in the evening to see if it was necessary to check the traps at night, but no hares were caught in the evening so a nightly check was deemed unnecessary. When it was necessary to suspend trapping, trap doors were wedged open to permit hares to frequent the traps without being captured.

Captured animals were removed from traps by quickly thrusting an arm in the trap and firmly grasping the hare's hind feet (Fig. 12.). This procedure had to be performed quickly because the hares became belligerent in the traps and were capable of inflicting cuts and scratches. After removal from the trap the hare was placed in a burlap bag and weighed to the nearest ounce with a 4 pound capacity Chatillon spring scale (Fig. 14.). The burlap bag was weighed after each capture so the actual hare weight could be determined. A National Band and Tag style 1005 number 3 monel metal ear tag was placed on the lower outside edge of each ear by means of a special pair of pliers (Fig. 15.). Printed on one side of the tags were the letters FWS (Fish and Wildlife Service) which designated the tagging agency. Each tag was numbered consecutively for identification purposes. Figure 13 shows the tagging and measuring tools used during the study.

Loss of tags was at a minimum as evidenced by the fact that only two retrapped animals had lost one of their original tags. One hare was captured a year later and both tags were intact

Fig. 12. Removing a snowshoe hare from trap A4. The legs are grasped close to the body to prevent jerking and escape.

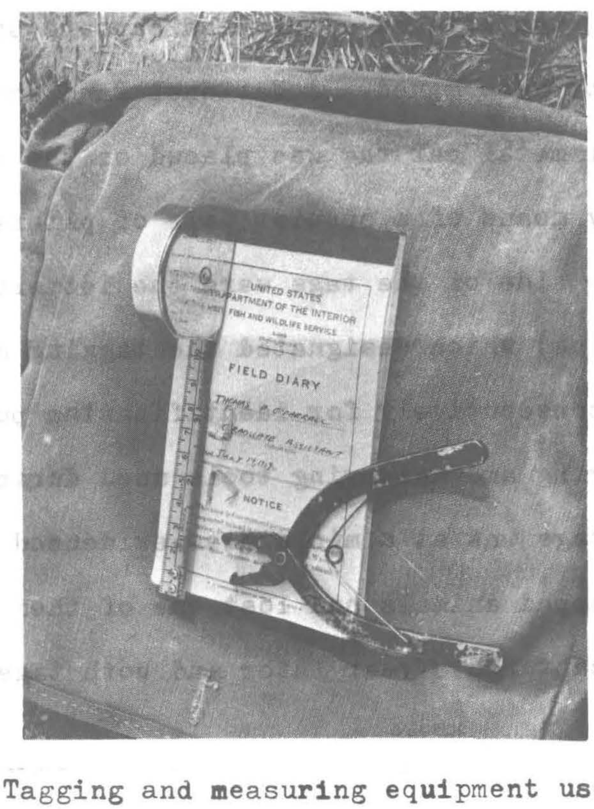


Fig. 13. Tagging and measuring equipment used in the Alaska hare study.

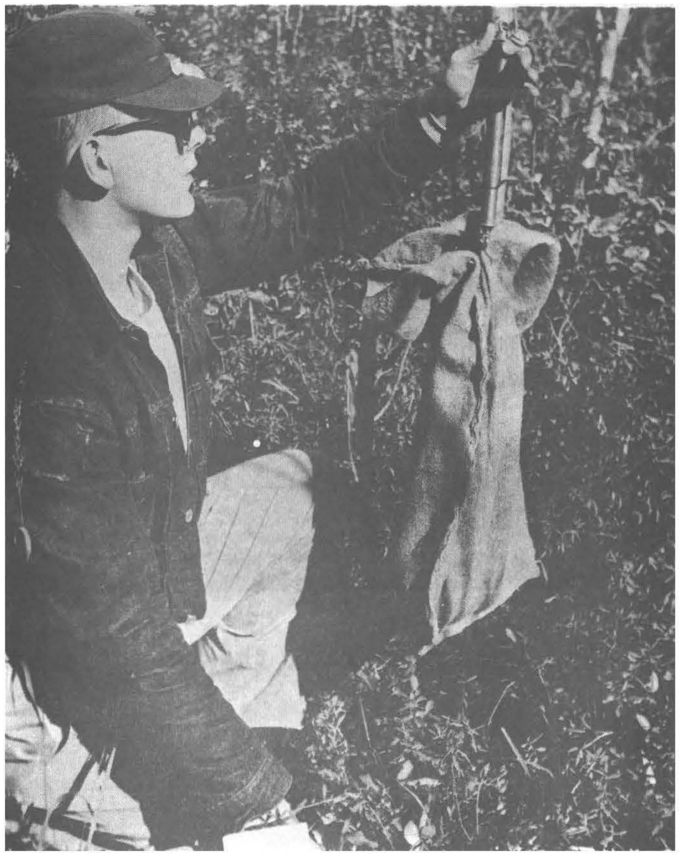


Fig. 14. Weighing a hare on a spring scale.

Fig. 15. Tagging a snowshoe hare.

Fig. 16. Measuring the ear of a hare.

Fig. 17. Taking the hind foot measurements of a hare.

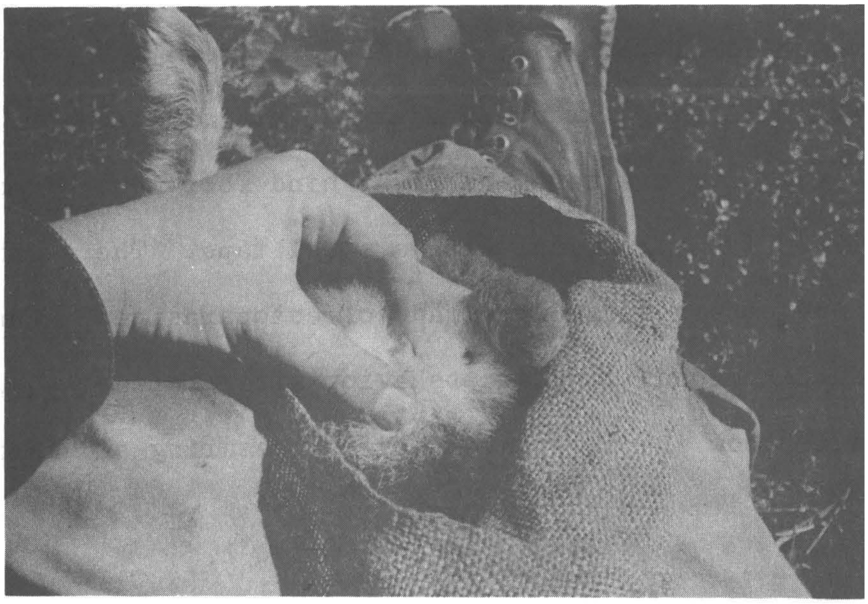


Fig. 18. Sexing a juvenile hare. The skin around the genitals is stretched to aid in observations.

Fig. 19. A juvenile snowshoe hare--tagged, measured and ready to be released.

and secure. In no case was there any indication that the tags caused infection.

After tagging, standard measurements of the ear from the notch, ear from the base and right hind foot length were taken to the nearest millimeter with a steel tape. The rabbit was sexed and observations were made of ectoparasites, abnormalities, reproductive condition, and behavior after release. Figures 16, 17 and 18 show the procedure used in measuring and sexing the hares.

Census Methods

The second objective of this study was to test various hare census methods to determine which techniques were usable in Alaska. Because this phase of the investigation was secondary, only five methods were attempted with varying degrees of success.

Track Count

Since snow covers the region for almost eight months, it was logical that the first census index to try was the track count method. While the traps were being checked, all snowshoe hare trails were counted and listed on a chart. It soon became apparent that the track count would not work well without more investigation and modification. After a fresh snow almost no hare trails were observed on the plot. Two days after a snow, barring cold weather, the hares were so active that the trails and runways were too well-used to permit an accurate count of the number of individual trails. In a population low, the track-count index might be useful, but as the population grows this census method seems to become less practical.

Pellet Count

MacLulich (1937) described how pellet counts may give an index of hare population size. This technique was tried after the last litter of 1959 had become active. Twenty circular one-ten-thousandth (1/10,000) acre sampling units were placed along the trails on the plot. Each sampling unit had a stick in the center with a string 1.2 feet in length attached to facilitate describing the one-ten-thousandth of an acre when sampling. None of the sample plots had pellets deposited on them during the winter. Upon investigation it was noted that the only place that hare pellets were found was under logs and in old forms. The hares did not seem to randomly deposit their droppings as other investigators had stated (Adams, 1959). Frequent snowfalls also hindered the collecting of pellets during the study and possibly some of the droppings were buried.

Strip Census

Webb's (1941) modification of the King strip census was carried out daily, from October, 1959, to January, 1960, using the trails through the plot as sampling strips. As noted by Seton (1953) and Adams (1959), snowshoe hares tend to "freeze" rather than flush when approached and because of their protective coloration they are almost undetectable. It was this freezing tendency that rendered Webb's method unfeasible. The greatest number of hares seen in any one day was three, and that was after a week of no hare sightings in the summer, when the population was at its highest level. This method requires further study to determine its usefulness in Alaska.

Calendar Graph

Adams (1959) correlated his trap-retrap and pellet count census estimates with a chart which he described as a calendar graph. On this graph he plotted all of the hares captured and recaptured against the periods in which he trapped. By extrapolating from dates when hares were known to be alive, he estimated the population by totaling all the hares present on a certain date. His use of an island as a study area, coupled with a very high recapture percentage, made the calendar-graph method quite workable under the circumstances. Unlike the work of Adams, however, this study was carried out in an area where immigration and emigration could have occurred. After plotting a calendar-graph for an Interior Alaska hare population, it was obvious that errors were introduced by movements, mortality and births and the chart was usable only as an index to the minimum population.

Trap-Retrap

Trap and retrap data lend themselves to analysis by the Lincoln Index (Lincoln, 1930) and the Schnabel Method (Schnabel, 1938). These methods are subject to bias from many sources as Scattergood (1954) has pointed out, but they were the best means available to determine the population level on the hare study area. Both methods entail tagging individuals during a pre-census period and then capturing them, both tagged and untagged, during a census period. The Lincoln Index gives an estimate of the population size during the census period only whereas the Schnabel Method gives both daily and total population estimates.

Observation

To compile natural history of hares in Alaska observations of snowshoe hares and their activities were kept in a daily diary throughout the field studies. This information was supplemented with observations of hares kept in captivity.

An attempt was made to mark hares with colored plastic strips to aid in observations. Three hares were marked by crimping 1 inch by 0.5 inch plastic strips to their ears with the ear tags. One hare was captured two months later with both plastic tags missing and the metal tags intact. A second color-marked hare was trapped one year later and had both metal tags but no plastic tags. The plastic used was apparently too brittle for color-marking purposes. Vinyl 0.010 in. thick was used.

To aid in observing the hares seen after the fall molt, 12 hares were sprayed with orange "Day Glo" paint. Because of the wetness of the snow, however, the paint remained vivid for three or four days and then faded rapidly. It appeared that spray painting of hares was impractical for long-term observation use.

Estimation of Home Range

Burt (1953) considered home range to be the area over which an animal travels in its daily activities. In this study, however, home range was considered to be the total area frequented by a snowshoe hare during the ten months of trapping because data were lacking to calculate home ranges for shorter periods of time. Burt (1953), Blair (1941), Hayne (1949), Davis (1953 and 1956) and Stickel (1954) are only a few of the authors who have either described a new method of determining home range, or have evaluated the present techniques. Basically all of the techniques for determining home range are modifications of a trap-retrap method.

To approximate the home range for snowshoe hares in Interior Alaska a modification of the boundary inclusive method of Blair (1941) was used. To calculate home range using this method the points of capture for each hare are plotted on a map of the study area and connected by straight lines. Then a boundary strip equal to one-half the distance to the next trap is drawn around the connected capture points. The area within the geometrical figure drawn is considered to be an approximation of the true home range. A boundary strip width equal to one-half the distance to the next trap is arbitrarily used because the true distance moved by an animal around a trap is unknown. Blair (1941) believed that if the movements around a trap could be plotted, the mean distance would probably be equal to half the distance to the next trap. This method assumes that home range is beyond the trapping stations since only a few animals will have a range coinciding exactly with the pattern of trapping. This method accepts the presence of traps in the home range that are not visited since an animal probably never gets a chance to be captured in every trap within its range. Hayne (1949) considers Blair's method to be entirely objective.

RESULTS

Population Estimate

The capture data gathered were analyzed by the Lincoln Index, the Schnabel Method and the calendar-graph. Each month was treated as a separate trapping period. The first two weeks of each month were considered the trapping period, and the last two weeks of the month were considered the sampling period for each census technique. Monthly population estimates based on the three methods were made to determine the population trends.

Both the Lincoln Index and the Schnabel Method give inflated population estimates when recruitment is occurring because some hares are nursing during the trapping period and become active during the census period, thus biasing the sample. Conversely, the calendar-graph method underestimates the population during recruitment since it is merely a count of the actual animals handled. It took eight months, from June to December, 1960, to tag enough of the population so that 90 per cent of the captures were tagged hares. Undoubtedly during the eight month period a number of hares, both adults and juveniles, died before being handled and consequently were not entered on the calendar-graph. Since recruitment occurred throughout five months of the study, actual population size was probably between the inflated estimates of the Lincoln Index and the Schnabel Method, and the minimum estimate of the calendar-graph. Table 3 shows the monthly population estimates as calculated by the three indices.

Confidence limits were calculated for the Lincoln Index and Schnabel Method population estimates and they are shown in Table 3. The confidence limits are very wide because recruitment

TABLE 3. ESTIMATES OF THE HARE POPULATION SIZE ON A 160 ACRE INTERIOR ALASKA STUDY AREA DURING 1959-1960.

Month	Calendar Graph	Schnabel Method	95 per cent Confidence Limits	Lincoln Index	95 per cent Confidence Limits
June	80	155	0, 562	155	0, 610
July	85	85	0, 953	130	0, 1,113
August	85	230	0, 695	255	0, 710
September	85	210	0, 674	240	0, 690
October	50	180	0, 621	215	0, 636
November	25	55	10, 93	55	11, 105
December	15	16	7, 25	16	5, 22
January	5	8	0, 19	8	0, 16
April	50	36	12, 54	68	42, 94

was occurring, the sample sizes were small and the recapture percentage was not high enough to achieve statistical accuracy. The population estimates are listed in spite of the poor confidence limits so that some idea of the population size can be determined. During June the hare population was between 80 and 155 animals. The actual population size was probably closer to 80 animals since recruitment was inflating the estimate of 155 hares. In July the population was estimated to be between 85 to 130 hares and in August between 85 and 255 hares. The September estimates showed between 85 and 240 hares, and in October there were between 50 to 215 hares.

Recruitment, which was occurring when trapping operations began in June, ceased in August, but three more months were required to tag the greater part of the population. When 50 per cent of the hares captured were recaptures in November, 1959 (Fig. 21.), all three population indices agreed more closely in their estimates of the population size. By November the hare population estimate had dropped to 25 to 55 animals. The decline in population size continued throughout December and January. According to the indices there were 15 to 20 rabbits in December, and by January the population was down to between 5 and 10 hares. Trapping records during April, 1960, however, indicate that the low population estimates from November, 1959, to January, 1960, were partially biased by the poor trap response of hares during the winter. For example, during January, 1960, only five different hares were captured on the study area. In April, 1960, 50 hares, including 16 untagged hares, were captured on the study area. Only two of the tagged hares had been trapped in January. It is evident, therefore, that there were at least 32 tagged hares on the hare study area in January that were never recaptured during that month. A closer estimate of the minimum population during January, 1960, is 37 hares if the number of hares captured during January is added to the number of untrapped hares known to have been on the study area during that month.

Capture data gathered during April, 1960, was analyzed in the same manner as the data of the previous months. The population size was estimated to be between 36 hares (Schnabel Method) and 68 hares (Lincoln Index). The calendar-graph estimate was 50 hares on the 160 acre study area.

The estimated population size indicated that the hare population being studied was probably in the lower part of the ascending leg of the cycle. During the four month orientation period in 1958, only 17 hares were captured indicating that the population size was growing steadily in 1959.

<u>Calculation of Home Range</u>

During this investigation 72 hares (44 males and 28 females) were recaptured a total of 177 times. The recapture data obtained (Table 4.) for each hare were plotted on a map of the area and consecutive recaptures were connected by straight lines (Fig. 20.). Traps were located 500 feet apart so a 250 foot boundary strip was added around the points of capture. The area contained within the boundary strip around each trap was equal to 5.7 acres. To approximate home range the number of squares equal to 5.7 acres that a hare was captured in were

TABLE 4. RECAPTURE DATA COLLECTED FROM APRIL, 1959, TO APRIL, 1960, ON A 160 ACRE SNOWSHOE HARE STUDY AREA IN INTERIOR ALASKA

No.	Sex	Date	Trap No.
2137	M	4/21/59	A3
		6/18	B4
		4/24/60	A2
2139	F	5/20/59	A4
		4/26/60	B4
2149	F	6/18/59	E3
		8/ 8/59	E3
2153	M	6/19/59	C5
		1/ 1/60	B1
		1/16	B1
2157	M	6/20/59	C2
		4/10/60	D2
		4/12	C2
		4/15	C3
2159	M	6/20/59	C5
		11/ 9	C5
		4/10/60	D5
		4/15	C4
		4/20	D5
		4/21	C4
		4/25	C4
		4/28	C4
2161	M	6/21/59	C2
		7/17	D1
2165	M	6/24/59	C4
		6/29	C4
2169	M	6/25/59	E4
		4/24/60	E5
2171	M	6/26/59	C4
		7/18	C4
		4/18/60	D4
2173	F	6/27/59	A1
		7/25	B2
2177	M	6/28/59	B4
		7/16	B4
		4/16/60	B4
2179	M	6/28/59	C3
		7/ 3	C4
2183	F	6/29/59	B3
		8/17	B1
		4/ 9/60	D2
2187	M	6/29/59	C3
		7/ 9	C3
2189	F	6/29/59	D4
		7/ 7	A1
		7/16	B2
		7/19	B2
		7/22	B2
		7/31	A1
		10/21	A1
		10/30	B2
2191	M	6/30/59	B3
		7/ 9	B3
2193	F	7/ 3/59	C3
		7/25	E2
		10/ 1	E2
2195	F	7/ 3/59	D2
		7/18	D1
		10/15	D1
2197	M	7/ 5/59	B3
		4/26/60	B5
2501	M	7/ 7/59	B3
		4/20/60	D4
		4/22	D4
2503	M	7/ 7/59	E1
		4/ 9/60	E2
2505	F	7/ 9/59	A3
		4/19/60	B4
2507	M	7/17/59	B3
		8/ 1	B3
		4/13/60	B2
		4/17	C2
		4/21	B2
		4/26	B2

TABLE 4. (Continued)

No.	Sex	Date	Trap No.
2511	F	7/18/59	A3
		11/11	A4
2519	F	7/19/59	E1
		10/30	E2
		11/ 6	E1
		11/12	E2
2523	F	7/25/59	B1
		8/ 6	B1
2525	F	7/25/59	D4
		7/30	D4
		9/23	D4
		9/30	D4
		4/19/60	D4
		5/ 1	D5
2533	M	7/31/59	D4
		11/ 3	D4
		11/10	D4
		11/26	D4
		11/27	D4
2539	M	8/ 3/59	C4
		10/21	B5
2541	F	8/ 6/59	B4
		1/30/60	D5
2545	M	8/ 7/59	B2
		12/16	A1
		4/16/60	A2
		4/19	A2
		4/22	B2
2551	M	8/ 8/59	C4
		11/10	B3
2557	F	8/ 9/59	D4
		10/22	D3
		4/16/60	D3
		4/19	D3
		4/23	E5
2563	F	8/10/59	D2
		10/ 4	B3
2565	M	8/13/59	D3
		4/21/60	E4
2577	M	8/15/59	E3
		11/25	D3
2579	F	8/16/59	B1
		4/10/60	B2
2581	F	8/16/59	C4
		10/26	C5
		10/30	C4
2587	M	8/17/59	D1
		4/12/60	D2
		4/16	E3
		4/23	E4
2597	F	9/22/59	D5
		10/13	D5
2603	F	9/23/59	A1
		10/29	A4
2607	F	9/23/59	B4
		12/30	A1
		1/ 3/60	B4
		1/ 6/60	A4
2611	M	9/30/59	C4
		4/14/60	B4
		4/20	C5
		4/22	C5
		4/23	B4
2613	F	9/30/59	E3
		12/24	E3
		12/29	E3
		1/ 1/60	E3
		1/ 4	E3
		1/ 7	E3
2617	M	10/ 5/59	C2
		4/22/60	C2
2627	F	10/12/59	C5
		4/23/60	A3
2629	F	10/13/59	B3
		11/13	B3
		4/25/60	B3

TABLE 4. (Continued)

No.	Sex	Date	Trap No.
2637	M	10/15/59	C2
		4/12/60	D3
		4/13	E5
2645	M	10/27/59	B3
		12/10	B3
		12/14	B3
		4/ 9/60	C3
		4/12	B3
		4/13	C3
		4/19	B3
		4/20	C2
		4/23	C3
		4/26	B3
2651	M	10/29/59	A5
		11/ 3	A5
		11/24	A5
2655	M	10/30/59	A4
		11/ 3	A4
		11/23	A4
		11/27	A4
		4/ 9/60	A4
		4/14	A4
		4/15	A2
		4/16	A4
		4/19	A4
2657	M	11/ 3/59	C4
		12/ 8	C4
2659	M	11/ 3/59	D5
		11/ 5	C4
2663	M	11/ 4/59	B3
		11/ 9	C3
		12/13	C2
		12/26	C2
		12/30	C2
		12/31	C3
2669	M	11/ 5/59	D1
		4/13/60	D1
		4/15	D2
		4/25	D2
2671	M	11/ 6/59	B5
		4/13/60	A5
		4/17	B4
		4/21	A5
2677	M	11/10/59	E2
		4/21/60	E1
2685	F	11/24/59	D1
		4/21/60	D2
2693	M	12/16/59	A4
		12/28	A2
		12/30	A4
		4/12/60	A4
		4/13	A2
		4/18	A3
		4/22	A3
2695	F	12/24/59	A2
		12/31	A1
		1/ 2/60	A1
		4/18	A2
2697	M	12/24/59	A5
		12/27	A5
		12/31	A5
		4/ 9/60	A5
2699	M	12/25/59	A3
		12/29	A3
		4/11/60	A3
		4/21	A2
		4/23	A2
2703	M	1/26/60	D1
		4/19	D1
2711	F	4/18	C3
		4/19	C2
		4/20	C3
		4/22	C3
		4/24	C3
		4/29	C3
2718	M	4/13	E3
		4/14	D3
		4/17	E3
		4/18	D3
		4/20	E3
		4/23	E3
2720	M	4/13	C5
		4/18	C5
		4/24	C5
		4/25	C5

TABLE 4. (Continued)

No.	Sex	Date	Trap No.
2722	M	4/13/60	C4
		4/17	C3
		4/18	C4
		4/21	C3
		4/24	C4
2728	M	4/24	E4
		4/27	E5
2732	F	4/26	C4
		4/27	B3
		4/30	C5
2734	M	4/26	E5
		4/28	E4
2738	F	4/28	C5
		4/30	C4

summed. This procedure was repeated for each hare, then an average home range was calculated mathematically for each sex. Since adults and juveniles could not be distinguished with certainty, no attempt was made to calculate separate home ranges for adults and juveniles. The recapture data gathered during April, 1960, were included in the calculation of home range size for the duration of the study. The April information was also treated separately to estimate the size of the home range during the early breeding season. During April, 1960, 26 hares (20 males and 6 females) displayed an approximate home range.

The estimated average home ranges for snowshoe hares in Interior Alaska were 11.8 acres for males and 13.0 acres for females. The approximate home ranges during the early breeding season were 12.5 acres for males and 12.4 acres for females (Table 5.). The calculated home ranges for both sexes during the two periods did not vary significantly from each other indicating that both male and female hares have a similar home range size.

The distance moved during the 177 recaptures were tabulated to check the accuracy of the calculated home ranges. Table 6 shows the movements between recaptures of 72 hares.

Eighty-nine per cent of the recaptures were within 1,000 feet of the last capture indicating that hares do not usually move great distances. If 1,000 feet is considered the diameter of a circle, the area contained within the circle is eight acres. This figure of eight acres implies that the trap indicated home range closely approximates the actual home range.

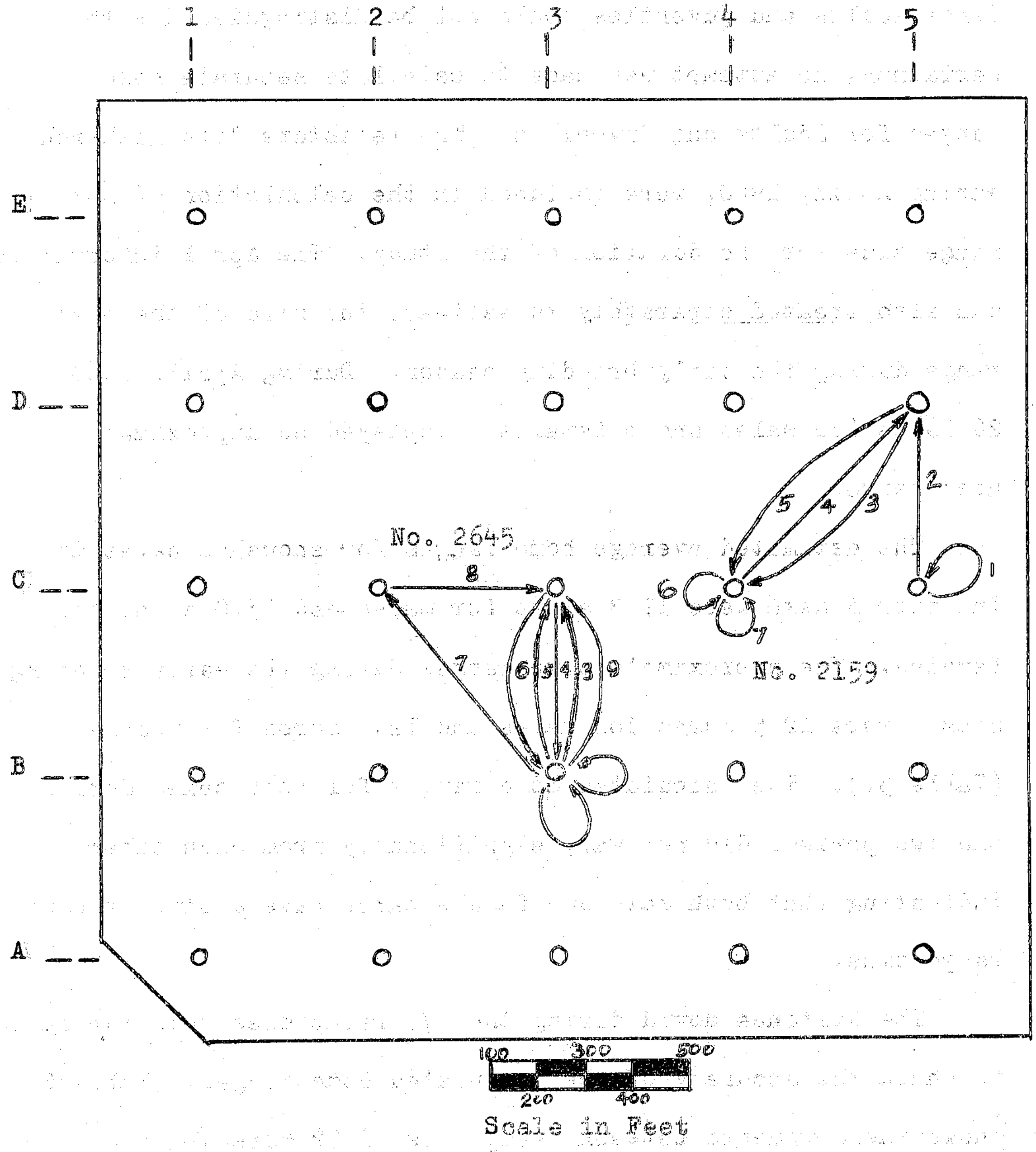


Fig. 20. Home range movements of hares 2159 and 2645 on the Interior Alaska study area. The lines of movement are numbered consecutively in the order of their occurrence between recaptures. These home ranges were chosen because they displayed the most typical home range shape.

TABLE 5. ESTIMATED HOME RANGES OF SNOWSHOE HARES IN INTERIOR ALASKA BETWEEN APRIL, 1959, AND APRIL, 1960.

	ENTIRE STUDY			EARLY BREEDING SEASON		
Sex	No.	Home Range (Acres)	95 per cent Confidence Limits	No.	Home Range (Acres)	95 per cent Confidence Limits
Male	44	11.8	2, 21.6	20	12.5	7.3, 17.7
Female	28	13.0	2, 24.0	6	12.4	3.2, 21.6

Further evidence that snowshoe hares do not usually move great distances and hence have small home ranges was gathered during the April, 1960, trapping period. Eight hares, five males and three females, were recaptured that had been tagged as adults during 1959 and were therefore at least two years old in 1960. The three females were recaptured at 0, 500 and 750 feet, respectively, from their initial capture point. One male was recaptured in the same trap while the other four males had moved only 500 feet from their last capture points. This evidence indicates that adult hares remain within a small area even over long periods of time.

Seton (1928) estimated the home range of snowshoe hares as 20 or 30 acres in brushy woods. Grange (1932a) pursued a hare and could not force it out of an area of about 10 acres, and he believed that this indicated the home range size. Adams (1959) calculated the home ranges for adult male and adult female hares in Montana. He found that the male home range was 25.2 acres and that of the female was 18.9 acres. The home range sizes calculated during this study vary significantly only from Seton's high estimate of 30 acres and Adams' estimate of 25.2 acres for adult males.

Neither male nor female home ranges during April were significantly different from the yearly home range estimates (Table 5.). This seems to indicate that the hares do not increase the size of their ranges during the early breeding season. Hares apparently increase the use of their home range and become more active during the breeding season. This increased activity is shown by the fact that of 34 hares captured during the winter and

TABLE 6. DISTANCES MOVED BETWEEN 177 RECAPTURES OF 72 SNOWSHOE HARES IN INTERIOR ALASKA

Distance Moved (Feet)	Number	Per cent of Total
Less than 500	75	42
750	61	34
1,000	23	13
1,075	7	4
1,100	3	2
1,400	1	0.6
1,450	1	0.6
1,500	1	0.6
1,575	1	0.6
2,075	2	1.0
2,250	2	1.0
2,300	1	0.6

and the breeding season, only 28 recaptures were recorded for the rest of the year, but during the breeding season the 34 hares were retrapped a total of 75 times.

Natural History

The life history of the snowshoe hare has been studied and described by Seton (1928), Grange (1932a), Aldous (1937) and Severaid (1942). The objective of this section is to review those facets of the hare's natural history which were observed during this study. The data in this section were collected through live-trapping, observations in the field and rearing three hares in captivity.

Trap Response

One of the first things learned about the hares was that they were more "trap-shy" than anticipated. Although great care was taken in the trapping procedures, very few hares were caught per unit of effort (trap night). Trapping success can be expressed in percentage form as the ratio between the number of hares caught and the amount of effort expended in catching them.

During the study 348 hares including retraps were captured in 4,098 trap nights for a trapping success of 8.4 per cent. From June to September the monthly trapping success ranged from 11 per cent in June to a high of 16 per cent in September. In the fall and winter months the trapping success dropped slowly from eight per cent in October to a low of two per cent in January. Only one hare was captured in 168 trap nights during the first two weeks in February, and because of the small sample during the month, no calculations of trapping success were made. During April, 1960, the trapping success was 20 per cent.

Recapture success may be defined as the proportion between the total number of hares captured during a given period and the

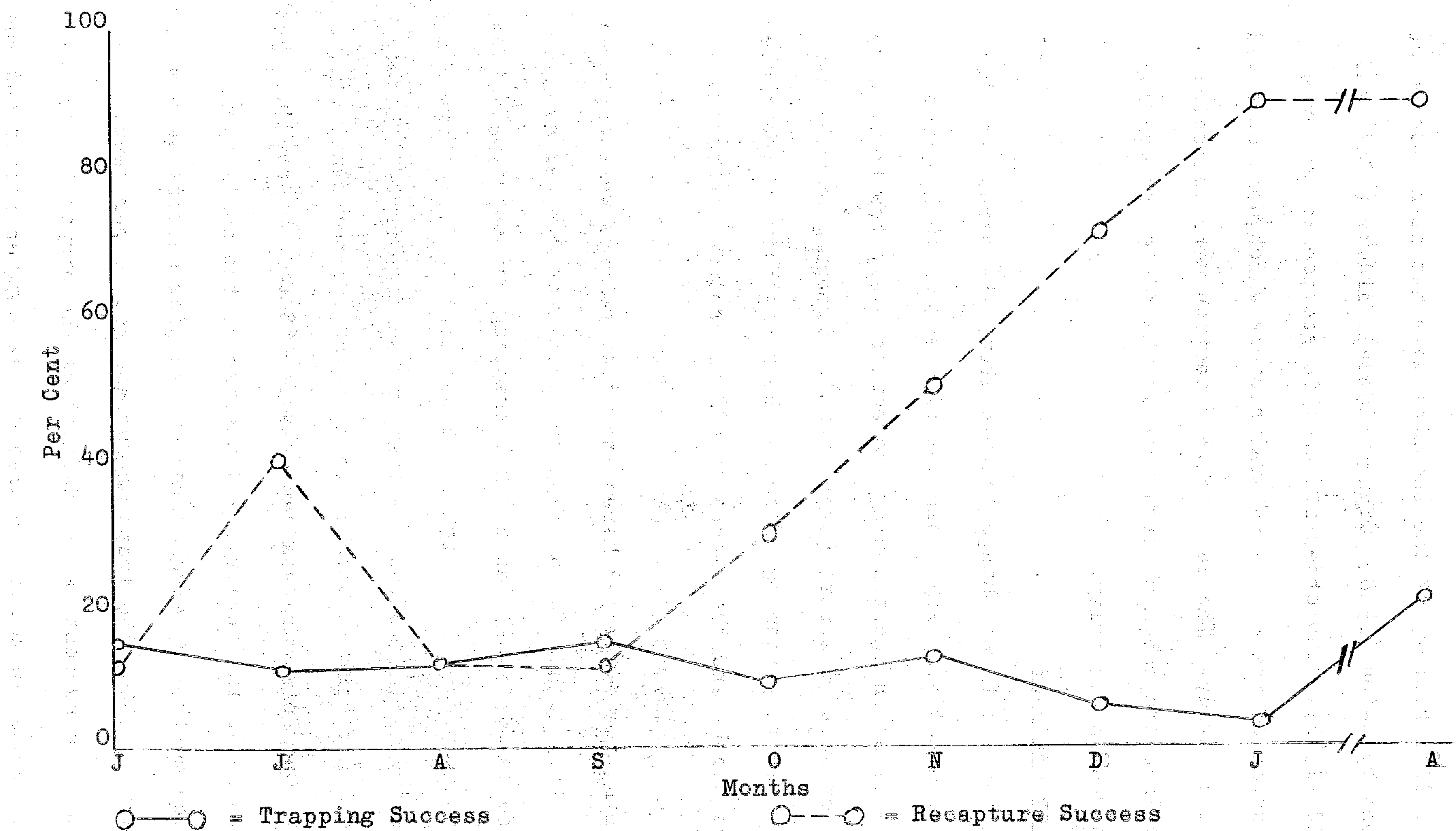


Fig. 21. Graph of trapping success and recapture success for an Interior Alaska hare study.

number of tagged hares in the total expressed in percentage form. Eleven per cent of the hares trapped in June, 1959, were recaptures. Recapture success rose to 42 per cent in July, probably due to the fact that most of the juveniles born in May and June were tagged during the two months of trapping. As more juveniles, born probably in late June and July, became active during August, the recapture success dropped to 12 per cent in August and September. The per cent of recaptures rose steadily from September to January when 89 per cent of the hares captured were tagged. During the April, 1960, trapping period the recapture success was also 89 per cent. The high recapture percentage during the last months of the study indicated that a large proportion of the hares on the study area were tagged. Figure 21 is a graph of trapping success and recapture success during this study.

A great part of the poor trapping success was due to the low level of the population, but at least some of the poor results can be blamed on trap-shyness. During the summer it was impossible to tell if hares that approached traps were usually captured or not, but on several occasions hares were seen regularly within 10 to 75 feet of traps that they did not enter. After the first snowfall notes were taken on any trap that was approached and avoided by hares. Throughout the winter at least four to five different traps were visited daily and avoided by hares. Several times hares came up to the trap entrances and then either leaped over the trap or hopped around the wooden barriers and snow covering the trap. The hares even avoided traps that presented the best path through an area of dense vegetation.

This trap-shyness on the part of hares can be explained in at least two ways. First, it can be assumed that the hares eventually associated the traps with confinement, and handling and thus avoided the trapping stations, even in areas where they had never been captured before. Another assumption is based on the type of traps used. During cold weather beginning in November, the steel traps were quite cold when the air temperature dropped below 0°F., and the merest touch resulted in a contact burn. Possibly the hares avoided walking into the traps because of the cold metal floors and sides. The fur on the hare's feet is quite dense and undoubtedly it is good insulation, but at -30°F. steel is probably cold enough to repel hares. Wooden live traps should be experimented with to see if trapping success could be increased.

A total of 150 different hares, 84 males and 66 females, was captured during the study. This does not vary significantly from an even sex ratio, indicating that males and females were equally susceptible to being captured. April, 1960, was the only month in which the sex ratio showed any distortion. During that month 26 males and 12 females were captured. This difference is probably due to the increased activity of the males with the beginning of the breeding season.

Use of Runways

The surface vegetation in the snowshoe hare study area was covered by networks of hare runways, especially in the muskegs. These paths were used so often that in areas of moss and soft ground cover, the runways were beaten down one to two inches below the ground level.

When the early winter snows fell in October the hares made use of well-packed runways. The surrounding snow was so loosely compacted that the hares rarely ventured off the runways. One hare was cornered by the investigator at the edge of some fresh snow. After touching the loose snow with its feet, the hare chose to run only two feet from the observer rather than flounder in the snow. Single trails were seen early in the winter, but only rarely. As the snow throughout the area compacted, the hare trails were seen more often off the runways. In January single hare trails were seen all over the snow cover, and well compacted runways were rare. However, hares still used definite runways when crossing open areas from one stand of dense vegetation to another.

As the thaw commenced in April the density of the snow changed still further, and once again the hares used runways almost exclusively. It was interesting to note that traps placed on snow runways in the winter were found resting on well-used summer runways after the thaw. Hares probably follow certain summer paths even in the winter months when the snow cover offers numerous avenues of movement.

The fact that hares alternate in their use and disuse of runways depending on the quality of the snow is in agreement with Pruitt (1960:60) who stated, "But wherever the hardness and density of the snow fall below a critical level, the hare too turns to packing the snow to form regular trails and runways." Further investigations are needed to determine what levels of snow density and hardness cause the hares to use trails.

Early in the study it was believed that the investigator's packed trails would alter the movements of the hares by providing paths for them. Surprisingly the hares made little use of human trails, preferring to cross over rather than walk on them. The longest distance any hare moved down a packed trail was 30 feet. There are at least two possible reasons for this response to human trails. Perhaps the density and hardness of the trail were not to the hares' liking. Also the investigator's trails were usually 18 to 24 inches below the surface of the surrounding snow. A hare moving at that depth would be unable to view his surroundings and consequently would be vulnerable to sudden attack. Behavioral investigations may show that snowshoe hares move more freely in areas where they can view their immediate surroundings. The latter seems to be the more logical reason for hares avoiding man-made trails, but a final answer must wait for an investigation of the snow factors influencing snowshoe hare movements.

Shelter and Concealment

Instead of making use of holes or hollow logs for hiding and resting, snowshoe hares use areas called forms. A rabbit form is nothing but a location that a hare rests in. Forms are not constructed by the hares, no lining is built up and they may be used only once. During the summer all hare forms were found in the middle of dense clumps of low spruce or willow. Generally the hares were seen resting between four or five small tree trunks.

Two types of winter forms were recorded. The more widely used winter type was found under spruce, willow or alder trees that were bowed over by the weight of snow. A canopy of snow and branches was thus formed under which a hare was protected from the elements and predators.

Three snow forms of a type similar to those used by grouse and ptarmigan were found in December. The snow forms were depressions in the snow measuring 10 inches long, four inches wide and five inches deep. The walls of the forms were glazed with ice and guard hairs were found imbedded in the ice. No correlation was noted between the occurrence of snow forms and climatic conditions or vegetation.

Hares dug at least six holes in the snow during this study. Each hole was about three to four inches in diameter and from four to 10 inches deep. In every case the moss ground cover was exposed, but no clues were found to explain why the holes had been dug.

One hare dug burrows in the snow between and under the trunks of the alder in the area around trap A4. The tunnels underlaid an area of approximately 300 to 500 square feet. This was the only evidence that snowshoe hares do any burrowing, and in this case the digging was in snow, not dirt.

Escape Behavior

When danger threatened, hares reacted in several ways depending upon the age of the hare and the season of the year. It was noted that during the summer months juvenile hares would immediately "freeze" in their location when the investigator walked close by. The adult hares, however, would make a few short hops, remain motionless for a few seconds, hop 10 or 15 more feet and then freeze again. In this way the adults quietly glided out of sight without any quick movements to draw attention to them.

During the fall when the molt was occurring, and in the winter months when the snowy surroundings provided excellent cover, hares of all age groups remained motionless at the slightest hint of danger. Hares depended on this "freezing" technique so much that it was possible to walk within five feet of hares before forcing them to bound away. Upon release from the traps, the hares invariably ran 50 to 75 feet and then froze, only to move slowly away when the investigator changed position.

The only time of the year when the hares seemed conspicuous was during the early breeding season. Relatively more hares were seen from mid-March to June than during any other period of the year. During the breeding season the hares seemed to be moving all the time, and their movements made them quite noticeable.

Food Preference

Information on the food habits of hares was collected by observing hares eating on the plot; feeding all the types of vegetation that could be collected to a captive hare; and by noting feeding signs in the snow.

The summer food of hares probably includes most of the green vegetation in the area. Willow, birch, aspen and alder leaves and twigs were the most widely used summer foods. Undoubtedly water is obtained from eating the succulent vegetation since no hares were observed drinking water from the stream or rain ponds.

After the first snows the hares ate the dried grasses and any greens that were left exposed. When the snow covered all of the grasses and greens the hares began to eat the bark of willow and alder trees. They ate the seedlings of all trees down to the snow level, and ate the needles of black and white spruce. Blueberry and rose bushes (*Rosa acicularis* Lindl.) were browsed quite heavily. In four instances the hares dug blueberry bushes out of the snow to nibble on them. Several clumps of rose bushes were eaten down to the snow line, thorns and all. During the winter hares get their water by eating snow, and it was a common sight to see a hare scooping snow into its mouth with its teeth and tongue after being released from a trap.

A captive hare ate all the foods utilized by its wild counterparts and in general confirmed all field observations of hare food preference. It was interesting to note that in spite of a two-day starvation period a captive hare would not eat rolled oats -- a standard hare bait.

Cover Preference

Adams (1959) showed quantitatively that there was a close association between hares and cover. During this study the hypothesis was formed that if hares have a cover preference, they should be trapped more frequently in the preferred vegetative types. A monthly table was kept of the number of hares captured and the per cent of the monthly total of capture for each trap (Table 7.). A chi-square test was worked for each month and for the total trapping period to test the null hypothesis that there is no correlation between vegetation and the number of

TABLE 7. A LIST OF THE NUMBER OF CAPTURES FOR EACH TRAP ON THE INTERIOR ALASKA STUDY AREA, JUNE, 1959, THROUGH APRIL, 1960.

	June		July		Aug.		Sept.		Oct.		Nov.		Dec.		Jan.		Feb.		Apr.		Total	
Trap	C.*	P.**	C.	P.	C.	P.	C.	P.	C.	P.	C.	P.	C.	P.	C.	P.	C.	P.	C.	P.	C.	P.
A1	2	7	3	7	1	3	1	8	1	3	2	6	5	20	1	10	-	-	-	0	16	5
A2	-	-	-	-	-	-	-	-	-	-	-	-	2	8	-	-	-	-	9	8	11	3
A3	-	-	2	5	1	3	1	8	-	-	-	-	1	4	-	-	-	-	5	4	10	3
A4	-	-	1	2	1	3	1	8	2	6	5	15	2	8	1	10	-	-	5	4	18	5
A5	2	7	-	-	1	3	-	-	2	6	3	9	3	13	-	-	-	-	3	3	14	4
B1	2	7	5	12	3	8	1	8	2	6	-	-	-	-	2	20	-	-	-	-	15	5
B2	1	3	6	14	2	5	-	-	2	6	1	3	-	-	-	-	-	-	5	4	17	5
B3	3	10	5	12	2	5	-	-	3	9	3	9	2	8	-	-	-	-	7	6	25	8
B4	3	10	3	7	1	3	1	8	-	-	-	-	-	-	1	10	-	-	5	4	14	4
B5	-	-	-	-	-	-	1	8	1	3	2	6	-	-	-	-	-	-	3	3	7	2
C2	2	7	-	-	1	3	-	-	1	3	-	-	3	13	-	-	-	-	5	4	12	4
C3	1	3	2	5	3	8	-	-	1	3	2	6	1	4	-	-	-	-	10	9	20	6
C4	4	13	2	5	3	8	1	8	1	3	2	6	1	4	-	-	-	-	9	8	23	7

TABLE 7. (Continued)

Trap	June C.*	June P.**	July C.	July P.	Aug. C.	Aug. P.	Sept. C.	Sept. P.	Oct. C.	Oct. P.	Nov. C.	Nov. P.	Dec. C.	Dec. P.	Jan. C.	Jan. P.	Feb. C.	Feb. P.	Apr. C.	Apr. P.	Total C.	Total P.
C5	1	3	1	2	1	3	-	-	3	9	1	3	1	4	1	10	-	-	8	7	17	5
D1	-	-	1	2	1	3	-	-	-	-	2	6	-	-	1	10	1	100	3	3	9	3
D2	-	-	4	10	1	3	1	8	1	3	-	-	-	-	-	-	-	-	7	6	14	4
D3	1	3	3	7	2	5	-	-	3	9	1	3	-	-	-	-	-	-	5	4	15	5
D4	2	7	2	5	4	11	2	15	2	6	5	15	-	-	-	-	-	-	5	4	22	7
D5	-	-	2	5	-	-	1	8	1	3	1	3	1	4	-	-	-	-	3	3	9	3
E1	1	3	2	5	1	3	-	-	1	3	1	3	-	-	-	-	-	-	2	2	8	3
E2	1	3	1	2	2	5	-	-	3	9	2	6	-	-	-	-	-	-	-	-	9	3
E3	2	7	-	-	4	11	1	8	1	3	-	-	2	8	3	30	-	-	5	4	18	5
E4	2	7	-	-	2	5	1	8	1	3	-	-	-	-	-	-	-	-	5	4	11	3
E5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	4	5	2

*Number of hares captured

**Per cent of the total monthly captured hares captured in the vegetation type. The tests failed to reject the hypothesis at the 0.05 level for each month and for the total. Thus, it would seem that the data gathered during this study failed to show a correlation between vegetation types and the number of hares captured in each type. Since this correlation could not be proved, it was assumed that during this study snowshoe hares did not show a cover preference.

One possible reason why the hares failed to show a cover preference is the fact that on the study area the various vegetation communities are interspersed in such a manner that a hare could move in a radius of less than 500 feet and be in several vegetation types without being captured. For example, a hare could have a center of activity or a form near trap D2, move less than 500 feet in four directions and it would be in four different floral communities without showing a preference through captures. If the vegetation types had covered enough area, a cover preference might have been detected.

Adams (1959:152) remarked, "Casual observations of pellet distribution showed early in the study that they occurred in greatest concentration where trees and shrubs were thickest." Since a cover preference could not be detected with the data gathered, no correlation between hares and density could be shown.

Pelage

Grange (1932b) and Severaid (1942) described pelage changes for snowshoe hares in Wisconsin and Maine, respectively. They found that in their areas the autumnal molt began in late September and was completed by early December. The vernal change began early in March and was completed in early June.

In Interior Alaska, during 1959, the fall molt began during the first week in August. The adult hares began to molt first, followed by the juveniles two weeks later in the month. Hares were observed in all stages of the color change from August 9, 1959, until November 1 when the molt was completed. Tagging records indicated that a complete molt required at least 68 days.

The vernal color change commenced late in March and was completed by mid-June.

The data collected during the autumnal molt were not complete enough to determine whether there was a difference in the molting sequence between the sexes. However, during the vernal molt of April, 1960, capture data indicated that the females precede the males in molting. Thirteen females captured from April 24, 1960, to April 30, 1960, had patches of brown fur extending over the head and down the back, but 16 males captured during the same period had brown fur on the head and neck only (Table 8.).

Nelson (1909) stated that the front feet and legs and the hind feet and lower legs of snowshoe hares in Interior Alaska remain white during the summer. Information on pelage collected during this study failed to substantiate the findings of Nelson since all adult hares captured during July had brown feet. A colored slide of an adult hare that had totally brown feet is on file at the Alaska Cooperative Wildlife Research Unit for reference purposes. Because the adults did not have white on their feet, it was impossible to use the aging technique of Adams (1959) that was based on foot color.

Movements

Hare movements seem to be influenced by the climate in at least two ways. During the summer, trapping success was poor on days after a heavy rain. For example, during the morning of July 3, 1959, three hares were captured. During the afternoon of the same day a rainstorm began which lasted until the evening of July 6. Between July 4 and July 6 the study area was wet and only two hares were captured during the two days. The sky cleared and by the morning of July 7, the study area was dry and four hares were captured.

Cold weather of -30° to -50°F. also restricted hare movements. For example, hares were being captured at an average rate of two per day during December until December 16 when the temperature dropped to -30°F. This cold spell lasted until December 23 at which time the low was -4°F. From December 16 to December 23 no hares were captured but on December 24 three hares were captured. On one occasion when the temperature was -35°F., the investigator approached within 5 feet of a hare in a form and could not force the hare to flush.

Besides the daily movements within the home range, dispersal movements were recorded for four hares. If a hare was recaptured several times in an area distant from the area of first capture, it was assumed that the hare had made a dispersal movement. Three juvenile hares made dispersal movements between traps of 1,125 feet, 2,075 feet and 2,125 feet, respectively, in 1959. A juvenile female hare tagged on August 24, 1958, yielded an unusual record. After being recaptured twice in 1958 the animal was not recaptured again. On September 27, 1959, a local sportsman shot the tagged hare at Mile 6 on the Livengood Road, a distance of at least 12.5 miles from the study area. This is the longest recorded movement of a snowshoe hare in the literature. Criddle (1938) reported seeing hare trails that were several miles long, but he never proved that any one hare traveled the entire distance.

Reproduction and Growth

The breeding season began in mid-March with the descent and enlargement of the males' testes. By early April all males had scrotal testes and showed courting behavior by chasing other hares and attempting to mount females.

By using the growth curve for Interior Alaska hares (Fig. 22.), an approximate date of birth was extrapolated for all leverets. Correlating the earliest possible litter by the graph method with the onset of courting, it was shown that the first litters were probably born during the last week in May. One captive female gave birth to three young on May 24, 1959. In contrast to the Alaskan breeding season, Adams (1959), Severaid (1942), and Aldous (1937) found that the hare breeding season in Montana, Maine and Minnesota began in mid-February with the descent of the males' testes. All males had scrotal testes by March and the first litters were born during the month of May.

After July 18, no males with scrotal testes were captured, indicating that the breeding season had ended. 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 are born at that time. Severaid (1942) and Aldous (1937) recorded hare births until late in August. Table 8 is a list of the breeding phenology of hares as recorded by five authors in

TABLE 8. VARIATIONS IN THE REPORTED REPRODUCTIVE PHENOLOGY AND PELAGE CHANGES OF SNOWSHOE HARES IN NORTH AMERICA

		Reproduction				Pelage Changes			
Investigators	Region	Testes Descend	First Litter	Testes Ascend	Last Litter	Vernal Begins	Vernal Ends	Autumnal Begins	Autumnal Ends
Adams (1959)	Mont.	Feb. 18	Early April	July 15	Aug. 1	--	--	--	--
Aldous (1937)	Minn.	--	--	--	Early Sept.	Early March	May	Oct.	Dec.
Grange (1932)	Wisc.	--	--	--	--	Mar. 17	June 21	Sept. 25	Dec. 15
Severaid (1942)	Me.	Mar. 1	Apr. 17	--	Late Aug.	Early March	Early June	Late Sept.	Dec.
O'Farrell	Alaska	mid-March	Early May	July 18	Late July	Late March	mid-June	Aug. 9	Nov. 1

North America.

Snowshoe hares have a gestation period of 36 days (Severaid, 1942) and breed soon after parturition. Since the first litter in the Fairbanks area was born in late May, and the leverets are weaned in 30 days, it would have been possible for a female hare to have had three litters during the 1959 breeding season. No data were collected on the incidence of pregnancy but the late Paul Tovey (vive voce) reported that his analysis of over 300 ovaries and uteri showed that some Interior Alaska hares have three litters per year.

A pregnant hare was trapped May 21, 1959, and kept in captivity. On May 24, at 11:00 p.m. the hare gave birth to three leverets. The young hares weighed 48 g., 50 g., and 58 g., respectively, for an average birth weight of 52 g. Adams (1959) recorded an average birth weight of 39.6 grams, whereas Grange (1932a) and Severaid reported 77.0 and 67.0 grams respectively as the average weight of hares at birth.

The following morning the 50 g. leveret had disappeared and the investigator was unable to determine its fate. Notes were kept on the behavior and growth of the remaining two hares until the female accidentally suffocated them two weeks after birth.

Only one observation differing from those of Grange (1932a) on juvenile hare characteristics was made. The Alaskan hares were darker at birth than their mothers and appeared almost black in certain light. Grange stated that Wisconsin hares were lighter in color at birth than their parents. Audubon and Bachman (1856) fide Grange (1932a) stated that young snowshoe hares were darker in color than their parents. The fact that the captive Alaska hares were darker at birth is probably due to the fact that their mother was still in vernal color change pelage. Later in the summer, when the adults are dark brown, the young of the year are lighter in color than adult hares.

Parental care did not seem well developed in the captive hares observed. On three separate occasions, however, a scene was repeated in the field that seemed to indicate that adult hares do care for the very young hares. Upon removal from a trap, a young (200 g.) hare screamed until placed in the burlap sack. When the screaming began a large adult hare stepped out of the brush only 15 feet away and watched the entire tagging procedure. When the investigator tried to frighten the adult hare away, it would move only a few feet. As the juvenile was released and bounded off, the adult hare likewise bounded away. Whether or not the large hare was the mother of the leveret is unknown.

A growth curve for Interior Alaskan snowshoe hares was drawn up in two ways. First, the method of Adams (1959) was tried. Briefly, this entailed matching the weights of Alaskan hares on the growth curve of Severaid (1942). A hare's weight was located on Severaid's graph irregardless of the point on the time scale. Later recapture weights were plotted according to the number of days since the last capture and at the correct weight ordinate, regardless of the points on the curve. If the Alaska hares grew faster or slower, it was assumed that the curve would be above or below the curve of Severaid. A second method was tried also. In the second method, the weights of the captive hares were used to fill in the first two weeks of growth on a

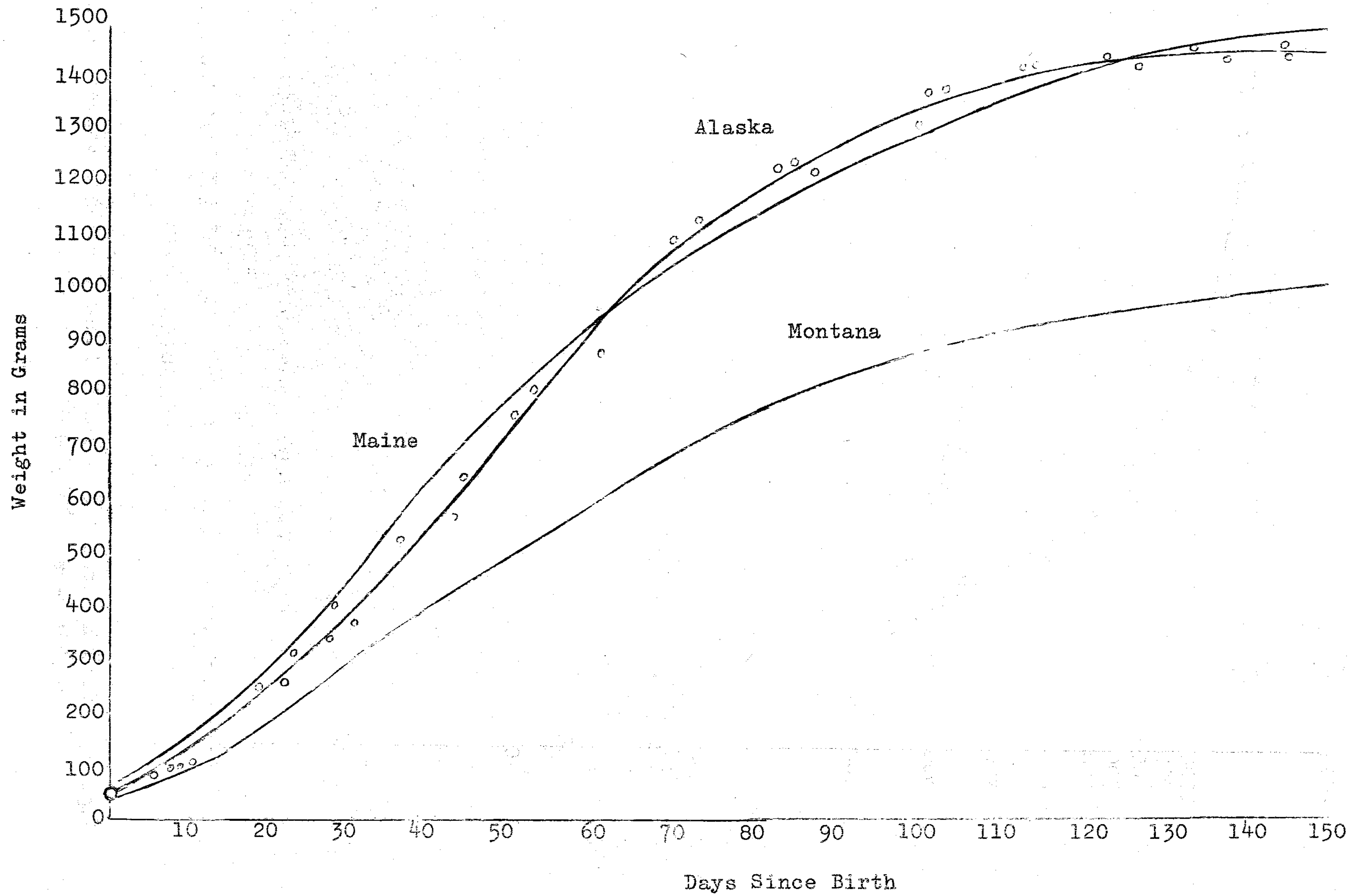


Fig. 22. Reported growth curves for snowshoe hares in Maine, Montana and Alaska.

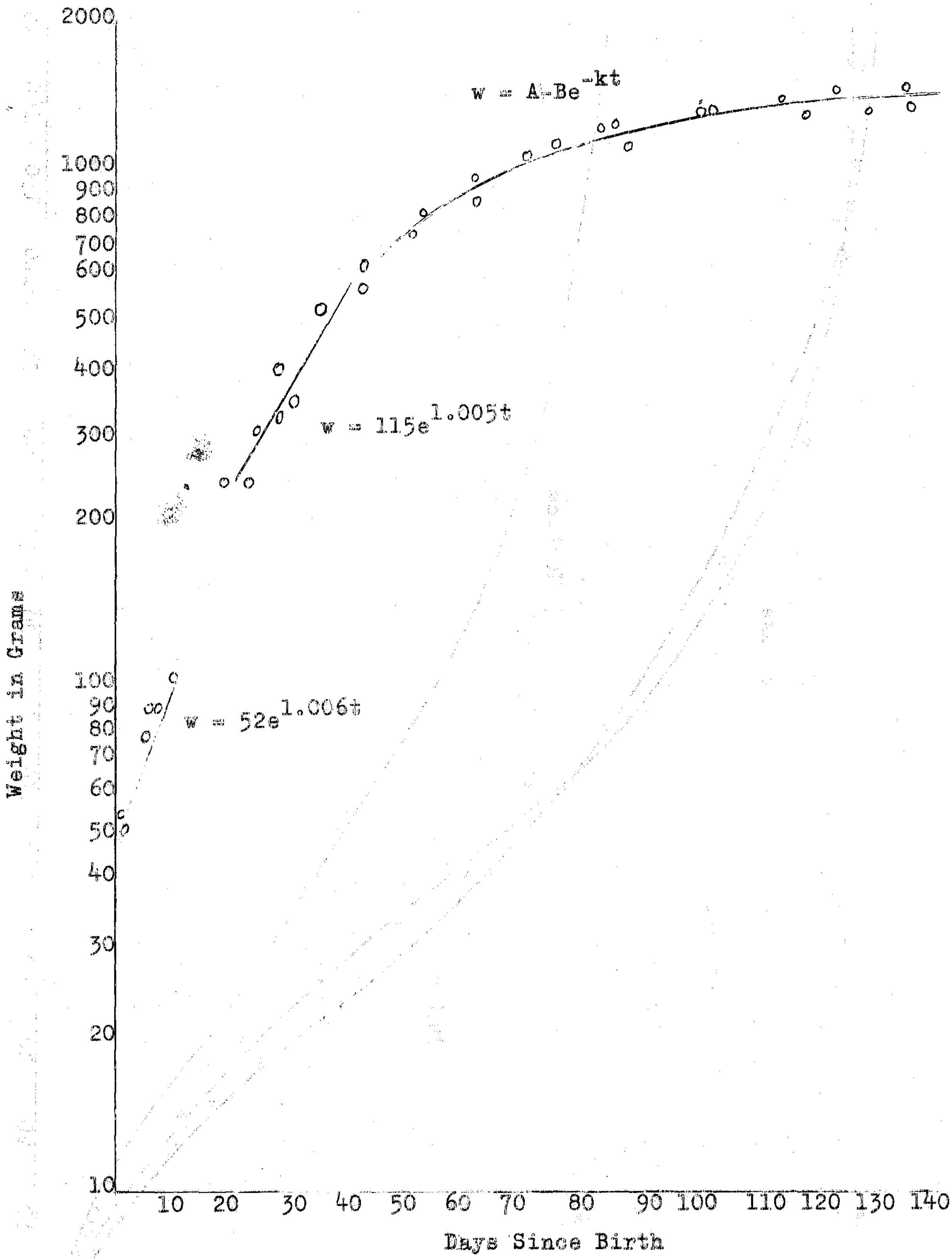


Fig. 23. Growth curve for Interior Alaska snowshoe hares plotted on semi-logarithmic paper.

graph. Then the weight of a wild hare which matched that of the captive hares at two weeks was placed on the chart in its proper place. When the hare was recaptured again the later weight was plotted at the correct time interval from the initial capture. By plotting the overlapping weights of hares and their subsequent recapture weights, it was possible to draw a growth curve which proved to be identical to the one drawn using the method of Adams (1959). The growth curve for Alaskan hares is shown in Figures 22 and 23.

The points on the growth curve were then plotted on semi-logarithmic paper to determine the components of the curve (Fig. 23.). On semi-log paper the curve broke into three separate parts. Each of the three parts was treated as a separate curve and a line of best fit was calculated mathematically by the method of least squares.

The first segment was a typical exponential growth curve from birth to 10 days. The generalized formula for a curve of that shape is $w = ae^{bx}$. A regression for the points between birth and 10 days, yielded the formula $w = 52e^{1.006t}$ where w = weight in grams, t = time in days from birth, and e = the base of the natural logarithms.

Between 10 days and 35 days the curve also fit the formula $w = ae^{bx}$. Using the points between 10 and 35 days a regression was calculated to determine the line of best fit. The regression yielded the formula $w = 115e^{1.005t}$.

A major point of inflection occurred at 35 days. After 36 days the rate decreased at a constant rate so the remainder of the curve was fitted using the graphic method of Brody (1945) for the formula $w = A - Be^{-kt}$. Finally, the three lines of best fit were united into the growth curve of Figure 22.

The curve shows that the hares in this study grew at a greater rate than the hares in Adams' study. The Alaskan hares grew at a similar rate to captive Maine hares until 60 days after birth at which time the Alaskan hares grew at a greater rate. It took the juvenile Alaskan hares between 90 and 120 days to attain adult weight. Grange (1932a) showed that it took Wisconsin hares at least four to five months to attain adult weight.

Because of the short period of succulent vegetation and the early arrival of dense snows, Alaskan hares have probably evolved a rapid growth rate to enable the young of the year to live through the long winter. Adams (1959) states that hares born early in the summer reach mature weight in fall but that hares born later continue to grow through most of the winter. The data gathered in Alaska indicated that all the juvenile hares regardless of birth date grow at the same rate. Hares born in the last litters reached mature weights in the same amount of time as those hares born in the first litters. All three juvenile classes grew to adult weight in the same amount of time. The late born hares did not grow through most of the winter.

Mortality

Hares are low on the food pyramid and supply protein to many predators. Lynx, fox, coyote, dogs, mink, weasels and black bear frequented the study area. The most important hare predator was the lynx, and at least 20 hares on the study area were known to have been killed by lynxes during the study. Mink killed and cached at least five hares, and black bears killed two hares in live traps. The other mammalian predators listed on page 17 are known to eat hares, but kills were not authenticated for them.

Goshawks and great horned owls were the most important avian predators. Goshawks were seen eating hares on four occasions. Undoubtedly the hawks and owls ate hares that were not recorded. An unsuccessful attempt was made to locate the hawk and owl roosts to obtain pellets for food analysis.

During May and June the heads and ears of all hares captured were literally covered with ticks. Several ticks were sent to the Rocky Mountain Laboratory where Dr. Glen M. Kohls identified them as <u>Haemaphysalis leporis-palustris</u>. The ticks were abundant on both adult and juvenile hares until late in August when the last observation of a tick was made. The role of these ticks in the mortality of Alaskan hares is uncertain.

Trap mortality was relatively low. Only 21 hares (20 juveniles, 1 adult) of 348 hares captured died in the traps. The one adult that died suffered from exposure when the trap was accidentally bypassed by the investigator. Of the 20 dead juveniles, 12 were found in the opisthotonic death position described by Green, Larson and Bell (1939), and it was presumed that they died of hypoglycemic shock. The investigator watched three juveniles die of symptoms exactly like those of shock disease. The following are the observations made of a hare that was carried around in a trap by a lynx on August 6, 1959:

1002 - Trap B1 lying at a right angle to usual location; on side and uncovered. Hare inside fine, no cuts. Retrap 2523-2524.

1004 - Picked up trap. Hare began to revolve longitudinally; kicked legs. Lay on side and moved legs as if it were running. Lay still 5-10 sec.

1010 - Took out of trap and placed on ground. Eyes glazed and covered with mucus.

1020 - Began jerking head.

1030 - Uttered muffled cries. Still twitching. Mucus coming out of nose and mouth. Acts like it is sneezing or coughing on mucus. Crying again.

1032 - Stopped jerking. Gasping for breath. Three violent head jerks. Breathing quickly. Head held back all this time. Nose and mouth filling with dirt. Cannot see breathing.

1036 - Head jerking, legs moving, body convulsing.

1038 - Hind legs stiffened straight out and a single convulsive wave moved up body to head. Chin and muscles of hind feet quivering.

1039 - Movement ceased. Dead.

1043 - *Rigor mortis* set in. 1½ loose scat at anus.

During this study shock disease was not recorded for adult hares. Seven male and five female leverets were found dead of shock disease indicating that the disease was common to both sexes of the juvenile class in an even sex ratio. Paul Tovey (*vive voce*) reported that during the cycle high both adults and juveniles died of shock disease so frequently that handling was enough to kill a hare.

Juveniles killed by shock disease were in the 200-300 g. weight class and had probably just been weaned. All of the deaths due to shock disease occurred in June, July and August; the months in which the juveniles were first out on their own. Why only juveniles were susceptible to shock disease was an unanswered question.

<u>Aging Technique</u>

There are no published field methods for determining the age of hares. Since average monthly weights, growth curves and other calculations depend on the ability of the investigator to distinguish the juvenile hares from adult hares, an effort was made to observe carefully any characteristics that might help to age hares. Two aging techniques were discovered that were useful in separating juvenile and adult hares. The penises of the juvenile males observed were knob-like when the fur around the genitals was stretched. The penises of the adult hares were very pointed and appeared much larger proportionately than the juvenile penises.

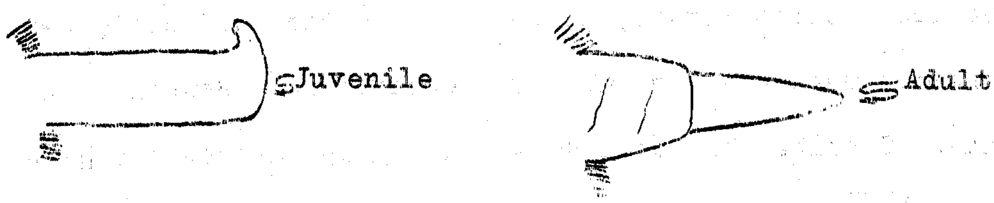


Fig. 24. Comparison of penis shapes in juvenile and adult hares.

From the information gathered it appeared that the juvenile hares had small penises until the first breeding season at which time the organ enlarged and became the pointed adult organ. Further work is needed to substantiate these observations and to determine when during maturation the penis changes shape.

Recapture data also indicated that the genitals of adult female hares differed from the genitals of female leverets. When the skin around an adult female's genitals was stretched, the vulva spread easily and appeared thick and fleshy. The vulvas of juvenile females had the characteristic ramp shape but were not fleshy and often would not spread open.

SUMMARY

A 160 acre study area was established two miles north of the University of Alaska to determine the home range of the snowshoe hare, to ascertain what census methods might be used under subarctic conditions and to gather natural history of the hare in its northern range. The topography, soils, climate, vegetation, and fauna of the area are described. The study was made between April, 1959, and April, 1960.

Live-trapping and tagging were used to gather the bulk of the data presented. To determine the level of the population several methods were attempted with varying degrees of success. The track count method, pellet count method and strip census were not usable under subarctic conditions. However, the Lincoln Index, Schnabel Method and calendar-graph method did give an indication of the population size.

Home range was calculated using the boundary inclusive method. It was found that the home range of males averaged 11.8 acres and that of females was 13.0 acres. There were no significant differences between the annual and the early breeding season home ranges.

Trapping success tended to be higher in the spring and summer and dropped quite low during the winter. The low level of trapping success during the winter was probably due in part to the cold metal traps and the tendency of the hares to remain relatively inactive during cold weather. Recapture per cent was low during the summer due to recruitment, but after September the recapture proportions rose steadily until 89 per cent of the

captured hares were recaptures.

Snowshoe hares varied in their use of runways depending on the density and hardness of the snow. During the early winter when the snow was loose, and again during the April thaw when the snow was in a state of flux, hares used packed runways. Throughout the rest of the winter hares used the entire snow cover for movements.

The summer and winter forms used by hares are described. Summer forms usually were between the trunks of small trees, whereas winter forms were established under trees bowed by the snow.

Hares reacted to danger in several ways, depending on the age of the hare and the season of the year. During the summer adult hares would hop and "freeze" until they were out of sight, but juveniles remained immobile. During the winter all age classes seemed to depend on immobility for protection.

Food preference is described as observed in the field and from feeding a hare in captivity. Summer food consisted of most of the green vegetation in the area. Winter foods were the bark of willow, birch, alder and spruce.

Data gathered indicated that the hares did not show a cover preference.

Interior Alaska hares began their autumnal molt in early August and were seen in all stages of color change until November 1 when the molt was completed. The vernal color change commenced late in March and was completed by mid-June. At least 68 days were required for a complete molt.

Hare movements were influenced by climatic conditions. During a heavy rain or cold weather (-30°F. or below) the hares remained inactive. Three dispersal movements are described. One hare was shot 12.5 miles away from its tagging site. This is the longest recorded movement of a snowshoe hare.

The breeding season extended from mid-March to mid-July. Three juveniles weighed an average of 52 g. at birth. A growth curve was drawn for Alaskan hares and is compared with two other hare growth curves. Alaskan hares grew at a greater rate than Montana hares. The Alaska hares grew at a similar rate to captive Maine hares until 60 days after birth at which time the Alaskan hares grew at a greater rate.

A field method for aging juvenile and adult hares based on the external characteristics of the genitals of both sexes is described.

Predation and shock disease were two mortality factors observed. Lynx, hawks and owls were the main predators.

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