SPRUCE SEED AS A FOOD OF THE SQUIRRELS
TAMIASCIURUS HUDSONICUS AND GLAUCOMYS SABRINUS
IN INTERIOR ALASKA

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<u>TAMIASCIURUS</u> <u>HUDSONICUS</u> AND <u>GLAUCOMYS</u> <u>SABRINUS</u>

IN INTERIOR ALASKA

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Photo by Karl Schneider

ABSTRACT

Red squirrels (Tamiasciurus hudsonicus) were censused from July through October, 1962, on a 27-acre, white spruce forested, island in the Tanana River. Time-area counts followed by an attempted complete kill produced an estimate of 0.74 squirrels/acre. This low density is believed to be the result of the failure of the cone crop on the island that fall. Observations indicate that a modification of the Schnabel method employing recorded red squirrel territorial and aggressive calls might be effective for future censuses.

Feeding trials conducted from November, 1962, through June, 1963, in an outdoor enclosure on the University of Alaska campus revealed that red squirrels can survive for 3 weeks (possibly longer) on nothing but white spruce (Picea glauca) seed and under such conditions consume about 144 cones per day per squirrel. Flying squirrels (Glaucomys sabrinus) do poorly on white spruce seed and, unlike red squirrels, probably do not consume large quantities of it in the wild. Red squirrels lose weight rapidly when given nothing but black spruce (Picea mariana) cones and show a marked preference for white spruce cones over black spruce cones, possibly because of the larger size and higher caloric content of white spruce seed. Red squirrels scatter about one sound seed for every two cones they strip, but it is unlikely that many of these scattered seeds successfully germinate.

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INTRODUCTION

Approximately 8%, or 28 million acres, of interior Alaska is covered with commercial grade forest, the principal species being white spruce (Picea glauca),[1] quaking aspen (Populus tremuloides), and paper birch (Betula papyrifera) and its Alaskan varieties. The mean annual net increment of the white spruce stands of interior Alaska is an estimated 412 board feet, of which only a fraction of 1% is being utilized at the present time (preliminary estimates, Northern Forest Experiment Station). Forest Service policy recognizes, however, that the demand for timber products from interior Alaska will increase. Research on the silviculture of interior tree species has been initiated at the Service's Northern Forest Experiment Station in order to have on hand the basic data which will be neces ry for effective timber management. The squirrel project reported on here was financed by the U. S. Forest Service through a contract with the University of Alaska; administration was through the Alaska Cooperative Wildlife Research Unit. This continuing project has been designed to provide information contributing to the larger picture of spruce ecology and management.

That red squirrels (Tamiasciurus hudsonicus) in

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[1]The scientific names of vascular plants follow Hultén (1941-1950). Those of mammals follow Hall and Kelson, (1959), and those of birds follow the 1957 check-list of the American Ornithologists' Union.

Alaska utilize large quantities of white spruce cones is obvious even to the casual observer. In August, before any significant natural seed fall occurs, the squirrels cut large numbers of cones, most of which are stored in piles or "caches" for use during the winter. The cones are utilized on or near the caches and the result is an accumulation of the bracts and stalks of shredded cones often (after several years) 30 to 60 cm deep over an area 3 to 4 m in diameter (Lutz, 1953). These accumulations, known as middens and often representing the remains of thousands of cones, are a common feature of white spruce forests. The effect of squirrels on seed dispersal, forest regeneration, and the long-term ecology of the spruce forests of interior Alaska is not known. This study, therefore, has been directed toward interpreting red squirrel-white spruce interrelationships.

The long-term objectives of the squirrel project are:

1. To determine the ecological relationships of red squirrels to the production and supply of white spruce seed and the regeneration of white spruce in interior Alaska.

2. To investigate management techniques that will improve these relationships from the standpoint of multiple use.

Two phases of this study are presented here: (1) a population study conducted from July through October, 1962, on an island in the Tanana River; (2) a food habits and consumption study conducted from November, 1962, through June, 1963, on captive red squirrels maintained either in individual cages within an outdoor enclosure on the University of Alaska campus or within an animal room at the University.

DESCRIPTION OF THE STUDY AREAS

Tanana River Island

Method of Selection

Since the investigation of red squirrel density required minimizing any immigration and emigration, one of the many forested islands in the Tanana River was selected as a study area. The choice was made after an aerial inspection of the river near Fairbanks and a ground check.

Location

The island used in this study is 10 miles SW of Fairbanks and 5 miles downstream (SW) from the confluence of the Chena and Tanana Rivers (Fig. 1). The island is included in the south one half of Section 7, and the northwest one quarter of Section 18, both within Range 2 west, Township 2 south, Fairbanks Meridian. It is approximately 420 feet above sea level, and its latitude and longitude are 64°45'N and 148°02'W, respectively.

Size

With an aerial photograph and a polar planimeter the size of the island was calculated to be 27 acres.

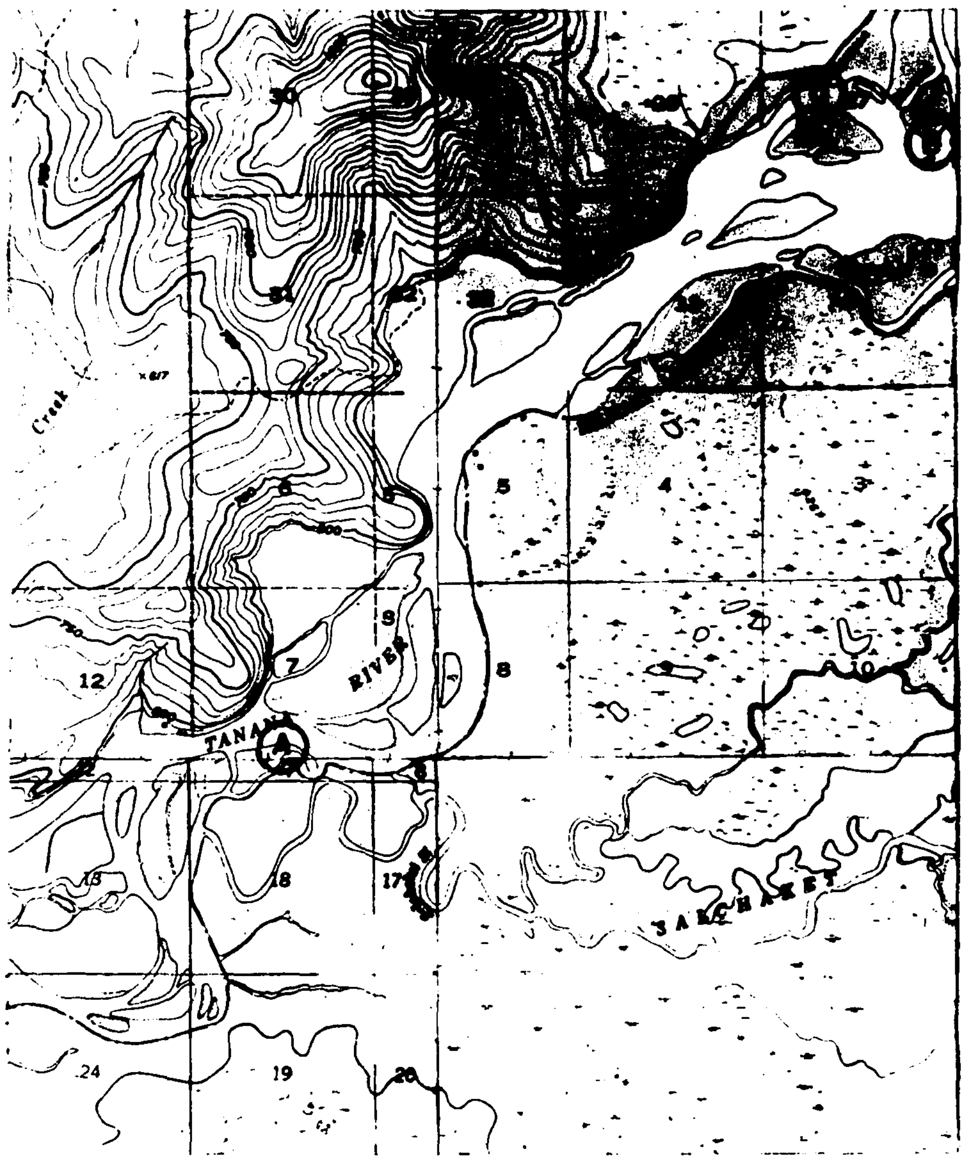

Fig. 1. Map showing: (A) the location of the study island, (B) the confluence of the Chena and Tanana Rivers, and (C) the location of the boat landing used during the study. (Composite of U. S. Geological Survey maps C-2, C-3, D-2, and D-3; Fairbanks Quadrangle with a scale of 1:63,360)

Vegetation

The vegetation of the island consists of a mature white spruce stand interrupted occasionally by alder (Alnus sp.)[1] and willow (Salix spp.) thickets. Scattered along the perimeter and near open areas are 25 to 30 white spruce trees with 25 to 30 in. dbh (diameter 4.5 ft off ground). The majority of the trees, however, are 4 to 10 in. dbh.

On the basis of gross vegetational characteristics the island was divided into six areas: the Dense Forest, the Open Forest, and four thickets (Fig. 2). Two 10 by 10 m plots were subjectively selected in the Dense Forest and density and basal area measurements were made on the species listed in Table 1. Similar measurements were made in the thickets on 4 by 4 m plots. No density or basal area measurements were made within the Open Forest, which is essentially a combination of the other areas. The aerial photograph gives an accurate impression of the gross aspect of the Open Forest. Being less completely canopied than the Dense Forest, the open area is drier and the mosses (Hylocomium alaskanum [Lesq. & James] Kindb., Rhytidiadelphus spp. and probably others) form a thinner and less continuous carpet than in the Dense Forest.

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[1]The Alnus and Ribes species were almost unquestionably A. crispa. and R. triste, but the specimens collected were lost and a positive identification was not made.

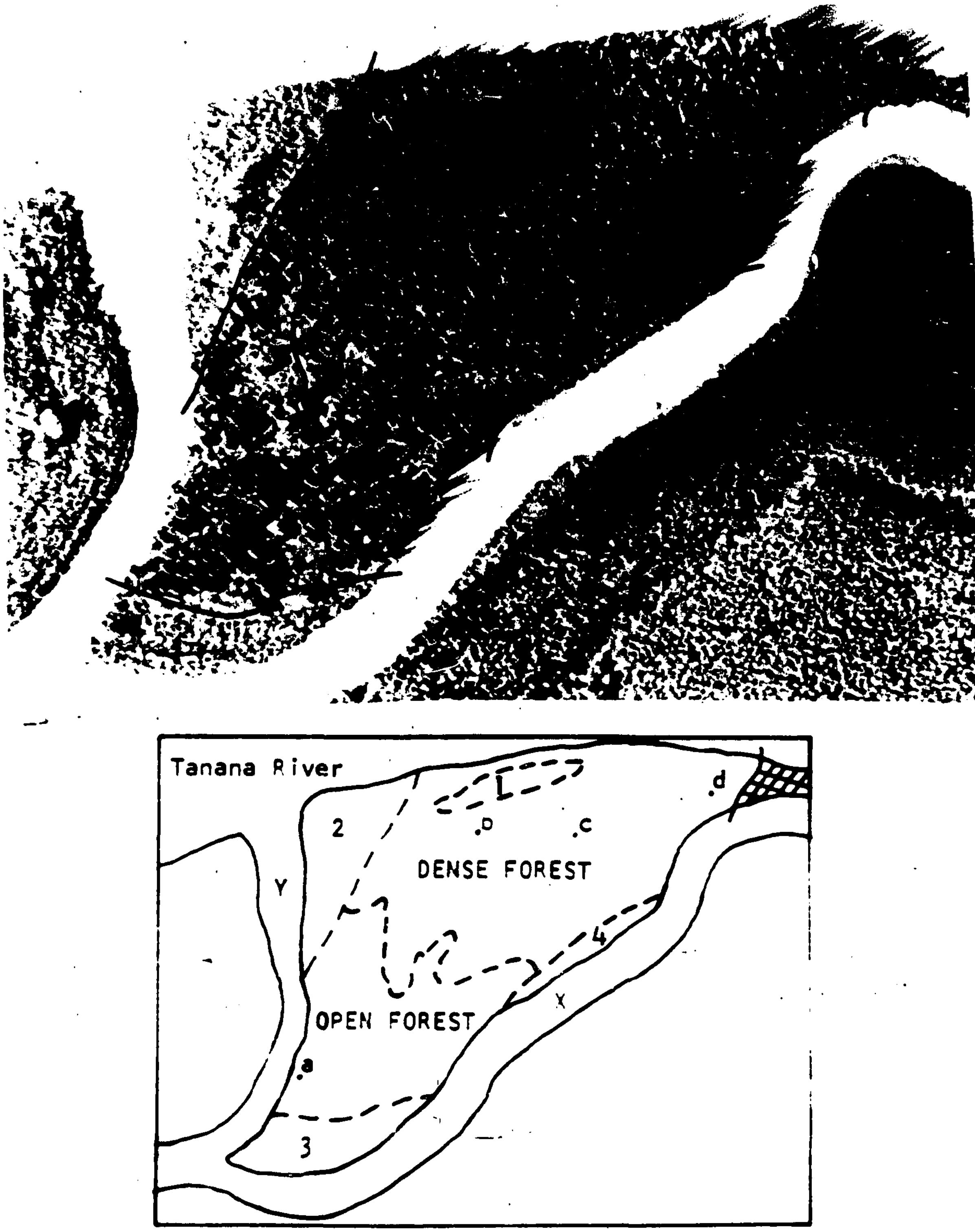

Fig. 2. Aerial photograph of the study island. The line drawing shows the major areas of vegetation. Numbers designate thickets mentioned in the text. Lower case letters designate the observation stations. Slough X separates the island from the mainland and slough Y separates the island from another island. Erosion has eliminated the crosshatched area.

Table 1. Vegetation analysis, Tanana River study island

Area and Species	Density	Basal Area*
	(per 100 m²)	
Dense Forest (average of two 10 X 10 m plots)		
Picea glauca	19	6,770 cm^2
Betula papyrifera	.5	150
***Alnus* sp.	1	50
Rosa acicularis	79	
Ribes sp.	14	
Thicket No. 1 (average of two 4 X 4 m plots)		
Picea glauca	3	10
Populus balsamifera	19	610
Alnus sp.	19	460
***Salix* spp.	6	1,420
Rosa acicularis	44	
Ribes sp.	47	
Thicket No. 2 (average of two 4 X 4 m plots)		
****Picea glauca*	216	
Populus balsamifera	41	290
Alnus sp.	16	280
Salix spp.	6	2,900
Rosa acicularis	56	
Thicket No. 3 (one 4 X 4 m plot)		
Populus balsamifera	19	30
Alnus sp.	19	1,230
Salix spp.	6	410
Rosa acicularis	156	
Thicket No. 4 (one 4 X 4 m plot)		
Populus balsamifera	69	650
Alnus sp.	25	1,420
Salix spp.	6	370

*Measured 61 cm above the ground.

**Most alder and willow plants divide into several main branches 61 cm or less above the ground. Branches (usually three to eight) derived from a common base were considered to be one plant for the purpose of calculating density, but the diameter of each branch was measured and used in the calculation of basal area.

***The tallest of these extended 5 cm above the ground.

In the Dense and Open Forests Linnaea borealis and Cornus canadensis are the most abundant of the small vascular plants. Several species of Equisetum are abundant in scattered areas throughout the island. Equisetum limosum was especially abundant along the beach near Thicket No. 4 and in other areas subject to flooding.

Mammals and Birds

The island is not equally isolated throughout the year, and most of the local mammals visit or inhabit it, at least occasionally. Isolation is comparatively high in spring and summer. By late fall the water is low enough for even the smallest mammal to swim the sloughs separating the island from the mainland. In winter, of course, ice forms a continuous bridge between the island and the mainland.

During the study, in addition to red squirrels, the following mammals, or their signs, were observed on the island by the author: flying squirrel (Glaucomys sabrinus), redback vole (Cleithrionomys rutilus), muskrat (Ondatra zibethica), beaver (Castor canadensis), snowshoe hare (Lepus americanus), moose (Alces alces), mink (Mustela vison), black bear (Ursus americanus), and wolf (Canis lupus).

The following birds were observed by the author on or near the island during the study: Canada Goose (Branta canadensis), American Widgeon (Mareca americana), Pintail (Anas acuta), Mallard (Anas platyrhynchos), Red-breasted Merganser (Mergus serrator), Ruffed Grouse (Bonasa umbellus), Common Raven (Corvus corax), Gray Jay (Perisoreus canadensis), Pine Grosbeak (Pinicola enucleator), Redpoll (Acanthis spp.), plus many unidentified small birds. David R. Klein observed two Goshawks (Accipiter gentilis) on the island during the study.

During winter the river and sloughs surrounding the island freeze over and the island becomes essentially a part of the adjacent forest. Consequently, although few squirrel predators were observed on the study island, it is safe to assume that the effect of predation upon the red squirrel population of the island is comparable to that on other squirrel habitat in interior Alaska.

Animal Enclosure

Location

The animal enclosure is located in a black spruce (Picea mariana) stand on what is now a remote portion of the University of Alaska campus about 1 mile NW of the Bunnell Building.

Dimensions and Construction

The enclosure consists of a 100 x 100 ft area, protected by a sturdy 8-foot wire mesh fence with pipe posts and barbed wire overhang (Fig. 3). The mesh was extended out from the base 1 ft or more along the surface of the ground to prevent dogs from digging into the enclosure. Although the mesh (approximately 15 x 15 cm) would not prevent a fox (_Vulpes fulva_) or a lynx (_Lynx canadensis_) from entering the enclosure, no sign of these animals was found during the study.

A fabric-covered Jamesway hut, located a few feet from the only entrance to the enclosure, was used as a storehouse and field laboratory until 22 April 1963 when the hut collapsed because of the weight of snow that had accumulated on it. After the loss of the building, the supplies and weighing table were kept inside the enclosure, the supplies being protected with tarpaulins.

Fig. 3. Detail of construction of the animal enclosure (August 1963)

METHODS

Census

Time-area Count

Four observation stations (a, b, c, and d) were subjectively established in portions of the island representative with respect to estimated squirrel activity (Fig. 2). On five different days between 18 September and 5 October 1962 each station was visited for one-half hour. The number of squirrels seen from each station was recorded. After the observation of one squirrel from a given station, all squirrels seen from that station on that day were considered to be the original squirrel, unless there was positive evidence to the contrary.

The area under observation at each station was determined by estimating the average maximum distance at which a squirrel moving on the forest floor could be seen from the station. This was done by subjectively selecting apparently representative radii within the four quadrants of each area under observation; these four radii were then averaged to get a mean radius for the area under observation. Since this census took place during the period when most of the deciduous plants were losing their leaves, it was necessary to measure the radii of visibility at both the beginning and the end of the census and to calculate mean values on this basis. The total red squirrel population of the island was estimated by assuming the following equality:

$$\frac{\text{Total observed area}}{\text{Area of island}} = \frac{\text{Average daily total of observed squirrels}}{\text{Squirrel population on island}}$$

Complete Kill

Two days after the time-area count was completed, a complete kill was attempted with the hope of making an absolute count of the squirrel population of the island as a check on the accuracy of the time-area count. Traps (191 rat-size Schuyler "Folding Animal Killers", 17 Victor rat traps and 21 National live-traps) were set approximately 25 m apart with heavier concentrations in the more promising areas, such as around cone caches, and with lower concentrations in the alder and willow thickets. Fifteen traps were set along the banks of the sloughs bordering the study island (X and Y in Fig. 2) in order to obtain an index of immigration and emigration. Since a complete kill was desired, all traps were set in likely looking places rather than in a specific grid pattern.

The snap-traps were baited with tough meat coated with a mixture of peanut butter and bacon grease. Schuyler traps are often hard to spring, but it is difficult for a squirrel to remove a piece of tough meat from one without getting caught. The live-traps were baited with bread coated with peanut butter and bacon grease.

This bait was suspended above and behind the treadle to prevent raiding by small mammals.

The traps were checked and reset where necessary on 10 and 11 October 1962. On 12 October the traps were again checked, and all but 16 of them were removed. On 13 October five additional traps were removed. On 16 October 1962 the attempted complete kill was discontinued. Each time the traps were checked the two to four people doing the checking were equipped with shotguns and shot all untrapped squirrels seen. In addition, the area was hunted for any remaining squirrels for from 2 to 4 hr during each visit.

Trapping

In order to build up a squirrel colony for the feeding trials, red squirrels were caught within 2 miles of the University campus in National live-traps. The bait used was peanut butter on bread suspended above and behind the treadle or Purina Laboratory Chow. Between 5 November and 1 December 1962, 106.5 trap-nights produced 22 squirrels including five flying squirrels. One trap-night equals one trap set for 24 hours. The traps were checked each morning and evening.

Cage Construction

The cages were made with 1 X 0.5 in. 16-gauge galvanized (after welding) wire (Fig. 4). Eight-foot lengths of the wire were cut from 4 X 100 ft rolls and bent with a sheet metal break, after which the loose ends, end pieces, doors and latches were fastened with hog rings. The nest boxes were made out of 1 X 12 in. untreated white spruce boards. Commercially-made 28-gauge galvanized metal trays were placed under the cages as catch-pans. This equipment served our purposes very well. The 30 cages constructed, including trays and nest boxes, cost approximately $17.00 each, not including labor, except that in connection with the trays.

Weighing

During the feeding trials the squirrels were weighed in live-traps of known weight. An Ohaus triple beam balance giving readings to the nearest 0.1 g and having a maximum capacity of 2,610 g was used. The weights recorded are believed to be accurate to within 1 g.

The weighing was done as close as possible to sunset to insure that most of the squirrels would have completed their day's feeding and would be in their nest boxes. The squirrels were frightened from their nest boxes into a trap as shown in Fig. 4. Often it was necessary to partially open the top of the nest box with a stick and blow into the opening in order to get the squirrel to come out. It was always necessary to be prepared to close the door quickly,

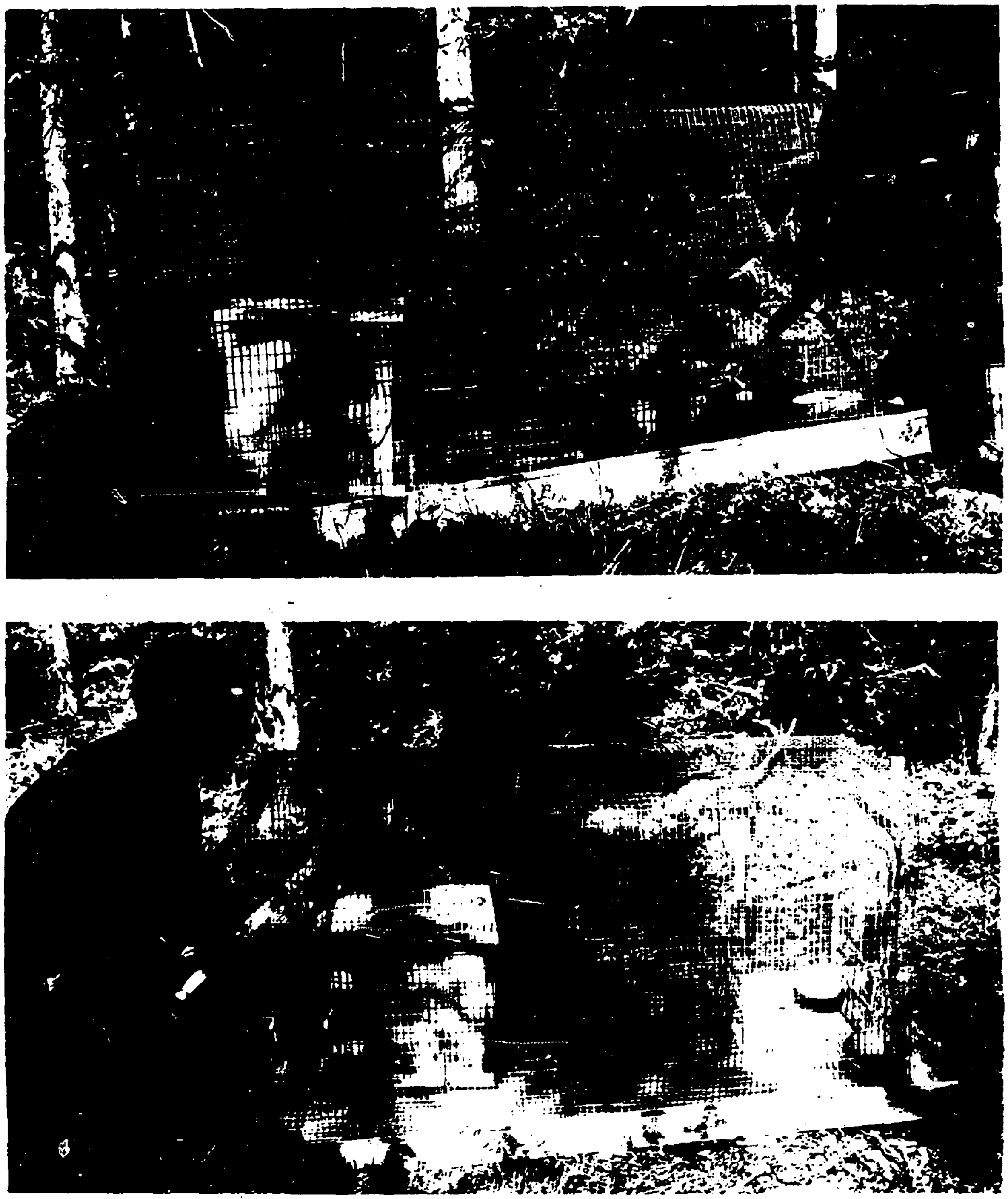

Fig. 4. Catching a squirrel for weighing. A trap is set in front of the nest box and sprung (upper photo) so that its door is held open by supports surrounding the entrance to the next box. Then the squirrel is frightened from the nest box into the trap (lower photo), and the nest box is pulled back allowing the door of the trap to close.

for occasionally a squirrel would be able to push the trap aside as he left the nest box. Only two squirrels escaped, however, and these during a practice session when the technique was being developed.

If a squirrel to be weighed was not in its nest box, it was caught by frightening it into a strategically positioned trap. This method was usually effective; however, about 10% (three to four) of the squirrels became exceedingly trap-wise and required the use of four to seven traps and as much as 20 min of effort prior to their capture. None of the trap-wise squirrels showed aberrant weight patterns, however.

Feeding Trials

The spruce cones used in the feeding trials were collected from a variety of red squirrel caches on or adjacent to University property. Most of the cones were collected in the fall of 1962. However, by early March it became apparent that the squirrels were consuming more cones than anticipated, and it was necessary to gather several thousand additional white spruce cones.

When not actually participating in an experiment, the squirrels were maintained on Purina Laboratory Chow, which was determined to have a caloric content of approximately 4,390 cal/g. No supplements were necessary. Snow and ice, provided as a water source, were utilized constantly by the squirrels. The captive squirrels maintained weights about 10% in excess of normal (i.e., wild) weights for red squirrels. The feeding trials were conducted from the second week of February through June, 1963.

I. Response of Red Squirrels to a White Spruce Seed Diet following Starvation

Two squirrels of each sex were randomly selected within each sex group from those that had been on a constant diet of laboratory chow for a week or more. On 11 February their cages and nest boxes were cleaned and all food was removed. On 15 February, after 4 days without food, the three squirrels that survived were each offered a predetermined number of cones. On the first day approximately 100 white spruce cones were offered each squirrel. The daily ration was increased by 50 cones each day until it became apparent that the squirrels were being given more cones than they could utilize. When the daily ration was stabilized, the cones were pre-counted and fed to the squirrels in groups of 200. On 21 February and at the end of the trial on 9 March, the intact cones remaining in the cages were counted in order to determine the total number of cones stripped by each squirrel. Partially stripped cones were counted as half cones. The squirrels were weighed at the beginning, end, and every second day (except 3 March) throughout the experiment.

II. Response of Red Squirrels to a White Spruce Seed Diet following a Constant Diet of Laboratory Chow

The individual cages of eight male and eight female red squirrels randomly selected within each sex group were cleaned, cleared of food, and subjectively positioned to give them approximately equal climatic exposure. For 10 days beginning 11 March each squirrel was presented with more white spruce cones than it could utilize. After the 10th day, because of a depleted cone supply, all cones were removed from the cages of the female squirrels which were then put back on laboratory chow. The males were supplied with cones for four more days, after which the remaining cones were removed and these squirrels were also put back on laboratory chow. The intact cones removed from the cages were counted to determine the exact number of cones stripped by each squirrel. Partially stripped cones were counted as half cones. The weight response of the squirrels to their return to laboratory chow was recorded through 10 April. The squirrels were weighed at the beginning, end, and every second day (except 31 March) throughout the trial.

III. Response of Flying Squirrels to a White Spruce Seed Diet

The cages of two male and two female flying squirrels were cleaned, cleared of food, and subjectively positioned to give them approximately equal climatic exposure. Each squirrel was given 150 cones on 21 February and never allowed to exhaust its supply. On 1 March they were put back on laboratory chow, and 2 days later the numbers of cones remaining in the cages were estimated. Since these squirrels utilized very few, if any, cones when the laboratory chow was available to them, we were able to estimate the number of cones utilized by the squirrels between 21 February and 1 March. The weight response of the squirrels to their return to laboratory chow was recorded through 6 March. The squirrels were weighed at the beginning, end, and every 2 or 3 days throughout the experiment. In addition, during 21 March through 8 April (with the exception of 25 and 31 March) the same squirrels were weighed at 2-day intervals while on a constant diet of laboratory chow in order to record weight fluctuations under such conditions.

IV. Response of Red Squirrels to a Black Spruce Seed Diet

Two red squirrels were randomly selected from those that did not participate in Trial II. Their cages were cleared of food and debris and positioned about 20 cm apart. Beginning 29 March the squirrels were continually supplied with more black spruce cones than they could utilize. The number of cones given to the squirrels was measured volumetrically. On 18 April the cones remaining in the cages were collected and counted, and the squirrels returned to a diet of laboratory chow. The weight response of the squirrels to their return to laboratory chow was recorded through 1 May. The squirrels were weighed at the beginning, end, and at various times throughout the experiment.

V. White Spruce-Black Spruce Cone Preference Tests

This trial was conducted during 13 April through 7 May and the squirrels used were those red squirrels that were adjusted to feeding in my presence. Four of the squirrels did this readily. Others cooperated to varying degrees. It was possible to run this test on two to four squirrels at one time, depending upon their rates of feeding. The squirrels were starved or placed on limited rations for about 24 hours before beginning a sequence of tests to encourage them to feed at the proper time. The cones were presented to the squirrels on boards with six evenly spaced holes 3 cm in diameter and 0.6 cm deep. The holes were numbered consecutively from left to right. Three white and three black spruce cones from the general population of cones on hand were randomly positioned on the board, the squirrel's preference being determined by the order of his choice. The board was placed on the bottom of the cage directly in front of the feed dishes opposite the nest box. The squirrels were allowed to feed with a minimum of disturbance until all the cones of one type had been selected (i.e., until no choice remained). Twenty or more sets of six were presented to those squirrels that fed readily under the conditions of the experiment. A test was considered to favor a given species only when all three of the cones of that species were selected and stripped before all three of the cones of the other species were selected and stripped.

VI. Seed Scattering Tests

Two male and three female red squirrels that had been maintained in a heated laboratory for two weeks or more were selected for this experiment, which was conducted during June. They were kept in the laboratory in approximately 30 X 60 X 30 cm rabbit cages equipped with mesh bottoms and catch-pans, the object being to feed the squirrels white spruce cones and then collect and analyze the uneaten portions. The mesh on the bottoms of the cages was 1.2 cm square and large enough for the seeds, bracts and other uneaten parts of the stripped cones to fall through to the catch-pans. Each squirrel was fed 10 cones, one at a time. When a squirrel had completely stripped a cone, the tray was removed and the remains of the cone were analyzed to determine the number of seeds in the productive zone of that cone, the number of seeds scattered (i.e., dropped) by the squirrel, and the proportion of the seeds scattered that was composed of filled seeds.

The number of seeds in the productive zone of each cone was determined by counting the bracts from that region and multiplying the total by two, since two seeds are normally produced at the base of each bract. The productive zone of a spruce cone is not easily recognized, especially after the cone has been stripped by a squirrel. These cones have a central productive zone which contains the larger, potentially viable seeds and two unproductive zones, one at the base and the other at the apex. However, with practice, one can readily determine which zone a given bract is from by the size and shape of the seed scar. Usually the productive zone lies between the upper six and lower two whorls of bracts. This agrees with the findings of Richard A. Werner, U. S. Forest Service, Juneau (personal correspondence).

The seeds scattered by the squirrels were picked out of the catch-pans with tweezers and placed in small dishes. Each seed was carefully examined to determine whether it had been cracked by the squirrel. Unfilled seeds that had been cracked were considered to have been intentionally rejected by the squirrels and were not counted as scattered seeds. All of the scattered seeds were cut transversely through the center with a razor blade and observed under a hand lens (if necessary) to determine if they were filled, unfilled or partially filled. Insect-infested and pitch-filled seeds were recorded as being unfilled. Seeds that contained some endosperm but were not completely filled were recorded as partially filled. The seeds recorded as filled had no spaces between the endosperm and the inner seed coat.

Determination of the Caloric Content of White and Black Spruce Seed

In October, 1963, four samples of white spruce cones and four samples of black spruce cones were collected from seven widely separated red squirrel caches on the University of Alaska property surrounded by Yankovich, Sheep Creek and Farmers Loop Roads. Although the samples were not strictly random, cones were taken from several parts of each cache and any deliberate bias was avoided. Arbitrarily selected cones from each sample were dried until open, after which the seeds were removed by shaking the cone in either a paper bag or a box. The seeds were de-winged and separated from all but an insignificant amount of debris. During 1 November to 4 November 1963, 1 g samples of the seeds from each cache were burned in an oxygen bomb calorimeter (Parr Instrument Company, Inc.).

It should be noted that the cones used in this analysis were from the 1963 crop, while those used in the feeding trials reported in this thesis were from the 1962 crop. See page 60 and Table 11.

Analysis of the Local 1962 White Spruce Cone Crop

A proportionate sample of each batch of white spruce cones collected for use in the preceding trials was held in reserve and then analyzed for the number of seeds in the productive zone and the proportion of filled seed in the productive zone. The samples used were not strictly random, but an attempt was made to avoid bias. The techniques employed were essentially those used in the seed scattering trial discussed above. However, some of the cones reserved for analysis had opened, allowing the seeds to dry and causing the endosperm to shrink, thus making it difficult, in some cases, to distinguish filled from partially filled seeds. Nevertheless, it was possible, after five to ten seeds had been cut and examined, to determine the effect of desiccation upon the endosperm and distinguish originally filled from originally unfilled seeds. Analysis was especially difficult when the degree of desiccation was not uniform for a given cone but I believe that the results obtained are accurate within the limits indicated.

RESULTS AND CONCLUSIONS

Census

The time-area count produced an estimate of 24 red squirrels, while the attempted complete kill and subsequent observations indicated that only 16 animals of this species inhabited the study island (Table 2). I am convinced, however, that a number of squirrels avoided detection during the attempted kill. During the last day of the study about half an inch of snow fell, just enough to permit tracking on the shores of the island and in a few open areas. The tracks of two squirrels (included in the 16) were observed, but it would have been possible for many squirrels to have been active on the island without leaving tracks on the snow. The remains of freshly shredded white spruce cones were also observed on the last day of the study, but they are believed to have been scattered by one of the squirrels whose tracks were observed. That more evidence of squirrel feeding was not found is not surprising since the island's cone crop failed that fall, and evidence of squirrel feeding on other available foods (alder cones and various fruits and buds) is difficult to detect.

My final, and admittedly arbitrary, estimate of the red squirrel population of the island during the period 19 September to 18 October 1962 is 20 or 0.74 squirrels per

Table 2. Summary of data from Tanana River study island

Time-area count:

	Squirrels seen at stations A	B	C	D	Estimated population
19 September	1	1	0	1	36
21 September	1	1	0	1	36
26 September	0	0	0	1	12
29 September	1	1	0	0	24
6 October	1	0	0	0	12
					$\bar{x}$ = 24

Coefficient of variation (C) = .5

90% confidence interval for true mean:

$$L_1 = 24 - 5.4(2.1) = 13$$

$$L_2 = 24 + 5.4(2.1) = 35$$

Attempted complete kill:

Trapping - 745 trap-nights from 8 to 18 October 1962 produced: 3 red squirrels
1 flying squirrel

Hunting - 40 man-hours from 10 to 18 October 1962 produced: 11 red squirrels

Tracks in the snow indicated that at least two squirrels survived.

Emigration and immigration were considered to be negligible.

Minimum population: 16 red squirrels

Number of dreys on the island: 23

Number of middens on the island: 14

Size of the island: 27 acres

Final estimate of the red squirrel population during the period of the study: 20 or 0.74 squirrels/acre.

acre. All previously reported censuses of red squirrels have been made in more southern latitudes, and the densities recorded are generally less than one squirrel per acre (Layne, 1954; Burt, 1957; and others). However, Klugh (1927) reports a spring population of nine squirrels per acre in ". . . a mixed forest of pine, hemlock, cedar, oak (red and white), beech, maple, butternut and hickory . . ." at Great Bend, Ontario, near the shore of Lake Huron.

An accurate and efficient method of censusing red squirrel populations would be an invaluable tool in future studies on the role of red squirrels in spruce forest ecology. Although the time-area count conducted on the island gave what appears to be a fairly reliable estimate of the population, without the results of the attempted complete kill we would have little knowledge of the squirrel density on the island. The 90% confidence interval of 13 to 35 is rather large, but the time-area counts made by Flyger (1959) and Fitzwater (1941) show even more variability. The location of the observation stations, the visibility (influenced by foliage density and weather), the degree of squirrel activity, and the ability and concentration of the observer introduce so much variability that it would be difficult to compare the results of two time-area counts. Goodrum (1940) and Uhlig (1956) claim considerable success using time-area counts to obtain rough estimates of gray squirrel populations over large areas (7,000 and 10,000 acres, respectively), but for relatively small study areas greater precision is needed. Layne (1954) and others believe the complete kill to be an effective method on small, isolated areas. When completed before an influx of new squirrels occurs, Layne believes that the majority of the remaining squirrels can be counted. In my experience, however, it is the quiet, inconspicuous squirrels that escape the kill and, therefore, it is difficult to estimate the number of survivors. Even if the complete kill technique were sufficiently accurate, the fact that it destroys the population being studied would prohibit its use in many cases.

When we know more about the relationships involved, perhaps the number of dreys per acre or the number of active middens per acre (see Table 1) will give us a satisfactory estimate of the population, but in order to learn these relationships, we need to develop a more direct method. The technique we are looking for may be a modification of that proposed by Schnabel (1938), which in turn is a modification of the Jackson-Peterson method or the so-called "Lincoln Index." The formula for this method, adapted from Schnabel (1938), is:

$$N = \frac{\sum (tM)}{\sum r}, \text{ where}$$

N = the estimated population
t = the number of squirrels captured in 1 day
M = the number of squirrels previously marked and available for capture on the day of trapping
r = the number of marked squirrels caught in 1 day

Flyger (1959) has shown that for gray squirrels the Schnabel method is more accurate when the number of marked and unmarked squirrels seen by an observer in the woods is used rather than the number of marked and unmarked animals caught in traps. Apparently the proportion of the population which can be seen by an observer is larger and more truly representative than the proportion of the population that is subject to trapping.

Although red squirrels are well known for their scolding chatter, the study on the island leaves little reason to doubt that some, perhaps many, remain quiet and go unobserved, even when observations are made in the early morning when the squirrels are most active. It may, however, be possible to make uniquely accurate censuses from late fall to early spring by taking advantage of the marked territorial behavior exhibited by red squirrels in Alaska during that part of the year. Territoriality in Tamiasciurus has been extensively studied by Smith (1963). A fellow graduate student, Karl Schneider, and I have trapped a number of squirrels this winter, marked them with a purple dye, and then released them where they were caught after holding them in captivity long enough for another squirrel to move in and take over the cache and territory of the trapped squirrel. Within a very short time (30 sec at the most) after the marked squirrel was released, the new owner betrayed its presence by excited behavior.

An observer equipped with a recording of red squirrel territorial and aggressive calls could observe a large percentage of the population and make an accurate estimate of the population using the Schnabel method. The recording would be easy to get; my captives elicited territorial and aggressive calls repeatedly while being fed. A decoy, such as a squirrel in a wire cage, might also be effective.

The density measured during this study appears to be low for a vigorous white spruce stand such as the one that occurs on the island and could be the result of the complete failure of the island's cone crop. Unpublished observations by T. Neil Davis, William O. Pruitt and myself indicate that the white spruce habitat in the vicinity of College, Alaska, supports fall populations of from two to eight red squirrels per acre; in addition, preliminary trapping and observations indicate almost as many flying squirrels. The degree of dependence of red squirrel populations on cone abundance has yet to be determined, but the situation on the study island, plus the feeding trials, indicates that it may be high.

Sufficient records have not been kept to establish whether red squirrels are cyclic, but Hatt (1929) believes they are most abundant every third year at Leland, Michigan, and Hamilton (1939) has data indicating that they are most numerous every eight years in western New York. White spruce cone crops fluctuate drastically. In the Lake States and southern Canada, excellent crops occur every 2 to 6 years (Roe, 1952). It is believed that excellent crops occur less frequently in interior Alaska (personal communication with Robert A. Gregory, Northern Forest Experiment Station). Whether there is any causal relationship between the fluctuations of red squirrel populations and the fluctuations of white spruce cone crops is a question that could best be answered by a simultaneous study of both phenomena over a period of years.

Feeding Trials

I. Response of Red Squirrels to a White Spruce Seed Diet following Starvation

One squirrel (no. 34) died after losing 28.7% of its body weight during the 4-day starvation period, but the three squirrels that survived responded well to the white spruce seed diet (Fig. 5 and Table 3). By the end of the experiment, after being on white spruce seed for 22 days, two of the survivors had regained the weight they had lost during the period of starvation. Squirrel no. 24 was still 2 to 3% below his initial weight, but, as Figs. 6 and 7 and Table 4 show, a change of 2 to 3% is well within the range of variation of red squirrel weights under the conditions of these experiments.

The low weights recorded on 25 February are the result

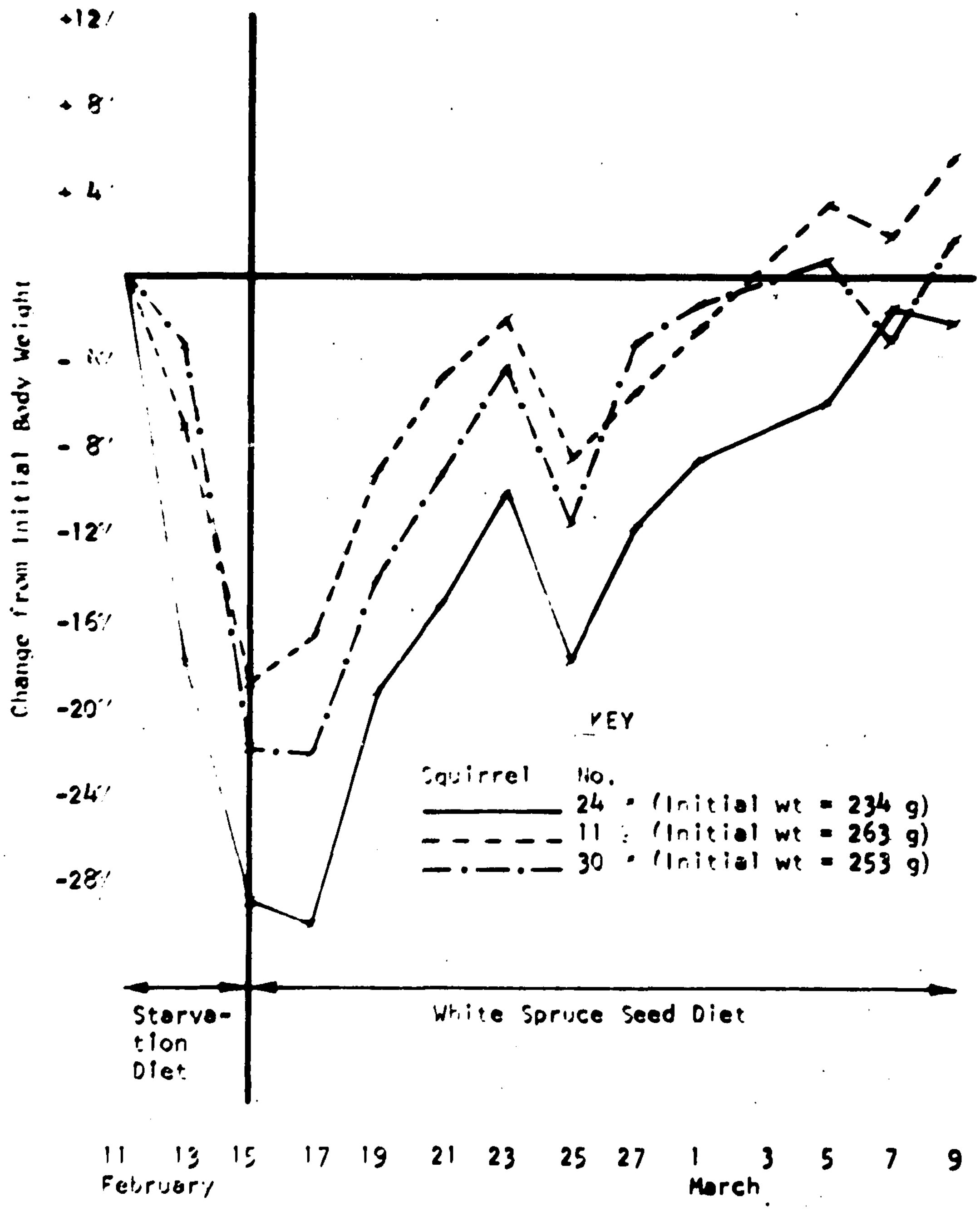

Fig. 5. Response of red squirrels to white spruce seed diet following starvation.

Table 3. Response of red squirrels to white spruce seed diet following starvation

Squirrel		Weight in Grams													
		On Starvation Diet			On White Spruce Seed Diet										
		February										March			
No.	Sex	11	13	15	15	17	19	21	23	25	27	1	5	7	9
11	F	263	245	213	213	218	239	251	258	241	249	256	273	267	277
24	M	277	228	197	197	195	224	233	249	228	245	254	261	273	272
30	M	253	245	197	197	197	218	230	243	224	245	250	254	246	257
34	F	247	203	176 (dead)											

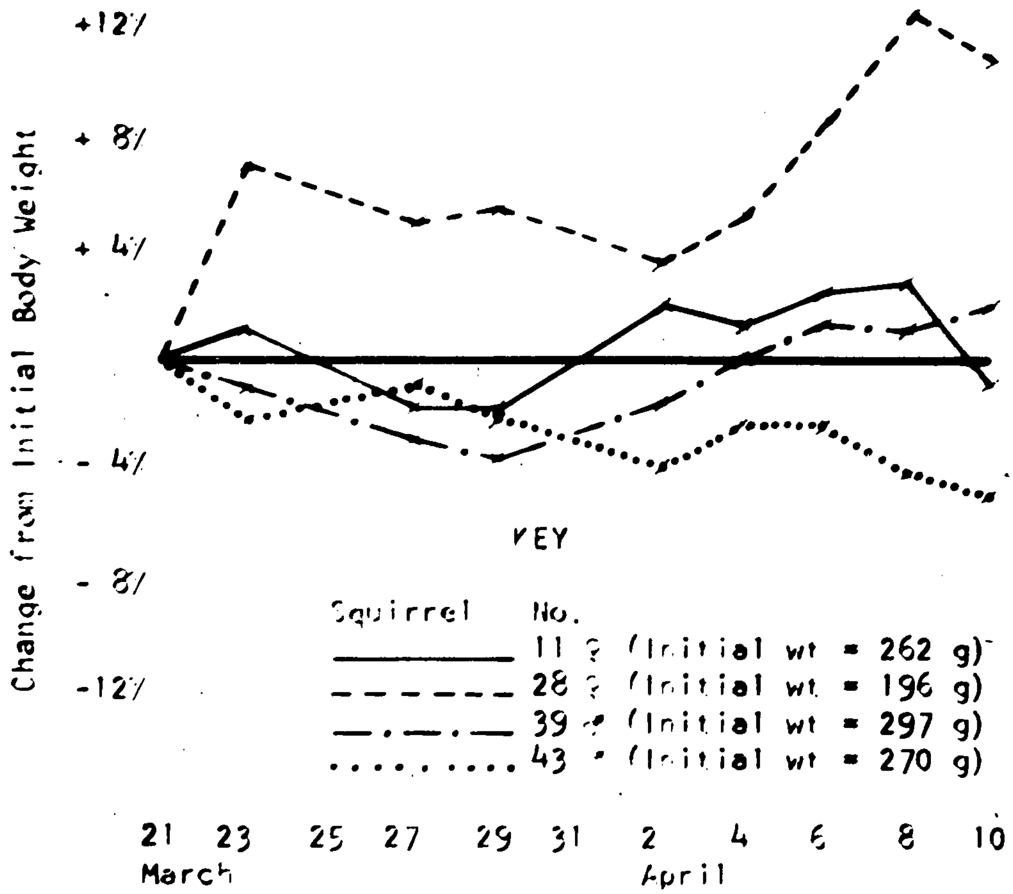

Fig 6. Changes in the weights of red squirrels on a constant diet of laboratory chow.

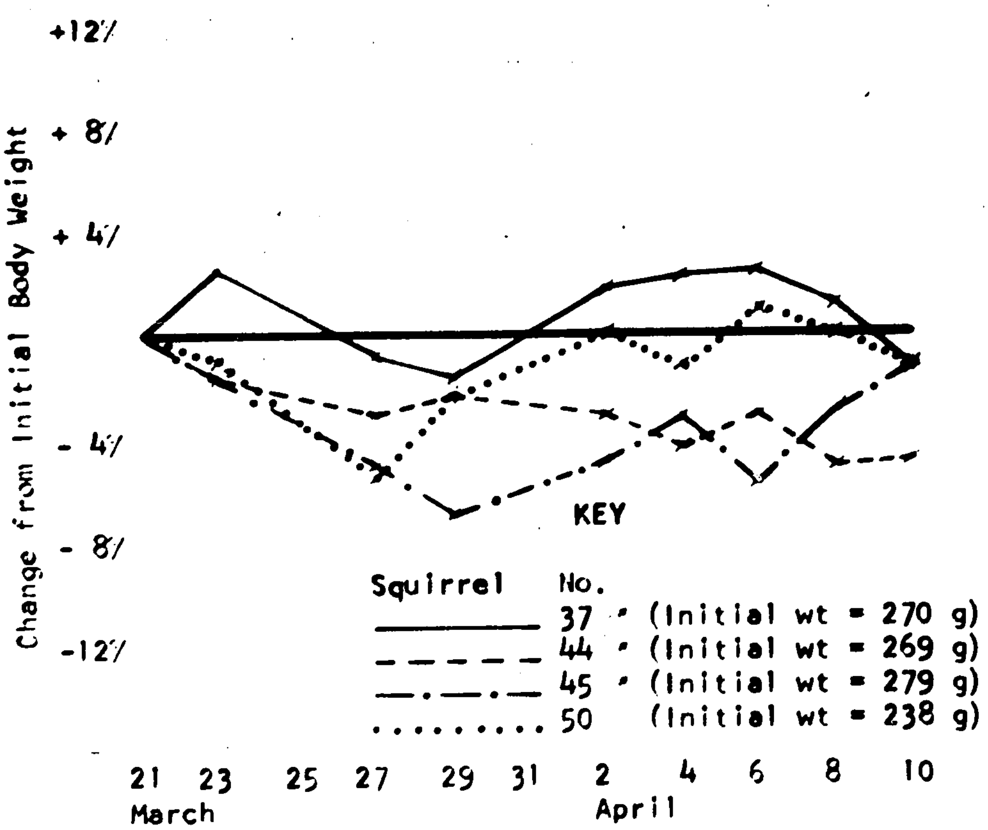

Fig. 7. Changes in the weights of red squirrels on a constant diet of laboratory chow. The sex of no. 50 was not recorded.

Table 4. Changes in the weights of red squirrels on a constant diet of laboratory chow (in grams)

Squirrel		March				April				
No.	Sex	21	23	27	29	2	4	6	8	10
11	F	262	265	258	258	267	264	268	269	259
28	F	196	211	206	207	203	206	213	221	217
37	M	270	278	268	267	275	276	277	273	268
39	M	297	294	288	286	292	297	301	300	292
43	M	270	265	269	264	259	263	263	259	256
44	M	269	265	260	262	260	257	260	255	256
45	M	279	274	266	259	266	269	263	271	274
50	?	238	235	225	232	238	234	240	238	234

of the squirrels exhausting the supply of cones provided on 25 February. The fact that they continued to gain weight on the white spruce seed diet, despite the temporary setback, may be significant. Certainly, this experiment demonstrates the potential importance of white spruce seed in the diet of red squirrels. These seeds alone contain sufficient nutrients to bring the squirrels from a severely undernourished condition back to an apparently normal condition.

During the 22-day interval the following numbers of white spruce cones were utilized:

No. 11	female	4,019 or 183/day
24	male	3,914 or 178/day
30	male	3,783 or 172/day

Red squirrels in the wild probably would not use this many white spruce cones. See page 52 for a discussion of the winter food habits of red squirrels.

There was no apparent correlation between the weather (Table 5) and the weight changes of the squirrels in this or any of the feeding trials.

II. Response of Red Squirrels to a White Spruce Seed Diet following a Constant Diet of Laboratory Chow

When transferred from a laboratory chow diet to a white spruce seed diet, all of the squirrels participating in this trial (except no. 10) showed an immediate loss of from 3 to 12% of their individual initial weights (Figs. 8,

Table 5. Climatological data

Date	Temperature (°F) Max	Min	Precipitation (in.) Snow	Water equiv.	Remarks
Feb.					
10	3	-14			
11	3	-12			
12	2	-15			
13	7	-12	1.0	.05	
14	10	3			
15	10	5			
16	15	9			
17	20	5			
18	29	3			
19	20	8	1.0	.07	
20	22	15			
21	29	- 2			
22	9	- 3			
23	24	2	1.4	.06	
24	29	14			
25	43	10			
26	21	10	.3	.02	
27	35	8			
28	35	2			
Mar.					
1	11	4	.5	.02	
2	16	7	1.0	.01	
3	26	8			
4	25	8	.7	.07	
5	28	16	T	T	T=trace
6	33	19	1.0	.04	
7	29	19			
8	38	28		.01	Rain
9	37	27		.20	Rain and snow
10	32	12	4.0	.40	Blizzard winds
11	13	-21			Blowing snow
12	2	-12			
13	12	-21			
14	0	-18			
15	12	-13			
16	4	-17			
17	20	-11			
18	20	- 6			
19	18	-13			
20	8	-18			

Table 5 (continued)

Date	Temperature (°F) Max	Min	Precipitation (in.) Snow	Water equiv.	Remarks
Mar.					
21	11	- 7			
22	22	2			
23	23	- 3			
24	31	10	3.5	.16	
25	33	28	7.0	.70	
26	32	2	8.0	1.07	
27	10	-10	T	T	
28	-2	-27			
29	8	-12			
30	15	-13			
31	23	6	.5	.06	
Apr.					
1	27	5			
2	23	- 8			
3	25	7			
4	25	- 1			
5	32	13	.3	.03	
6	37	13			
7	37	15			
8	37	22			
9	42	26	1.5	.07	
10	31	1			
11	31	0			
12	26	0			
13	41	17			
14	41	17			
15	26	15	2.0	.08	
16	16	5	2.0	.18	
17	17	-11			
18	15	- 7	T	T	
19	23	2			
20	32	11			
21	43	21			
22	51	33			
23	45	28			
24	41	29			
25	45	30			
26	48	26			
27	52	34			
28	54	33			

Table 5 (continued)

Date	Temperature (°F) Max	Min	Snow	Water equiv.	Remarks
Apr.					
29	54	36			
30	56	34			
May					
1	46	34		.11	Rain
2	49	34			
3	44	33			
4	49	36			
5	42	30			
6	48	25			
7	48	32			
8	42	30			

U. S. Coast & Geodetic Survey
College, Alaska

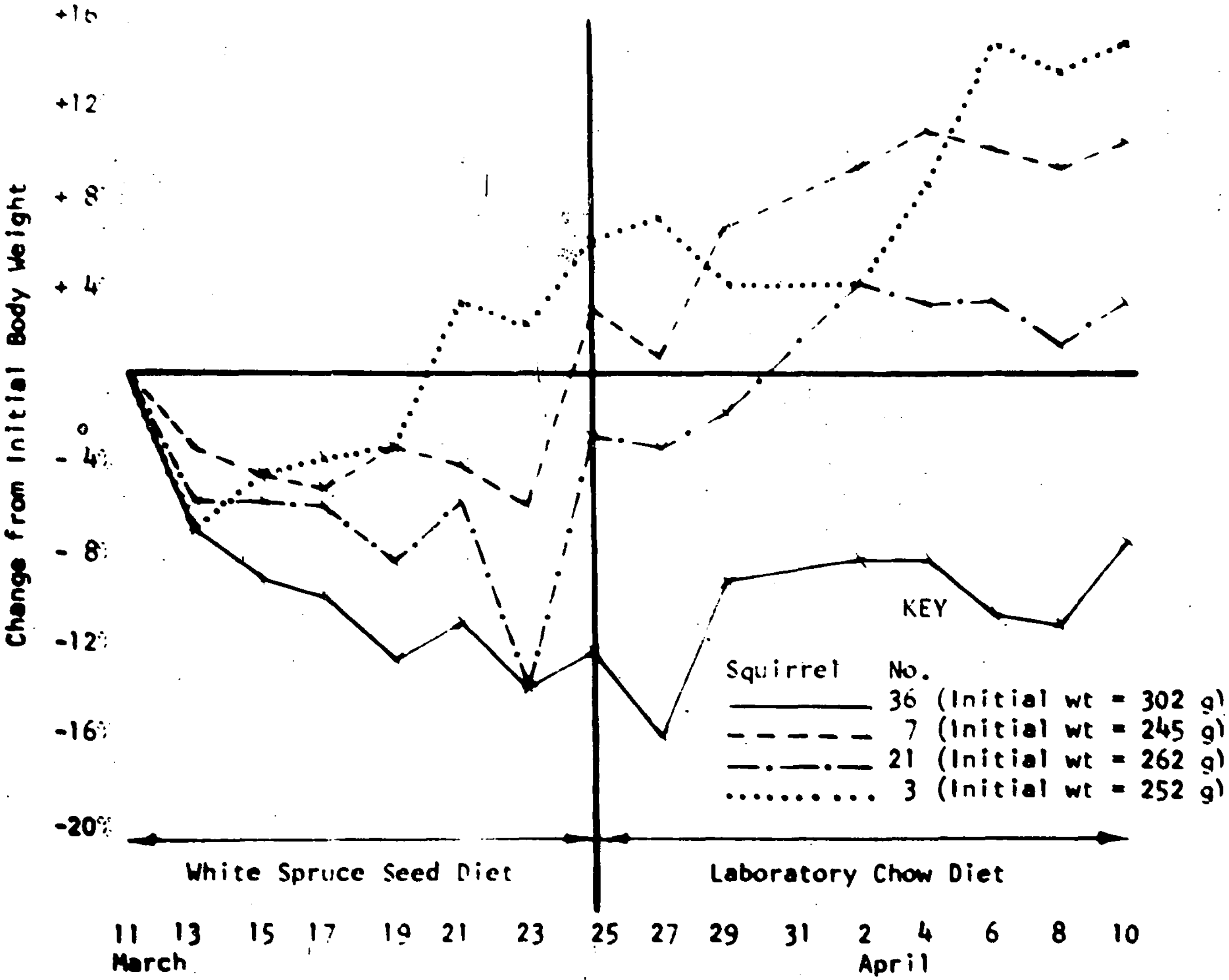

Fig. 8. Response of male red squirrels to white spruce seed diet following constant diet of laboratory chow.

9, 10, and 11 and Tables 6 and 7), most likely due to a reluctance to utilize the spruce cones after having become accustomed to the laboratory chow. After the initial drop, the general trend was for the weights to level off and then gradually return to the original level. There were, however, several exceptions. The weight losses that the male squirrels (Figs. 8 and 9) experienced between 21 and 23 March were apparently the result of a short supply of cones. The fact that the males gained weight steadily before and after the two dates indicates that something drastic happened to them during the 2-day interval. Since the females (Figs. 10 and 11), which were then on laboratory chow and subject to the same environmental influences as the males, gained weight during that interval, the weight loss experienced by the males is assumed to have been associated with the food supply.

Squirrel no. 10 gained weight consistently throughout the experiment (Fig. 11). Although it always had an abundance of laboratory chow available, no. 10's weight dropped from 324 g (unusually heavy) on 19 December to 239 g on 30 January and to 213 g on 11 March, the day this experiment was started. Perhaps the excitement of being trapped and weighed somehow stimulated its appetite. One of the "controls" (no. 28) produced a similar response (Fig. 6). It had weighed 225 g on 30 January. Squirrel no. 36 (Fig. 8)

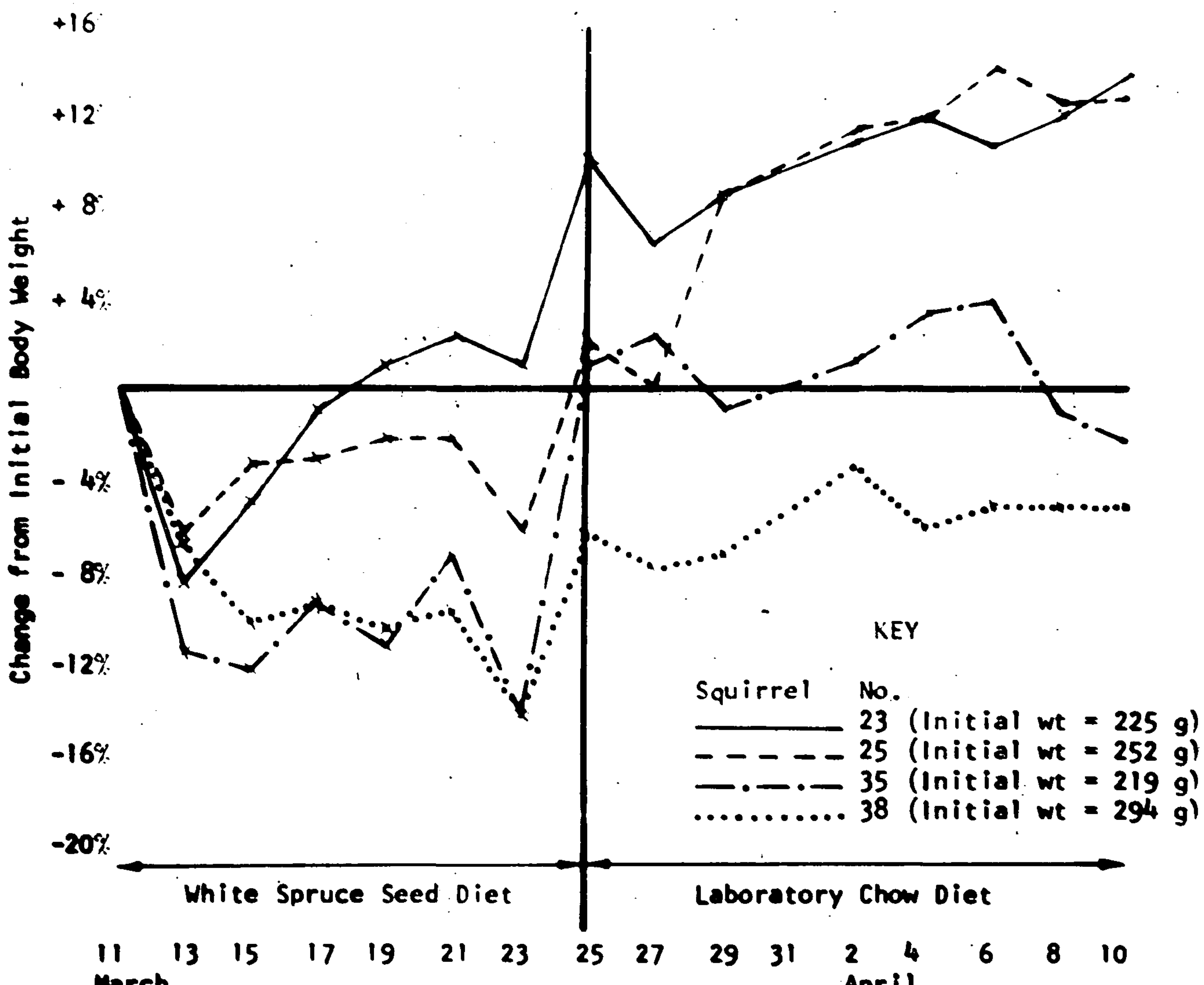

Fig. 9. Response of male red squirrels to white spruce seed diet following constant diet of laboratory chow.

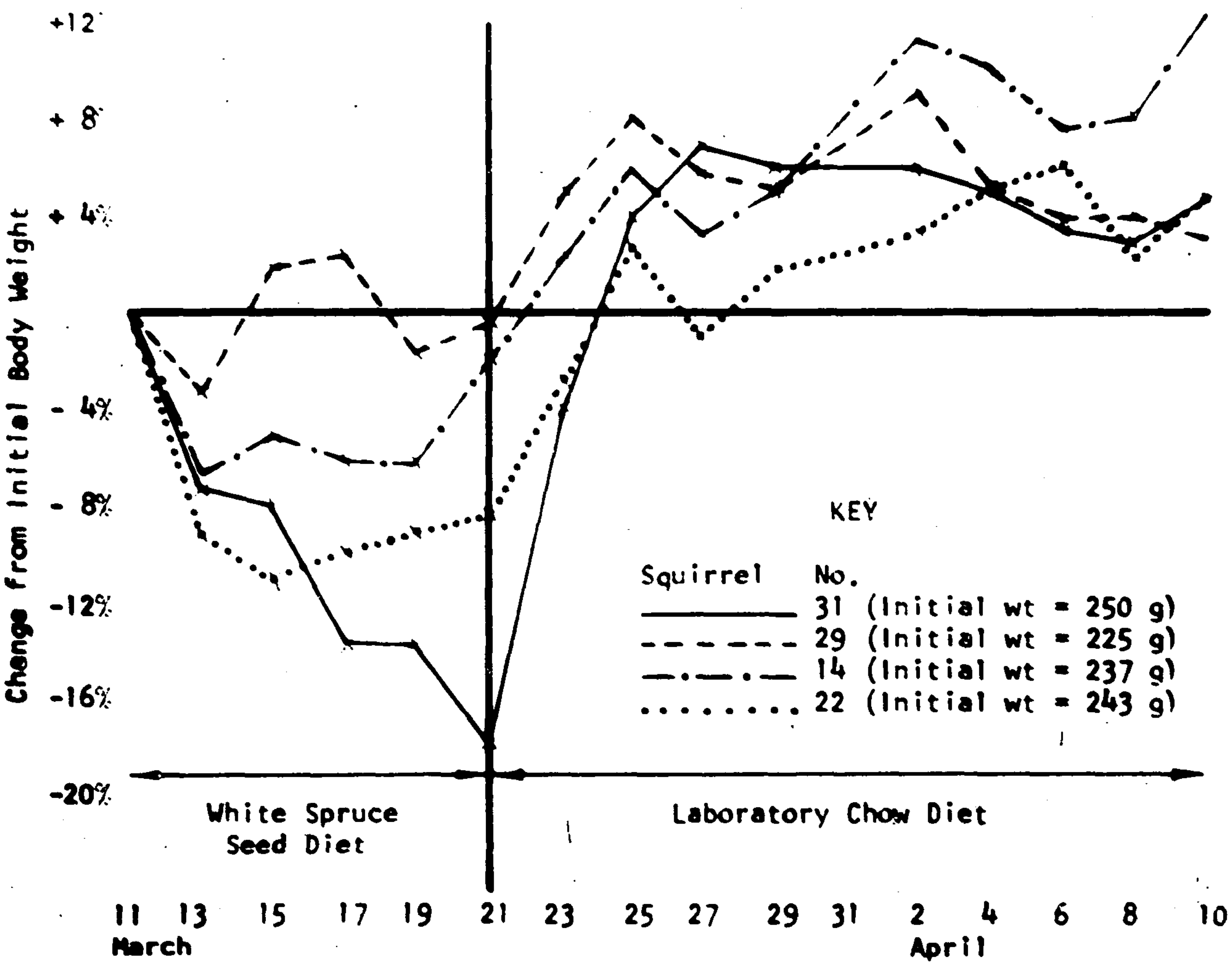

Fig. 10. Response of female red squirrels to white spruce seed diet following constant diet of laboratory chow.

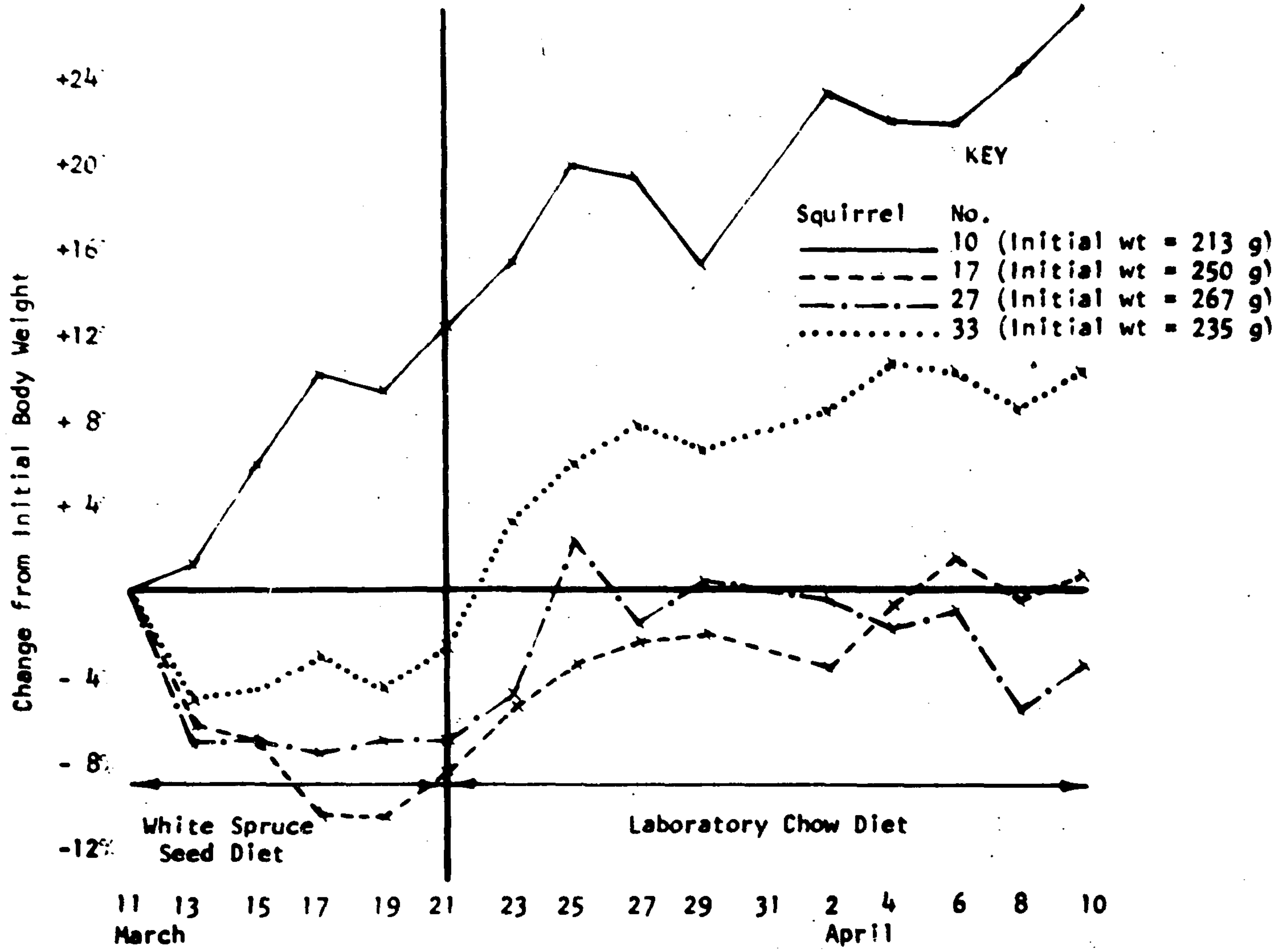

Fig. 11. Response of female red squirrels to white spruce seed diet following constant diet of laboratory chow.

Table 6. Response of male red squirrels to white spruce seed diet following constant diet of laboratory chow

Squirrel No.	Weight in Grams															
	On White Spruce Seed Diet								On Laboratory Chow Diet							
	March 11	13	15	17	19	21	23	25	25	27	29	April 2	4	6	9	10
3	252	233	238	242	243	260	258	267	267	270	262	262	273	289	286	289
7	245	236	234	232	236	235	251	252	252	246	261	267	273	270	268	271
21	262	246	246	246	240	245	225	253	253	252	257	273	270	270	266	271
23	225	206	214	222	227	230	227	248	248	242	244	250	252	250	252	256
25	252	235	243	244	247	247	236	258	258	252	273	281	282	285	283	284
35	219	193	192	198	194	203	187	222	222	224	217	222	227	228	217	214
36	302	280	274	272	261	268	258	265	265	252	275	276	276	269	268	280
38	294	274	263	266	262	265	252	275	275	270	272	283	276	278	278	279

Table 7. Response of female red squirrels to white spruce seed diet following constant diet of laboratory chow

Squirrel No.	Weight in Grams															
	On White Spruce Seed Diet						On Laboratory Chow Diet									
	March 11	13	15	17	19	21	21	23	25	27	29	April 2	4	6	8	10
10	213	216	226	235	233	239	239	245	256	255	245	263	261	260	266	271
14	237	221	225	222	222	233	233	245	251	244	250	265	262	255	256	266
17	250	233	232	224	224	229	229	236	241	244	245	241	248	253	249	252
22	243	220	216	219	221	222	222	236	251	240	247	251	256	258	249	255
27	267	247	247	247	248	248	248	255	274	263	268	266	263	265	252	258
29	225	217	229	230	221	224	224	237	243	238	236	245	237	234	234	232
31	250	231	230	216	216	205	205	240	260	268	265	265	262	259	258	261
33	235	223	224	228	225	229	229	244	249	253	251	255	260	259	254	259

continued to lose weight after the initial loss and never did approach its initial weight, even when returned to a diet of laboratory chow. This squirrel had weighed 257 g on 11 February, but on 11 March, when the experiment was started, it weighed 302 g. Apparently the squirrel was considerably overweight and the change in diet and circumstances of the experiment somehow caused it to lose some of its excess weight. The response of squirrel no. 38 (Fig. 9) was similar to that of no. 36, apparently for the same reasons.

Squirrel no. 31, a female, was the only squirrel to show no indication of being able to maintain its weight on the white spruce seed diet (Fig. 10). Possibly even this squirrel would have regained its initial weight if the interval during which the squirrels were given white spruce cones could have been extended.

During this experiment the squirrels consumed an average of 144 cones per squirrel per day (Table 8). It seems unlikely, however, that red squirrels in the wild, despite greater activity, consume this many white spruce cones. In the fall of 1962 the author excavated about 15 red squirrel caches, in the largest of which were found approximately 6,000 white spruce cones. Undoubtedly, many cones were not found; in addition to large caches a few meters in diameter, red squirrels in this area make many small, auxiliary caches over a relatively large area.

Table 8. Number of white spruce cones utilized by red squirrels during Feeding Trial II

Squirrel No.	Sex	Total Consumed	Daily Average
3	M	2,156	154
7	M	2,136	153
21	M	2,138	153
23	M	2,221	159
25	M	2,423	173
35	M	2,414	172
36	M	1,922	137
38	M	2.152	154
		Mean for males =	157
		C =	.74
10	F	1,442	144
14	F	1,265	127
17	F	1,156	116
22	F	1,379	138
27	F	1,328	133
29	F	1,372	137
31	F	1,397	140
33	F	1,102	110
		Mean for females =	131
		C =	.92
		Over-all mean =	144
		C =	1.1

Nevertheless, I would estimate that none of the squirrels whose caches I excavated had stored more than 8,000 white spruce cones. Thus, it appears that if the squirrels strip 100 or more cones per day, their supply will become exhausted long before the winter is over. I would guess that red squirrels in the wild utilize an average of 40 to 50 white spruce cones per squirrel per day during the winter. General field observations and the cursory examinations by the author of red squirrel stomach contents at various times throughout the winter indicate that although white spruce seed is the primary winter food of the red squirrel, supplementary foods (discussed below) are frequently, if not always, utilized.

It is almost certain that red squirrels in Alaska clip shoots from the ends of upper branches of white spruce trees in late winter and early spring. I have seen 100 or more of these shoots, all about 5 cm long, scattered around individual trees, and a local resident (Ann Larson) has observed these shoots falling from the upper parts of trees in which she knew there were squirrels. Wagg (1963) reports that red squirrels at Hinton, Alberta, ". . . were observed cutting the lateral and terminal twigs and feeding on the vegetative and flower buds of white spruce." Red squirrels on Bull Island in Flathead Lake, Montana, caused similar damage to ponderosa pine (Pinus ponderosa Dougl.) in winter in their efforts to get at the cambium layer (Adams, 1955). It is not known what portion of the shoots the squirrels utilize in Alaska. Since most of the shoots that are cut come from the upper part of the tree, it is almost certain that some of them bear reproductive as well as vegetative buds. Thus red squirrels may affect the fall cone production through their action in cutting shoots from the crown of the tree during the spring. Adams (1955) believes that the damage he observed may occur mostly in poor cone crop years and may lead to ". . . intensified damage extending into the years immediately following." This could also be the case in Alaska.

Red squirrels eat mushrooms throughout the winter (personal observations and Buller, 1920). Other supplementary foods probably include the buds, fruits and, possibly, the bark of most of the woody plants found in the tiaga. Whether these supplementary foods can effectively buffer red squirrel populations in the absence of white spruce seed is not known. Data from the study island (see page 27) suggest that the amount of available white spruce seed does influence the squirrel population, at least locally.

III. Response of Flying Squirrels to a White Spruce Seed Diet

That flying squirrels, unlike red squirrels, are unable to maintain themselves on a diet of nothing but white spruce seed, is clearly demonstrated in Fig. 12 and Table 9. These squirrels would have undoubtedly died if they had been forced to remain on the white spruce seed diet for two or three more days, for their weights had already dropped to a critical level. Gerstell (1942) demonstrated that relatively small mammals usually cannot withstand weight losses exceeding 30% of their body weight. The right-hand portion of Fig. 12 shows fluctuations in the weights of the same flying squirrels while on a constant diet of laboratory chow.

Although no formal preference tests were performed with flying squirrels, they consistently preferred other foods to either white or black spruce cones. Immediately after capture they preferred laboratory chow to spruce cones. In contrast, the red squirrels, when first caught, always preferred spruce cones to laboratory chow. Gradually the red squirrels would develop a taste for the chow and after 2 or 3 weeks they would prefer it, but never to the degree that the flying squirrels did. A local resident, Glen Haddock, who successfully bred a pair of flying squirrels in captivity, found that his squirrels would eat a variety of foods such as milk and most dairy products, assorted unsalted nuts, most fruits, raw or cooked potatoes, and chicken readily but would not utilize spruce cones even when nothing else was available.

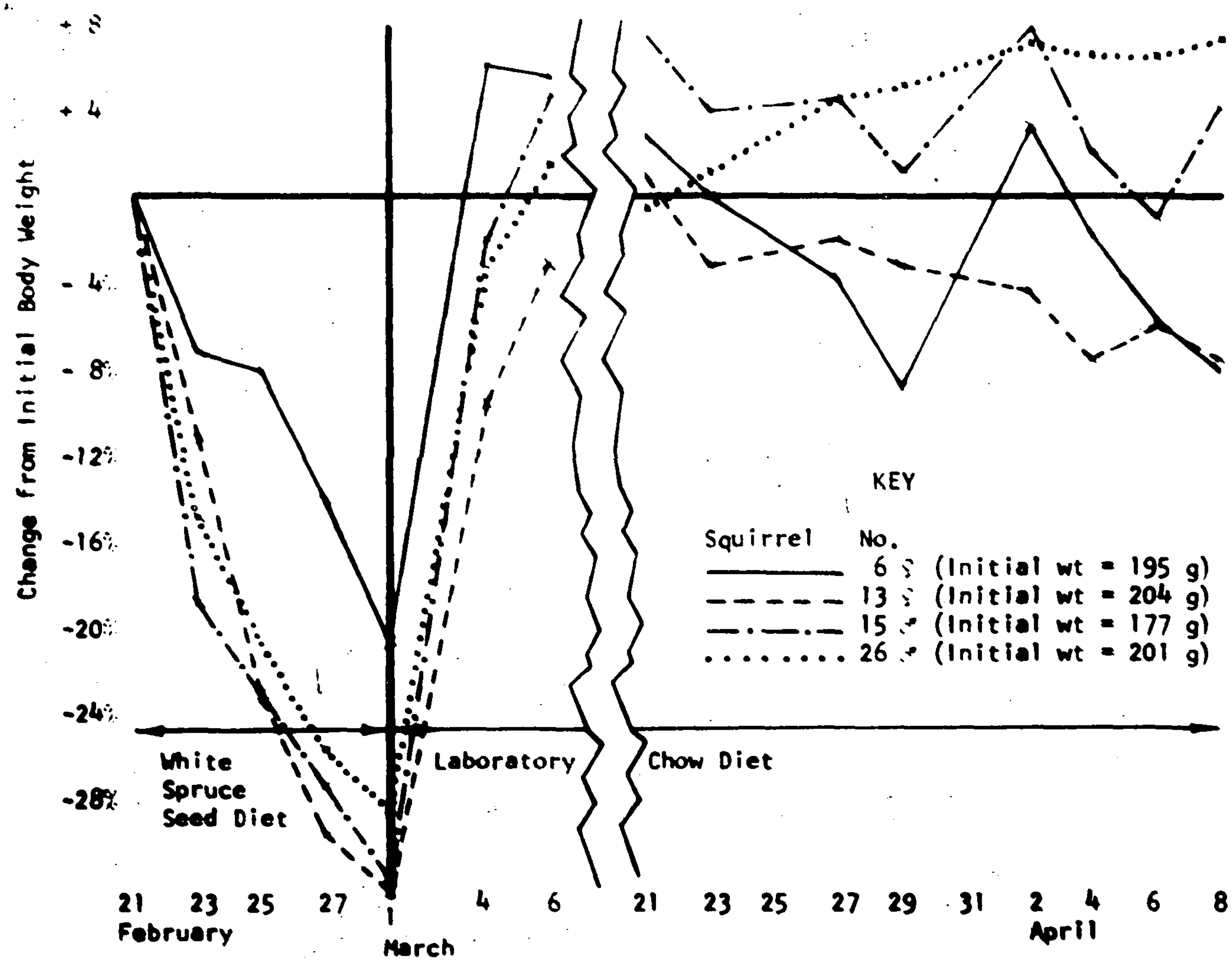

Fig. 12. Response of flying squirrels to white spruce seed diet.

Table 9. Response of flying squirrels to white spruce seed diet

Squirrel		Weight in Grams															
		On White Spruce Seed Diet					On Laboratory Chow Diet										
		February				March								April			
No.	Sex	21	23	25	27	1	1	4	6	21	23	27	29	2	4	6	8
6	F	195	180	179	167	154	154	207	206	201	195	187	177	201	191	183	179
13	F	204	180	155	145	138	138	184	198	206	197	200	197	195	188	191	188
15	M	177	144	135	128	120	120	173	186	191	184	185	179	191	180	175	184
26	M	201	171	159	149	143	143	194	204	200	203	210	211	215	214	214	216

During this experiment the flying squirrels utilized the following numbers of cones:

No. 6	female	530 ± 10	or about 66/day
13	female	530 ± 10	or about 66/day
15	male	330 ± 10	or about 41/day
26	male	530 ± 10	or about 66/day

What relationship these figures have to the amount of white spruce seed consumed by flying squirrels in the wild is not known. However, since flying squirrels do poorly on white spruce seed and prefer many other foods to spruce cones, it seems unlikely that they consume a significant amount of spruce seed in the wild.

IV. Response of Red Squirrels to a Black Spruce Seed Diet

Although the two squirrels that participated in this trial utilized about 242 black spruce cones/day, they consistently lost weight and it seems unlikely that they could have survived more than two or three additional days without a change in diet (Fig. 13 and Table 10). Notwithstanding the fact that two squirrels constitute a small sample on which to base conclusions regarding an entire population, it appears that red squirrels are not able to gain as much nourishment from black spruce seed as they can from white spruce seed.

Analysis of the caloric content of white and black spruce seed demonstrates a small but statistically significant difference between the energy values of the seeds of

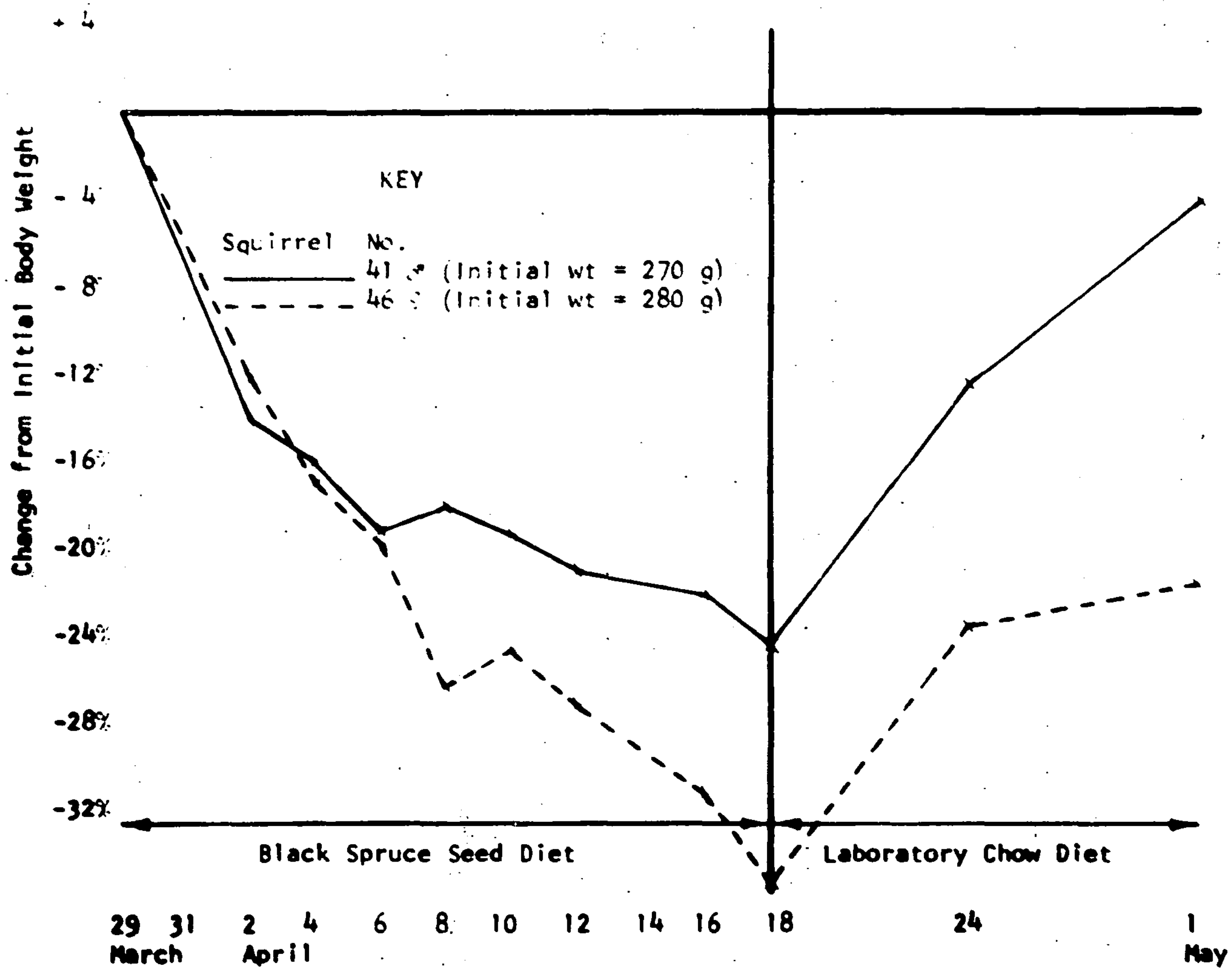

Fig. 13. Response of red squirrels to black spruce seed diet.

Table 10. Response of red squirrels to black spruce seed diet

Squirrel		Weight in Grams											
		On Black Spruce Seed Diet									On Laboratory Chow Diet		
		Mar.	April										May
No.	Sex	29	2	4	6	8	10	12	16	18	18	24	1
41	M	270	232	226	218	221	218	214	211	204	204	236	254
45	F	280	246	233	224	206	209	204	192	180	180	214	219

the two species (Table 11). These analyses were made on seed from the 1963 crop, while 1962 cones were used in the feeding experiments. However, it is assumed that during both years seed quality was comparable. It is interesting to note that although samples 5W and 4B were from the same cache and, therefore, developed in the same mixed stand of white and black spruce, their energy content was quite different.

Why red squirrels maintain relatively constant weights and survive very well for extended periods on laboratory chow, which has about 4,390 cal/g, but lose weight steadily on black spruce seed, which has about 6,053 cal/g, is not known. The fact that these squirrels survive well, at least for limited periods, on white spruce seed, which has only about 9% more calories per gram than black spruce seed, indicates that the critical difference between the seeds of the two species as a food for red squirrels involves something other than caloric content per gram of seed. Since black spruce cones are harder and smaller than white spruce cones, it is likely that a squirrel must expend more energy in order to extract the seeds of the former, but it is unlikely that this would account for the difference in the squirrels' responses to the two seed diets. The squirrels in this experiment had daylight time to eat three or four times as many cones as they did. Therefore, it appears that

Table 11. Caloric content of spruce seed from the 1963 cone crop

White Spruce

Sample No.	Calories/Gram
2W	6,669
3W	6,570
4W	6,491
*5W	6,731
	$\bar{x}$ = 6,615
	C = .016

99% confidence interval for true mean:

L_1 = 6,615 - 5.841(53) = 6,305

L_2 = 6,615 + 5.841(53) = 6,925

Black Spruce

Sample No.	Calories/Gram
2B	6,127
3B	5,961
*4B	6,014
5B	6,108
	$\bar{x}$ = 6,053
	C = .013

99% confidence interval for true mean:

L_1 = 6,053 - 5.841(38) = 5,831

L_2 = 6,053 + 5.841(38) = 6,275

*Samples 5W and 4B were taken from the same cache.

black spruce seed is lacking in one or more essential nutrients that are present in both white spruce seed and laboratory chow; or that black spruce seed contains something undesirable which white spruce seed does not; or the two squirrels that participated in this experiment are unique and unrepresentative in their inability to maintain relatively constant weights, even for a short interval, while on a black or white spruce seed diet.

V. White Spruce-Black Spruce Cone Preference Tests

Red squirrels were found to have a marked preference for white spruce cones over black spruce cones (Fig. 14 and Table 12). In 65.3% of the tests all three of the white spruce cones were selected and stripped before any of the black spruce cones were selected and stripped. Conversely, in only 1.7% of the tests were all three of the black spruce cones selected and stripped before any of the white spruce cones were utilized. One squirrel, no. 25, selected and stripped white spruce cones in favor of black spruce cones every time without exception through 20 complete sets. After the white spruce cones were gone, most of the squirrels would strip the black spruce cones readily. However, although he had frequent opportunities to utilize more, on only two occasions did no. 25 shred one of the remaining black spruce cones. He seemed to be waiting for more white

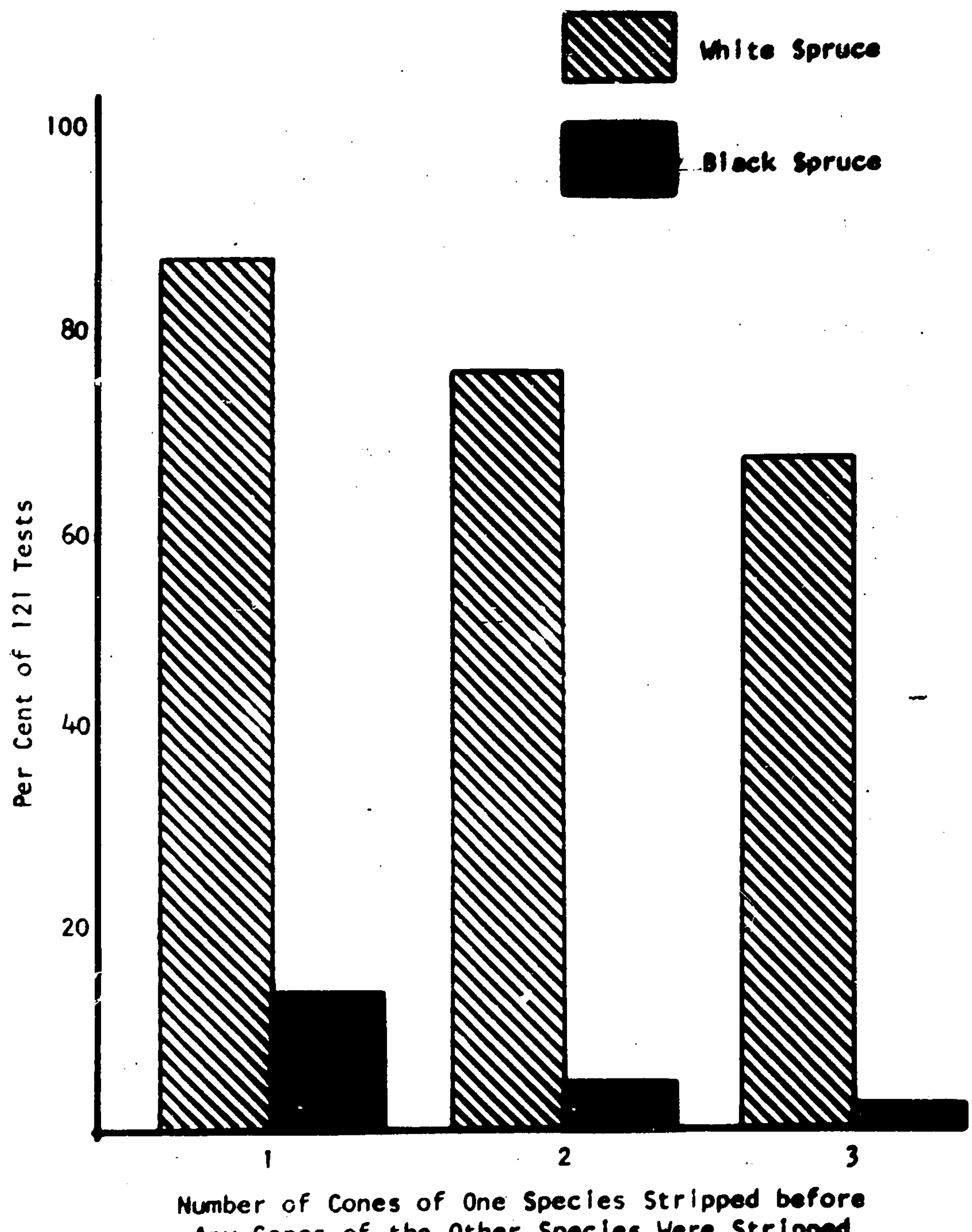

Fig. 14. Results of preference tests in which red squirrels selected cones from a board on which three white spruce cones and three black spruce cones were randomly positioned.

Table 12. White spruce-black spruce cone preference tests

Squirrel No.	Sex	Tests completed	Tests favoring white spruce	Number of times all white spruce cones were stripped before any black spruce cones	Number of times all black spruce cones were stripped before any white spruce cones
11	F	20	19	14	0
14	F	20	15	9	1
23	M	22	19	11	0
25	M	20	20	20	0
27	F	2	2	2	0
28	F	5	5	5	0
29	F	18	15	11	1
35	M	3	1	0	0
37	M	1	1	1	0
38	M	8	8	4	0
39	M	2	2	2	0
	Totals:	121	107 (88.4%)	79 (65.3%)	2 (1.7%)

spruce cones. After he had completed 20 tests, I presented him with five large black spruce cones and one unusually small white spruce cone. He sniffed each of the cones and selected and shredded the white spruce cone as expected.

All of the squirrels appeared to use the sense of smell more than that of sight to distinguish between the two species of cones. About 10% of the time a squirrel would start at one end of the board on which the cones had been placed and smell each cone in order until a white spruce cone was encountered. That white spruce cone would be stripped, and then the process would be repeated until all of the white spruce cones had been selected and shredded in a surprisingly orderly fashion.

There are a number of possible reasons why red squirrels prefer white spruce cones to black spruce cones. The seeds of white spruce are almost twice the size of those of black spruce (U. S. Forest Service, 1948). Also, as previously demonstrated, white spruce seeds contain more calories per gram, perhaps partly as a reflection of the higher seed coat to endosperm ratio in the smaller seeds. The feeding trials suggest that white spruce seeds also contain important nutrients not present in black spruce seed. In addition, black spruce cones are noticeably harder than white spruce cones and appear to be more difficult for the squirrels to strip. The evidence indicates that in terms of energy and nutrition it is more economical for red squirrels to utilize white spruce cones rather than black spruce cones.

This preference for white spruce cones over black spruce cones appears to influence the distribution of red squirrel densities within the taiga. Dice (1921, according to Hatt, 1929) and others have found red squirrels to be rare in the black spruce forests of Alaska. My observations in the vicinity of College indicate that in the areas where stands of white and black spruce meet and intergrade, red squirrel populations are at least as dense as those in the white spruce. Within the black spruce stands proper, however, the squirrel populations seem to be less dense than in the white spruce. Apparently, red squirrels compete for the white spruce habitat, the less successful squirrels being forced into the marginal black spruce.

VI. Seed Scattering Tests

As shown in Table 13, 6.6% of the seeds in the productive zone were scattered or rejected by the squirrels used in this experiment. Only 10.6% of these scattered seeds were filled, significantly less than the 46.1% that would be expected on the basis of viability tests for the entire population of cones (Table 14). Apparently the squirrels can distinguish between filled and unfilled seeds without breaking the seed coat. Thus, ~~the filled~~ seeds that

Table 13. Results of the seed scattering tests

Per Cent of the Seeds in the Productive Zone That Were Scattered or Rejected

N. = 50
Range = 1.8 to 20.8
$\bar{X}$ = 6.6±1.2 at 95% level
C = .62

Per Cent of the Above Scattered or Rejected Seeds That Were Filled

N = 50
Range = 0 to 100
$\bar{X}$ = 10.7±5.8 at 95% level
C = 1.9

Per Cent of the Estimated Number of Filled Seeds in the Productive Zone That Were Scattered

N = 50
Range = 0 to 14.8
$\bar{X}$ = 1.6±0.8 at 95% level
C = 1.8

TOTALS:

Cones used	50
Seeds in the productive zone	4,250
Seeds scattered	282 (6.6%)
Scattered seeds that were filled . . .	30 (10.6%)
*Estimated number of filled seeds in the productive zone	1,959 (46.1%)
Per cent of the estimated number of filled seeds that were scattered.	1.5

A chi-square test shows the difference between the expected per cent of filled seeds among those scattered (46.1) and the actual per cent of filled seeds among those scattered (10.7) to be highly significant at the 1% level.

X^2 = 142.7
Tabular value = 6.63

*Based on data presented in Table 14.

Table 14. Analysis of the local 1962 white spruce cone crop

Number of Seeds in the Productive Zone	
	N = 100
	Range = 46 to 160
	$\bar{X}$ = 86.9$\pm$4.0 at 95% level
	C = .25
Per Cent of the Seeds in the Productive Zone That Were Filled	
	N = 40
	Range = 14.6 to 74.2
	$\bar{X}$ = 46.1$\pm$4.2 at 95% level
	C = .36

are scattered are either accidentally dropped or mistaken for unfilled seeds.

It was found that approximately 1.6% of the estimated number of filled seeds in the productive zone (i.e., 0.016 X 0.461 X the number of seeds in the productive zone) were scattered. This means that red squirrels scatter about one filled seed for every two cones they strip. It is doubtful, however, that many of these seeds ever germinate. Red squirrels strip most of their cones in the immediate vicinity of their caches, the result being an accumulation of bracts and stalks called a midden (see INTRODUCTION). I have never seen any indication of spruce regeneration on a midden; in fact, my observations indicate that most plants, including large alder bushes and spruce trees up to 5 cm in diameter, in the area of a midden are killed by the decaying mass of shredded cones.

It should be pointed out that because of the very large amount of variability encountered in this experiment, the results should be considered as only a qualitative indication of what occurs in the wild.

<u>Analysis of the Local 1962 White Spruce Cone Crop</u>

The cones used in this experiment had an average of about 87 seeds in the productive zone, of which approximately 46% were potentially viable (Table 14). Werner

(1962) reports about the same number of seeds in the productive zone, but less than half as many filled seeds in a sample taken from 60 stands along the Nenana and Alaska Highways in late August, 1962. Apparently seed destruction by insects was less intense in the vicinity of College than in interior Alaska as a whole. However, since Werner collected his cones directly from the trees instead of from red squirrel caches, it is possible that the squirrels cache only those cones with the highest percentage of filled seeds.

Recommendations

Continued research is necessary if the long-term objectives of this project are to be achieved. Future investigators should approach the problem of red squirrel-white spruce relationships directly. Care should be taken to select a study area that is suitable for all phases of the study and that will be available for a number of years so that the results of successive investigators can be readily compared. I recommend:

1. That a method be devised for estimating with significant accuracy the number of cones on the trees of a 10- to 20-acre white spruce stand both shortly before and after the period of cone cutting by red squirrels.

2. That the modified Schnabel method of red squirrel census, as described on pages 30 through 32, be perfected and used in conjunction with the analysis of the cone crop damage inflicted by the squirrels.

3. That the extent of white spruce shoot clipping by red squirrels in late winter and early spring be determined, and that a method be devised for estimating the ratio of vegetative to reproductive buds on the clipped shoots so that the effect of this damage on the subsequent cone crop can be estimated.

4. That the seed scattering tests be expanded to verify the inital results and to examine the importance of this behavior to tree regeneration in the wild.

5. That the food habits of flying squirrels be studied by means of stomach content analyses.

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