RED SQUIRREL (<u>TAMIASCIURUS</u> <u>HUDSONICUS</u>) ECOLOGY

DURING SPRUCE CONE FAILURE IN ALASKA

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RED SQUIRREL (*TAMIASCIURUS HUDSONICUS*) ECOLOGY DURING SPRUCE CONE FAILURE IN ALASKA

A

THESIS

Presented to the Faculty of the
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MASTER OF SCIENCE

By

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ABSTRACT

Observations were made on a red squirrel (*Tamiasciurus hudsonicus*) population in a mature white spruce (*Picea glauca*) forest near Fairbanks, Alaska, during two years of spruce cone crop failure (July, 1964, to April, 1966). An adequate supply of old spruce cones, cached in previous years, was available during the first winter. A 67% drop in numbers of the squirrel population followed the second crop failure with the remaining squirrels utilizing spruce buds as their primary food during the winter. Stomach analyses revealed that when present, spruce seed is the major constituent in the diet. In its absence, heavy utilization of mushrooms in summer and spruce buds in winter occurs. Feeding trials conducted with captive red squirrels in March, 1965, and April, 1966, showed that about 194 old cones per day were necessary to sustain a squirrel, approximately 35% more than for cones from the current year's crop. Three squirrels survived for eight days on a diet of only white spruce buds. Analysis of old spruce cones showed that 31% of the seed was potentially viable (filled), but that only 1.4% of the seed germinated. Calorimetric determinations of old seed (minus coat), spruce buds, and mushrooms yielded values of 5,976, 4,986, and 4,552 cal/g respectively. Excavation of middens revealed up to 8,518 old, cached cones per midden, despite a crop failure. In years of normal cone production, squirrels may cut and cache 12,000 to 16,000 cones; the excess accrues each year and eventually a sufficient supply exists to maintain the squirrels through a winter following a cone crop failure.

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INTRODUCTION

This thesis represents the second part of a study aimed at determining the ecological relationships of red squirrels (Tamiasciurus hudsonicus) to the production and supply of white spruce (Picea glauca) seed and the regeneration of white spruce in interior Alaska. The project was financed by the U. S. Forest Service's Northern Forest Experiment Station (Contract No. 12-11-010-1650) and administered through the Alaska Cooperative Wildlife Research Unit at the University of Alaska at College. The time period included in this study was from July, 1964, to April, 1966.

The thesis presents some aspects of red squirrel ecology during two consecutive years of cone crop failure in a mature white spruce forest in interior Alaska. Since red squirrels utilize large quantities of white spruce seed as the major constituent of their diet during years of normal cone production (Brink 1964), this study was oriented to determine food habits in the absence of a fresh supply of cones. One phase deals with observations of natural conditions on a study area within a mature white spruce forest. The second phase consists of a series of feeding trials conducted with captive red squirrels within an outdoor enclosure on the University of Alaska campus. The feeding trials were set up in such a way that the data would be directly comparable to that obtained by Brink (1964) in a similar study.

STUDY AREA

The study area was situated within the Bonanza Creek Experimental Forest approximately 25 km southwest of College (Fig. 1). The major portion of the field work was conducted within a large stand of mature white spruce on a south-facing slope with an average elevation of 305 m above sea level. A permanent grid system 457 m square, or 21 ha (52 acres), was established within this stand to facilitate the mapping of midden locations and territories (Fig. 2). The largest spruce are over 125 years old, standing greater than 34 m in height with a diameter at breast height (d.b.h.) of 45 cm. Quaking aspen (*Populus tremuloides*) is common around the small and scattered blowdown-caused openings in the canopy. Alder (*Alnus crispa*) and paper birch (*Betula papyrifera*) are the only other large vascular plants on the area. Two 30 X 30 m sample plots were randomly selected, and density and basal area measurements were made on these tree species (Table 1). The forest floor is a continuous carpet of moss (primarily *Hylocomium splendens* and *Dicranum fuscescens*). Mushrooms are common and bracket fungi are found on most paper birch throughout the area. Beard lichens (*Parmelia sulcata* and *P. physodes*) are abundant on the lower dead branches of the spruce. Table 2 contains a listing of the major plant species on the study area.

All birds and mammals, or their sign, observed on the study area are listed in Table 3.

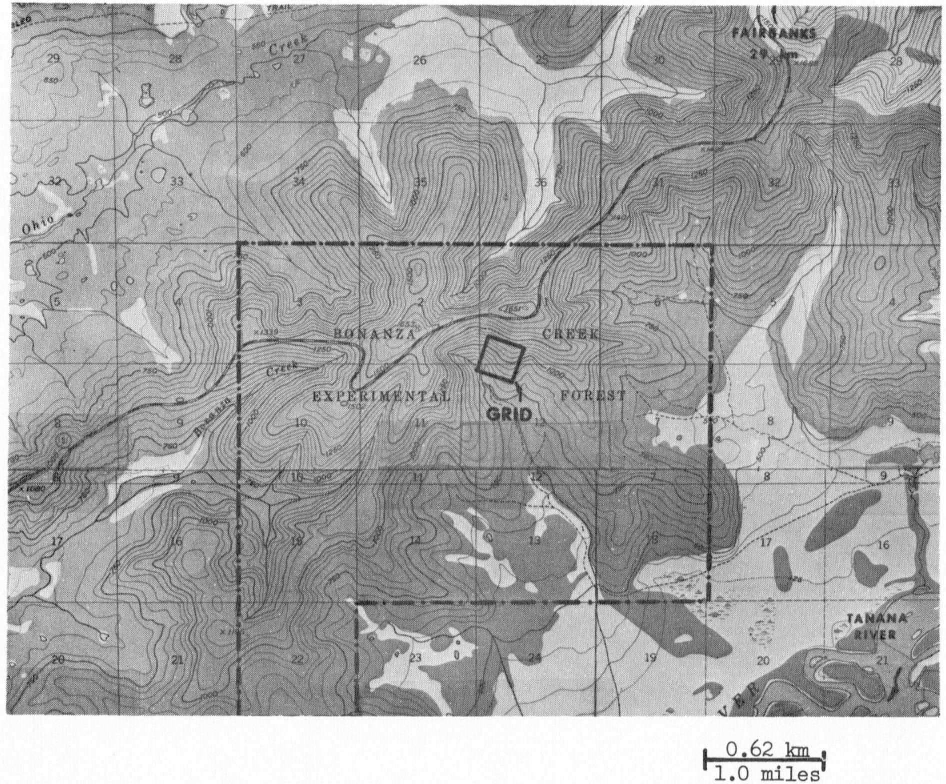

Fig. 1. Location of grid system within the Bonanza Creek Experimental Forest.

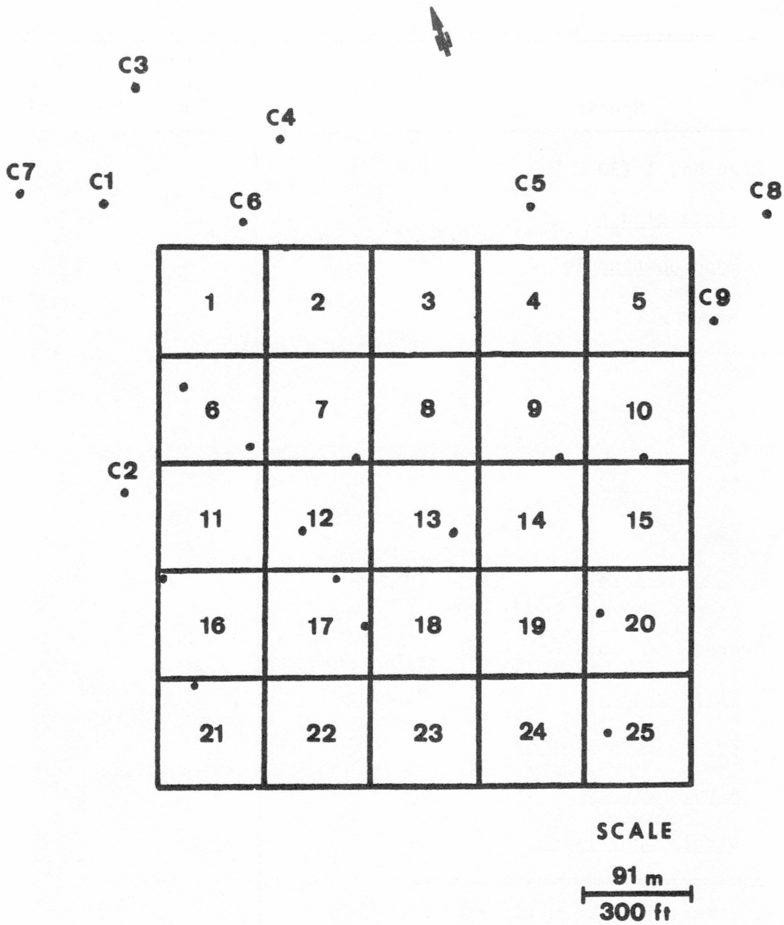

Fig. 2. Grid system and midden locations on the Bonanza Creek study area.

Table 1. Density analysis of tree species, Bonanza Creek study area.

Species	Density per Hectare	Density per Acre	Average Diameter* (cm)	Basal Area* (M^2 per Hectare)	Basal Area* (Ft^2 per Acre)
Plot No. 1 (30 X 30 m)					
<u>Picea glauca</u>	1042	422	21	43	132
<u>Populus tremuloides</u>	183	74	34	17	52
<u>Alnus crispa</u>**	64	26	-	0.2	0.6
<u>Betula papyrifera</u>	11	4	10	0.1	0.3
Plot No. 2 (30 X 30 m)					
<u>Picea glauca</u>	849	344	27	56	169
<u>Populus tremuloides</u>	32	13	31	2.5	8
<u>Alnus crispa</u>	43	17	-	0.2	0.6
Average of Plots No. 1 and 2					
<u>Picea glauca</u>	946	383	24	49	150
<u>Populus tremuloides</u>	108	44	34	10	30
<u>Alnus crispa</u>	54	22	-	0.2	0.6
<u>Betula papyrifera</u>	6	2	5	-	0.2

*Measured 1.4 m (4.6 ft) above the ground.

**Since most alders divide into several main branches less than 1.5 m above the ground, such plants were counted as one when calculating density, but the diameter of each branch was used in calculating basal area.

Table 2. Major plant species on the Bonanza Creek study area.

Mosses	
Hylocomium splendens	
Dicranum fuscescens	
Lichens	
Peltigera aphthosa	
Parmelia physodes	
P. sulcata	
Alectoria jubata	
Usnea comosa	
Vascular Plants	
Equisetum pratense	Horsetail
Lycopodium complanatum	Ground Cedar
Picea glauca	White Spruce
P. mariana	Black Spruce
Platanthera obtusata	Small Northern Bog Orchid
Populus tremuloides	Quaking Aspen
Betula papyrifera	Paper Birch
Alnus crispa	Green Alder
Geocaulon lividum	Northern Comandra
Delphinium glaucum	Glaucus Larkspur
Rubus idaeus	Red Raspberry
Rosa acicularis	Wild Rose (Rose hips)
Epilobium angustifolium	Fireweed
Cornus canadensis	Bunchberry
Pyrola secunda	One-Sided Pyrola
Vaccinium Vitis-idaea	Lowbush Cranberry
Galium boreale	Northern Bedstraw
Viburnum edule	Highbush Cranberry

The scientific names of mosses follow Conard (1956). Those of lichens follow Mason and Culberson (1960), and those of vascular plants follow Hultén (1941-1950).

Table 3. Birds and mammals observed by the author on the Bonanza Creek study area.

BIRDS

<u>Accipiter gentilis</u>* Goshawk
<u>Canachites canadensis</u> Spruce Grouse
<u>Dendrocopos villosus</u> Hairy Woodpecker
<u>D. pubescens</u> Downy Woodpecker
<u>Picoides tridactylus</u> Northern Three-toed Woodpecker
<u>Empidonax hammondii</u> Hammond's Flycatcher
<u>Perisoreus canadensis</u> Gray Jay
<u>Corvus corax</u> Common Raven
<u>Parus atricapillus</u> Black-capped Chickadee
<u>P. hudsonicus</u> Boreal Chickadee
<u>Certhia familiaris</u> Brown Creeper
<u>Ixoreus naevius</u> Varied Thrush
<u>Regulus calendula</u> Ruby-crowned Kinglet
<u>Dendroica coronata</u> Myrtle Warbler
<u>D. townsendi</u> Townsend's Warbler
<u>Pinicola enucleator</u> Pine Grosbeak
<u>Acanthis hornemanni</u> Hoary Redpoll
<u>A. flammea</u> Common Redpoll
<u>Junco hyemalis</u> Slate-colored Junco

MAMMALS

<u>Lepus americanus</u> Snowshoe Hare
<u>Tamiasciurus hudsonicus</u> Red Squirrel
<u>Glaucomys sabrinus</u> Northern Flying Squirrel
<u>Clethrionomys rutilus</u> Northern Red-backed Vole
<u>Erethizon dorsatum</u> Porcupine
<u>Vulpes fulva</u> Red Fox
<u>Ursus americanus</u> Black Bear
<u>Martes americana</u> Marten
<u>Lynx canadensis</u> Lynx
<u>Alces alces</u> Moose

*The scientific names of the birds follow the 1957 check-list of the American Ornithologists' Union, and those of mammals follow Hall and Kelson (1959).

METHODS

Field Study

Twenty-four of the middens on the study area, 15 within the grid system and nine located outside but within 140 m of the grid, were each marked with fluorescent orange flagging, plotted as to size and location, and repeatedly checked for activity throughout the study (Fig. 2). No attempt was made to accurately determine the exact size of the individual territories.

In October, 1964, the nine middens outside the grid system were searched, and all cones which could be found were dug out and removed. In November, 1965, four of the remaining six active squirrels on the study area were live-trapped and marked to determine if any change in midden ownership occurred during the winter. Aside from this live-trapping and marking, the squirrels and middens within the grid system were in no way disturbed. During the study, over 300 hours were spent in observing red squirrels. Since the squirrels quickly adjusted to being observed from a distance, it is believed that these observations did not significantly affect normal red squirrel behavior.

Collecting and Marking

No squirrels were collected on the study area as its population was being constantly observed. However, squirrels were regularly collected from a similar white spruce stand approximately 1 km from the study area. Stomachs were immediately fixed in 10% formalin for future analysis.

"Nyanzol A" dye was used in marking squirrels, and was purchased from the Nyanza Color and Chemical Co., 109 Worth Street, New York, N. Y., 10013, for $5.50 a pound (.45 kg) delivered. Two grams of the dye were dissolved in 100 ml of distilled water. Just before application, this solution was mixed in a ratio of 2:1 with a 10 volume (3%) solution of hydrogen peroxide (Fitzwater 1941). Cotton swabs were used for application, and the fur was allowed to dry before the squirrel was released. Since just four squirrels were marked, only one shoulder or hip was dyed on each squirrel.

Stomach Analyses

A total of 29 red squirrel stomachs was analysed during the study. The contents of each stomach were observed under a dissecting scope, and approximate percentages by volume of the contents were estimated. While it is often difficult to determine accurately red squirrel stomach contents collected in areas with a greater variety of foods, the usually monotonous diet of the red squirrels near the study area permitted reasonable accuracy.

Analysis of Old White Spruce Seed

During February, 1965, a germination test to determine the percentage of viable seed was conducted with the "old" cones used during the feeding trials. A sample of 1,000 seeds from the productive zone of 100 randomly selected old cones, collected on the study area in the fall of 1964, was put on moist cotton gauze in petri dishes and placed in a controlled temperature seed germinator for 28 days. A self-timing device maintained the temperature between 28° and 32° C for 12 hrs and at approximately 22° C for the remainder of the day. Brink (1964) described the productive zone of a white spruce cone as lying between the upper six and lower two whorls of bracts.

A second random sample of 1,000 old seeds, selected in the same manner as described above, was analysed to determine the percentage of filled seed in the productive zone. Each seed was opened and the endosperm examined. Seed containing even shriveled endosperm was considered filled. Hollow or resin filled seed was recorded as unfilled.

Calorimetric Determinations

Approximate caloric values were determined for three of the foods utilized during the study: the old white spruce seed, white spruce buds, and mushrooms. The seed was taken from cones collected from middens on the study area in October, 1964. Only endosperm and embryo, the part of the seed the squirrels actually eat, were used. The bud samples were cut from the crowns of four white spruce near the study area in March of 1966. Since squirrels discard the outer sheath of bud scales and eat only the inner portion of undifferentiated meristematic tissue, only the latter was used. Both the white spruce seed and buds were kept frozen until tested. The mushrooms were picked in the summer of 1965, and were preserved by drying. The mushroom values represent a ground up mixture of pilei from six species of mushrooms known to be eaten by the squirrels on the study area. The measurements were made in a Parr adiabatic oxygen bomb calorimeter, model 1221, after all food samples had been dried for 10 days in an oven at 75° C.

Feeding Trials

The feeding trials were conducted within a 30.5 X 30.5 m wire enclosure in a black spruce (Picea mariana) stand about 1.6 km northwest of the main campus. The squirrels were kept individually in 61 X 61 X 122 cm galvanized wire cages each furnished with a 30 X 30 cm wooden nest box. See Brink (1964) for construction details.

An Ohaus triple beam balance reading to the nearest 0.1 g was used for weighing, and the weights are believed accurate to within 1 g. Squirrels were weighed in live-traps of known weight. The weights were recorded at two-day intervals for Groups I, II, and III, and daily for Group IV. Weighing was done close to sunset when the squirrels had finished feeding and were in their nest boxes. After covering the small opening in the nest box, the box was removed from the cage to the weighing table where the squirrel could be easily frightened into a live-trap.

The squirrels used for the feeding trials were captured in National Live Traps within 3 km of the University campus. All squirrels were taken from white spruce middens and were captured from 5 to 36 days before the trials began. During this period and when not participating in a feeding trial, the squirrels were maintained on Purina Laboratory Chow which was determined to have a caloric value of approximately 4,390 cal/g (Brink 1964). Snow was provided as a water source.

Feeding trials with Groups I, II, and III were conducted from 11 to 31 March, 1965, utilizing only "old" white spruce cones. In the absence of a cone crop on the Bonanza Creek study area in the fall of 1964, the only supply of spruce cones available to red squirrels was that which they had cached in previous years and could excavate from their middens. Approximately 27,000 of these old white spruce cones, collected mainly from eight middens adjoining the grid system, were used for the trials. The ability of a squirrel to maintain body weight was the criterion used in determining success or failure of a trial. Three groups of squirrels, with five in each, were fed in the following manner. Group I acted as a control and received a constant diet of laboratory chow. Group II was fed only old white spruce cones and made an abrupt change in diet from the laboratory chow to spruce cones. The cones were pre-counted, and 250 were fed daily to each squirrel. At the end of the trials, the remaining cones were removed from each cage to determine the total number of cones stripped by each squirrel. Group III made a gradual change from the laboratory chow diet to old spruce cones during a seven-day period. As the original daily ration of 50 g of laboratory chow was reduced by 7 g each day, the ration of cones was increased by 35 each day until the squirrel was entirely dependent upon the 250 cone daily allotment. The cages and nest boxes were checked each day to remove any laboratory chow or spruce cones remaining from the previous feeding.

The feeding trial with Group IV was conducted from 29 March to 18 April, 1966, to determine if red squirrels could maintain body weight on a diet of only white spruce buds. The branch tips fed during the trials were cut between 2 and 24 March, 1966, from the crowns of white spruce growing near the study area or in the vicinity of the University. Tips averaged approximately 5 cm in length with six buds per tip. The lateral and terminal buds, including vegetative and reproductive buds, usually remained intact on the tips. The branch tips were kept frozen in plastic bags until fed to the squirrels. The five squirrels used for this test were gradually changed from a laboratory chow diet to one of white spruce buds during a five-day period. As the initial daily ration of 35 g of laboratory chow was reduced by 7 g each day, the ration of white spruce tips was increased by 500 each day until the squirrel was entirely dependent upon the 2,500 branch tip daily allotment. The initial daily ration of 35 g of laboratory chow was fed to Group IV when results from Group III showed that the 50 g daily allotment was higher than necessary for normal consumption. The cages and nest boxes were checked daily to remove any laboratory chow or branch tips remaining from the previous feeding. No attempt was made to count the number of tips or buds utilized.

RESULTS AND DISCUSSION

Field Study

This section is a synopsis of the chronological sequence of events relating to red squirrel ecology on the Bonanza Creek study area during the two consecutive years of cone crop failure (July, 1964, to March, 1966).

In July of 1964, it became evident that no white spruce cone crop of any consequence would be produced on the study area. Using the 10-category crop rating system applied by Werner (1964), the crop would have received a rating of "2" (few cones on occasional trees).

In a year of "normal" cone production by white spruce in interior Alaska, the cutting and storage of cones by red squirrels will usually begin sometime between 1 and 15 August, depending upon the individual squirrel and the cone crop. The seed usually matures and begins to fall about 20 August with at least 50% falling by 15 September (Robert Gregory, personal communication). Within this six week period, the major portion of red squirrel food gathering and storage normally takes place. While some squirrel-cached cones have undoubtedly shed a portion of their seed, the large majority of cones are probably cut before they open.

In the absence of a cone crop, the squirrels during August remained active primarily on the ground or in the lower branches of the spruce, very seldom venturing as high as the cone bearing portion of the crown. On three occasions squirrels were seen moving about in the tops of large white spruce. They would run out on a limb, check the branch tips, then climb to another limb. They were not seen cutting or eating anything during this time. At no time during this period were any squirrels observed cutting or caching new spruce cones.

During the first two weeks of September the squirrels began digging within their middens and retrieving old, scattered white spruce cones which had been stored in previous years. Many of these cones were rotten, mildewed, or insect infested, but were nevertheless re-cached in large numbers in active middens. By early October most middens had large quantities of these cones cached throughout the tunnel systems, often with many cones easily visible on the surface. Mushrooms were abundant on the area, and the squirrels were often observed eating and storing them among the lower dead branches of the white spruce in the vicinity of their middens.

The typical red squirrel social structure of the northern coniferous forests (Smith 1965) was constantly in evidence during this period and continued throughout the winter. Established territories were aggressively defended. Territorial calling was frequent and usually elicited similar responses from neighboring squirrels.

In early October, 18 of the 24 marked middens on the study area were active (C1, C2, C3, C4, C5, C6, C7, C8, 1-SW, 3-S, 6-NW, 7-SE, 9-SE, 10-S, 12-C, 13-SE, 17-E, 25-W) (Fig. 2). These included eight of the nine "coneless" middens (those middens adjoining the grid system which had been searched for cones). By mid-November two of the coneless middens, C3 and C7, were inactive. These had yielded only 472 and 0 cones respectively when searched, and their desertion was probably due to lack of a cone supply. It is believed that both squirrels were young-of-the-year.

Determining whether a midden was active was an easy task since active middens contained from three to seven fresh bract piles, often up to 30 cm in height and 45 cm in diameter. New snow soon covered the bract piles on inactive middens.

From late November until mid-March the squirrels continued to strip large numbers of cones, and with the exception of midden 1-SW, there was no change in the active status of the other 15 middens. About mid-January midden 1-SW became inactive. On 9 February the squirrel from midden 6-NW, approximately 55 m from 1-SW, was seen digging for cones on 1-SW. For the next six weeks this squirrel regularly visited 1-SW and utilized some of its cached cones, though this represented only a small number compared to the number of cones being stripped on its own midden. In late March a new squirrel occupied 1-SW and successfully defended the midden as its territory. While cones were still available to some degree on this midden, the large bract piles characteristic of the other active middens were not evident. Perhaps the absence of a large cache of cones was the cause for abandonment in mid-winter.

In early March midden C-1, inactive since November, was again occupied, but like 1-SW the characteristic large bract piles were not in evidence.

During late February and March, squirrels were occasionally observed cutting branch tips high in the white spruce and feeding on the spruce buds. Scattered branch tips were also frequently observed on the snow under these trees. While buds may have constituted a part of the late winter diet, the major portion still consisted of spruce seed.

By mid-April spring had arrived. The 1964-65 winter was one of the coldest on record with prolonged periods of temperature below -36° C (-32.8° F). Despite the severe winter and absence of a 1964 cone crop, 15 of the original 18 middens active in October remained active throughout the winter, and two, C7 and 1-SW, were active for parts of this period.

Between mid-April and late May the spruce cone supply on all middens became depleted. This was a gradual process with squirrels apparently finding small, previously undiscovered, caches of cones from time to time. By June little sign of freshly stripped cones could be found anywhere, and for all practical purposes white spruce seed ceased to constitute any significant part of the diet.

The normally rigid territorial structure which had persisted throughout the winter seemed to loosen a bit during May and June. While many squirrels remained on and actively defended their normal territory, others moved a great deal through the study area, and many territories changed ownership during June and July. Territorial calling, while still evident, was not as prevalent as during the preceding summer nor were these calls answered as regularly by neighboring squirrels.

By July, 1965, it was obvious that for the second consecutive year there would be no significant white spruce cone crop on the study area. Using Werner's (1964) rating system, this crop received a rating of "1" (no cones on any trees).

In early September the normal bustling activity of the red squirrels was conspicuous by its absence. As in the preceding autumn, squirrels were seldom observed high in the spruce. The squirrel population on the study area had dropped considerably and with territorial calling at its nadir, a person could have walked through the area without realizing red squirrels were present.

By early October only six middens were still active of 18 active at the same time the preceding year (C1, C8, 6-NW, 10-S, 17-E, 25-W). This represented a 67% drop in the number of squirrels. Since the squirrels had exhausted their cone supply the previous winter, no cones were available as they began the 1965-66 winter. While they had relied upon mushrooms to a large extent for food from July to October, the squirrels did not seem to store any more mushrooms than in the preceding autumn despite the absence of a cone crop. Tips of white spruce branches were found in some quantity on the snow in late October, indicating that utilization of buds had begun a full four months earlier than during the winter of 1964-65.

The six middens remained active throughout the winter with large quantities of spruce buds being eaten by the squirrels as their primary food. The four squirrels marked in November remained on the same middens during the winter with no change in midden ownership observed. Home ranges were considerably larger than in the preceding year as squirrels were lower in numbers and traveled greater distances in search of food. The lower frequency of territorial calling also continued until the conclusion of field observations in March.

Food Habits

The great variety of foods utilized by the red squirrel at lower latitudes has been amply discussed by Klugh (1927), Hatt (1929), Seton (1929), Hamilton (1939), Layne (1954), Hazard (1960), Smith (1965) and others. The red squirrel in interior Alaska, however, is limited in its diet by the homogeneous character of the white and black spruce forests which it inhabits. In the interior, spruce seed constitutes the major portion of the year-round diet during a normal cone crop year (Dice 1921, Murie 1927, Brink 1964). Therefore, in a homogeneous stand of spruce such as exists on the Bonanza Creek study area, a cone crop failure leaves no alternative source of conifer seed.

Table 4 lists the approximate percentages by volume of 29 red squirrel stomachs collected from August, 1964, to March, 1965.

Spruce seed.--During the summer of 1964, red squirrel middens on the study area contained large numbers of white spruce cones cached there in previous years. These cones constituted the major single portion of the summer diet, supplemented with mushrooms, fruits, and other available foods. With the failure of the cone crop, the squirrels riddled their middens with tunnels and exhumed

Table 4. Approximate percentage by volume of red squirrel stomach contents collected near the Bonanza Creek study area from August, 1964, to March, 1966.†

Date	Spruce Seed	Fungi	Spruce Buds	Lichen	Green Plant Matter	Insects	Fleshy Fruits	Bone	Misc.*
Aug., 1964	80%	20%							T
"	70	30							T
"	20	60		10%					10%
"	50	50		T					T
"	40	60							
Oct.	90	T		T					T
"	60	40							T
Dec.	80					20%			T
"	100								T
Jan., 1965	100								T
Feb.	20	70		10					T
"	100		T						T
Apr.					100%				
" **	90		10%						T
" **	80			10				T	T
May	90	10							T
"	100								T
"	60	20		10					10
July	T	50			50				
"		70					30%		T
"	30	60							10
Aug.					20		80		T
"		90		10					T
Sept.		100							
Oct.	T	60				40			T
"		70		20					10
Dec.			90					10%	
Mar., 1966			100					T	T
"		10	90						

† Each line represents one stomach.
* Wood, bracts, hair, dirt, moss, or gravel.
**Collected in white spruce stand near the University.

large numbers of these cones in preparation for the coming winter. Between 30 to 50% of these cones were rotten, mildewed, or insect infested. While a small amount of insect damage may occur after the spruce cones are cut and stored, the major portion occurs while the cones are still on the tree (Roy Beckwith, U. S. Forest Service, personal communication). Even though red squirrels may selectively distinguish between healthy and infested cones when harvesting, in years of normal cone production squirrels probably cut and store a certain small percentage of these damaged cones. The high percentage of infested cones exhumed from the middens in 1964 could have been the result of selection of uninfested cached cones from the middens by the squirrels for eating during years of normal cone production. With the cone crop failure, this previous selection could have resulted in the high proportion of infested cones remaining in the middens. However, Halvorson (1963) found that even a cone crop failure in Montana did not induce red squirrels to use insect infested cones of Douglas-fir (Pseudotsuga taxifolia).

In October, 1964, excavation of all the old cones which could be found in the nine middens adjoining the grid system produced a total of 24,457 cones (Table 5). Three of the nine middens (C3, C8, C9) produced less than 500 cones apiece while a fourth (C7) failed to yield any. The remaining five middens produced an average of 4,627 cones each, with one (C1) yielding 8,518. While an attempt was made to remove all the cones from these nine middens, it became obvious during the winter that many thousand cones were still available to the squirrels from areas within the middens not uncovered during the search. All 15 squirrels that remained active during the winter had cone supplies which lasted until mid-April or May.

Table 5. Old cones excavated from nine middens adjoining the grid system in October, 1964.

Midden Designation	No. of Cones
C1	8,518
C2	6,020
C3	472
C4	3,963
C5	1,750
C6	2,866
C7	none
C8	461
C9	407
	Total 24,457

Spruce seed remained the primary food in the squirrels' diet throughout the winter and was found in 11 of 12 stomachs analysed between December and May (Table 4). After the supply of cones on the middens became depleted in April and May, spruce seed ceased to constitute any significant portion of the diet. Only three of 11 stomachs analysed between July, 1965 and March, 1966, showed some trace of spruce seed. Any seed utilized by squirrels after May, 1965, probably resulted from chance discovery of an occasional cached cone.

Fungi.--Fungi, primarily mushrooms, constituted an important part of the red squirrels' diet throughout the study. While spruce seed was the major food during the summer and fall of 1964, fresh mushrooms were eaten constantly before they rotted or were covered by snow. These mushrooms probably supplied a major portion of the moisture requirement as no open water supply was available. Five stomachs collected in August, 1964, contained approximately 20 to 60% mushrooms by volume, indicating more or less alternate ingestion of mushrooms and spruce seed (Table 4).

Mushrooms were stored singly or in small groups among the lower branches of many of the white spruce surrounding the active middens. Within a 7 m^2 area on one midden near the study area, three white spruce contained a total of at least 24 mushrooms stored at heights of 2 to 9 m. Most of these were well preserved, but a few were soft or rotten. Buller (1920) mentions a squirrel's store containing two to three hundred mushrooms in an unused house. There was no evidence of such large numbers stored in any single location either within the middens or in trees or stumps. However, a squirrel could have possibly stored an equivalent total number of mushrooms in various smaller caches within its territory. During the winter partially eaten mushrooms were found on stumps or small dead branches almost in the center of active middens, but the squirrels would often leave these untouched for two or three weeks time. One large mushroom remained in such a conspicuous position for over three months on midden 17-E with the squirrel only occasionally eating a few mouthfuls.

During the winter, squirrels utilized their stores of mushrooms sparingly. Seldom was a squirrel seen eating a mushroom, and only one of eight stomachs collected between December and April contained mushrooms. However, that one stomach contained approximately 70% mushrooms by volume.

With the depletion of the spruce cone supply in late spring of 1965, mushrooms became the most important food in the diet. Species of *Clavaria*, *Hydnum*, *Boletus*, *Amanita*, several of *Russula* and other genera were commonly eaten. Squirrels were twice observed feeding on the pilei of *Amanita muscaria*. On both occasions the mushrooms were collected for identification. Seven of eight stomachs collected between July and October, 1965, contained mushrooms. These constituted over 50% by volume in all instances (Table 4).

While mushroom production on the study area in 1965 was similar to that of the preceding summer, the squirrels did not seem to store them in greater quantities despite the absence of a cone supply. Utilization of mushrooms was again spread out over the entire winter, and they were again found in conspicuous places on the middens, not being disturbed for two or three weeks at a time. Although stored mushrooms were generally scarcer in the spring of 1966 than in the preceding year, thawing snow brought down many uneaten mushrooms originally stored well up in the spruce. The squirrels had therefore failed to utilize all the mushrooms available to them during the winter.

In March and April, 1965, portions of chewed bracket fungi were found on five middens. Bracket fungi were common in the area, but no other evidence of such utilization was found. Layne (1954) mentions that bracket fungi were occasionally eaten by red squirrels in central New York. It is doubtful that these fungi were an important source of food for the squirrels.

Smith (1965) lists over 40 species of fungi eaten by red squirrels in the primarily coniferous forests of southern British Columbia. Interpolation of his feeding observations of six adult red squirrels (four females, two males), conducted during various periods in July and August, showed that the squirrels spent an average of approximately 23% of their daily feeding time eating fungi. This occurred when both old and new conifer cones were available to the squirrels. Although I do not have similar data from the study area, 23% is a reasonably close approximation of the amount of time spent eating fungi, primarily mushrooms, when old cones were still available in the summer of 1964. However, during the complete absence of cones in 1965, a figure approaching 60% would not be unreasonable. In the absence of a plentiful cone supply, mushrooms seem to constitute a major portion of the red squirrels' diet from late June until early October in interior Alaska.

<u>Spruce buds</u>.--The first evidence of white spruce bud utilization was found in late February, 1965. Since all the active middens still retained fair quantities of old cones, buds were apparently

eaten more out of a desire for variety of diet than from necessity. The squirrels continued to occasionally eat buds during March, gradually tapering off in April as the buds opened and growth began.

In late October, 1965, cut spruce branch tips were again found in some quantity on the study area. The complete absence of a cone crop for the second consecutive year had apparently forced squirrels to utilize spruce buds four months earlier than during the preceding winter. For the remainder of the 1965-66 winter spruce buds constituted the major portion of the diet. Large numbers of tips were regularly found at the base of the white spruce surrounding the six active middens. One squirrel stomach collected in December and two in March contained almost 100% spruce buds by volume (Table 4). Two of these squirrels were shot while feeding on buds near the study area.

Utilization of white spruce buds by squirrels has been reported by Klugh (1927), Hatt (1929), Hart (1936), Rowe (1952), and Wagg (1963, 1964). Hosley (1928) and others seem to indicate that such utilization occurs primarily during periods of deep snow when the normal food supply is cut off. This is not the case in interior Alaska. Despite the snow cover, red squirrels maintain an open tunnel system within their middens and thus have constant access to their cone supplies during the winter. The heavy use of spruce buds during the winter of 1965-66 can be attributed to the lack of any suitable supply of a more preferred food. Very few buds by comparison were utilized the preceding winter when a good supply of old spruce cones was available.

Lampio (1952) states that squirrels (Sciurus vulgaris) in Finland rely upon the seed of spruce as their number one food, but if spruce and pine seed, an alternate food, are not available, the main winter food consists of the buds of the spruce. Vartio (1946), also studying S. vulgaris in Finland, found that in areas with a successful cone crop, the diet consisted of 58% conifer seed and 19% buds of the conifers. Squirrels in areas with a cone crop failure, however, utilized conifer buds as 49% of their diet. Rowe (1952) reported that the damage to leaders and upper branches of white spruce, which occurred in Manitoba during the spring of 1950, was apparently due to heavy utilization of the buds by red squirrels following the cone crop failure in 1949. This same situation existed on the Bonanza Creek study area during the 1965-66 winter. Observations made in the wild and during the feeding trials in this study agree with Wagg's (1963) report that red squirrels cut lateral and terminal twigs of white spruce and ate both the vegetative and flower buds. No evidence was found showing that the inner bark of the spruce tips was eaten as reported by some authors for other species of squirrels and conifers. All squirrels observed eating spruce buds were in the top third of the tree. To what extent such heavy utilization of spruce buds will affect future cone crops is not definitely known.

Individual squirrels apparently vary in their methods of eating spruce buds. Most squirrels seem to cut the tips of a branch immediately behind the first whorl of lateral buds and then hold them with their front feet while eating the buds. An average of 85% of the tips from two, 50-tip samples collected under white spruce trees on two squirrel territories showed that they had been cut immediately behind the first lateral whorl of buds. These tips averaged approximately 3 cm in length. A great variation in bud clipping existed, both with respect to the proportion of the terminal buds eaten and in regard to the total number of buds removed from the branch tips (Table 6). Whether this variation reflects differences in palatability between trees or merely the feeding habits of the squirrels is not known.

Table 6. Characteristics of red squirrel-cut white spruce tips collected from two squirrel territories in February, 1966.

	Sample 1	Sample 2
Length of tip	2.5 cm	3.3 cm
Tips cut at lateral whorl	92 %	78 %
Number of buds in lateral whorl	3.9	4.0
Buds eaten in lateral whorl	82 %	82 %
Terminal buds eaten	90 %	29 %
Average no. buds per tip	7.2	8.4
Total buds on tip eaten	84 %	67 %

Other squirrels were observed feeding upon spruce buds, but were not seen to cut the twigs in the process. The tips were bent upward with the front feet, and the buds pulled off with the teeth. Thus, some squirrels do not drop the tips which usually connote bud feeding. Observations also showed that up to two tips discarded by the squirrels will be caught in the lower branches of the spruce for every one tip which reaches to ground. The number of tips found under a tree is therefore at best only an index of the destruction which has occurred.

Miscellaneous foods.--While spruce cones, spruce buds, and mushrooms probably supplied over 90% of the red squirrels' diet during this study, a number of miscellaneous foods were also utilized.

Squirrels were seen at various times of the year eating lichen (*Parmelia* sp.) which grows on the lower dead branches of the white spruce. They would run their mouth along the top of the branch and scrape the lichen off, usually taking a portion of the dead wood with it. Most of the spruce surrounding a midden showed many of these scars, seldom more than 1.5 cm in length, on their lower branches. Eight stomachs collected during the study contained small amounts of lichen (Table 4). It is probably eaten incidentally as the squirrel moves about its territory.

Although two stomachs collected in July and August, 1965, contained raspberries (*Rubus idaeus*), no other evidence indicating fleshy fruits as a food was found. Highbush cranberry (*Viburnum edule*) and rose hips (*Rosa acicularis*) were the only fleshy fruits found over a good portion of the study area. Raspberries were available only to those squirrels near the road. Klugh (1927) and Hatt (1929) mention rose hips as a food eaten by red squirrels, and

Murie (1927) mentions two bushels of highbush cranberries stored by a squirrel in southcentral Alaska. Neither species was known to have been eaten by the squirrels during this study. One rose bush, within 30 m of an active midden, retained its fruit throughout the winter of 1965-66 when the squirrel was eating large numbers of spruce buds.

In December a squirrel near the University was observed tearing open a piece of wasps' nest and eating the larvae and dead adults. During the study portions of wasps' nests up to 15 cm in diameter were found on six middens, and two red squirrel stomachs contained the remains of wasp larvae and adults (Table 4).

Red squirrels seem to have a strong penchant for collecting the bones of various dead animals. Hatt (1943) found that bones of various animals were frequently encountered on the middens of the pine squirrel (*Tamiasciurus fremonti*) in Colorado. Carlson (1940), Coventry (1940), Keith (1965), and Smith (1965) all report squirrels eating bone. The feet of snowshoe hares (*Lepus americanus*) were found on 11 middens during the study. Three of these, observed under a dissecting scope, showed squirrel teeth marks. The feet are probably picked up by the squirrels and brought to the middens to be chewed. Traces of bone were found in three stomachs.

The stomach of a squirrel shot while feeding in a quaking aspen tree in April, 1965, contained 100% aspen buds. Klugh (1927) also observed red squirrels feeding upon these buds.

The remains of an egg were found on one midden in October of 1964. The size and shape suggest that of a spruce grouse (*Canachites* canadensis).

Although the following red squirrel foods, listed by other authors, were known to be available on the study area, no evidence of their utilization was found: the green outer bark of quaking aspen (Seton 1909), bark of paper birch (Lutz 1956), catkins of paper birch (Hatt 1929), alder cones (Murie 1927), bunchberry (Cornus canadensis) (Klugh 1929), and the young of various bird species reported by many authors. Since the normally preferred red squirrel foods were very scarce during the second year of this study, a number of these foods were possibly utilized to some extent.

Territoriality

The various "degrees" of red squirrel territoriality mentioned by Seton (1909), Klugh (1929), Hatt (1929, 1943), Gordon (1936), Clarke (1939), Hamilton (1939), Layne (1954), Kilham (1954), Hazard (1960), Smith (1963, 1965), and others seem to depend upon the type of habitat in which the squirrels were studied. They range from Layne's (1954) conclusion that red squirrels in central New York, "... do not normally establish exclusive property rights over specific areas within the home range, and that territorial behavior is usually restricted to a small area immediately surrounding a feeding station or particular den site...." to the conclusion by Smith (1965) that territories from one-half to three acres (.2 to 1.2 ha) are defended equally well by either a male or female during all seasons of the year in southern British Columbia. The situation in interior Alaska parallels closely the latter. For the purposes of this discussion, normal territorial behavior will be interpreted as defense of an area; calling, the harvesting and caching of a food supply, and certain other activities within that area are included as manifestations of the defense pattern.

Smith (1965) presents an excellent argument for the evolution of red squirrel territoriality built around food as a resource in limited supply. Since conifer seed is often the only major food source present in large quantities in the northern portion of the squirrel's distributional range, he concludes that the function of territoriality, "... is to allow each individual squirrel the optimum conditions for harvesting, storing, and defending a food supply that is naturally available in a usable form only part of the year, so that it will be available all year." This may explain the variation in degrees of territoriality as the red squirrel in the more eastern and southern portions of its range is not as dependent upon a single source of food which can be easily stored and defended. If the normally rigid territorial structure exhibited by red squirrels in conifer forests is dependent upon a defendable stored food supply, then the great singular dependence upon the white spruce cone crop by squirrels on the Bonanza Creek study area may explain their departure from normal territorial behavior following exhaustion of the old spruce cone supply in the late spring of 1965. Despite the failure of the 1964 cone crop, the availability of the previously cached old spruce cones permitted territorial behavior and structure to remain intact throughout the 1964-65 winter.

Smith (1965) found the frequency of territorial calling by

Douglas squirrels (Tamiasciurus douglasii) much higher in the spring of 1963 following a fair cone crop in 1962 than it was during the spring of 1964 following the cone failure of 1963. He attributed this drop in the frequency of calling to fewer squirrels calling because of a population decrease and fewer calls per squirrel because of the decreased threat of territorial invasion. Halvorson (1963), studying red squirrels in Montana, found that after a cone crop failure of the two available conifer species, ponderosa pine (Pinus ponderosa) and Douglas-fir, the squirrels in late summer and early fall, "... were rather inconspicuous because of subdued calling rates and general activity." Smith (1963) mentioned that, "In late August no squirrels were seen or heard in a half hour's walk and Douglas fir trees were almost bare of new cones." The decrease in territorial calling which became evident on the study area in May and June of 1965, and the absence of the normal bustling activity during late August and September can probably be attributed to the lack of a defendable food supply, the cone crop failure, and the decrease in population density as squirrels emmigrated into black spruce stands, thus lessening the threat of territorial invasion.

Population Density

Occupancy of one midden by a single red squirrel has been reported by Gordon (1936), Clarke (1939), Kilham (1954), and Smith (1963, 1965). The same situation exists in interior Alaska. Both males and females are equally aggressive in defending their territories, and the sex of a squirrel has no significant bearing upon the outcome of a territorial dispute. At no time during the study, except during mating and territorial disputes, was more than one adult observed on a territory.

While it is possible for red squirrels to occupy more than a single midden, only one such occurrence was observed during this study. In that instance, the second midden showed only minor evidence of use and was abandoned by the squirrel when another squirrel defended the secondary site as its territory. It is believed that the continuous observations made on the study area would have detected any other similar occurrences.

Assuming one squirrel per active midden, the red squirrel density on the study area during the winter following the cone crop failure of 1964 was approximately one squirrel per 1.6 ha (4 acres). The following winter, after a second cone crop failure, the density had decreased to one squirrel per 4.8 ha (12 acres). These figures represent only the winter populations which did not change significantly during either winter. A number of smaller, inactive middens were interspersed among the larger active ones. These middens probably represent territories normally occupied only during years of good cone production and when active might raise the density to one squirrel per 1.2 ha (3 acres). Seton (1909) felt that one squirrel per 3 acres (1.2 ha) indicated abundance. Klugh (1927) estimated approximately two squirrels per 100 yard square area, or one per acre (.4 ha), in the spruce woods of New Brunswick, and Fitzwater (1941) estimated one squirrel per 2.2 acres (.9 ha) on the spruce flats in the Huntington Forest in New York. Smith (1965) plotted territories in two different forests and estimated the amount of food energy available on territories in southern British Columbia. He found that stable adult territories in one forest, one squirrel per 1.27 acres (.5 ha), were significantly smaller (P .005) than those in the other forest, one squirrel per 2.24 acres (.9 ha). Since territories in both forests contained about the same amount of food, he concluded that territory size appeared to be adjusted to the quantity of food contained on the territory. The densities found by Smith would not be expected to fluctuate as greatly between years as those in interior Alaska since there were at least two major alternate conifer species in southern British Columbia for the squirrels to rely upon during a cone crop failure in the third and principal species. The failure of the white spruce cone crop on the Bonanza Creek study area, however, left the squirrels with no alternate supply of conifer seed. The sharp decrease in squirrel numbers during the intervening summer probably resulted from emmigration into surrounding black spruce stands when the second cone crop failure became evident and no old white spruce cones remained in the middens. There is no reason to believe that the drop in numbers was caused by predation or disease. Although three goshawks (Accipiter gentilis) were active on the study area during the summer of 1964 and accounted for at least one known red squirrel death, no evidence of predation was found during the summer of 1965. No squirrels collected near the study area showed any incidence of disease or abnormal parasitism.

The black spruce stands, 300 m removed from the study area at their nearest point, had two normal cone crop years during the study and could have supplied enough food to maintain most of the immigrating squirrels. Brink (1964) found that red squirrels presented with both white and black spruce cones showed a definite preference for the former. Although Dice (1921) found red squirrels only rarely in black spruce, Brink concluded from observations in interior Alaska that where stands of white and black spruce meet, red squirrel densities are about equal in both types. He felt that competition was for the preferred white spruce habitat with the less successful squirrels being forced into the marginal black spruce. My observations agree with those of Brink. Large active middens may be found in black spruce stands even in years of good cone production in white spruce. Numerous reports of movements in red squirrel populations when food shortages occur have been cited in the literature. The interspersion of white and black spruce stands in interior Alaska may therefore provide an ideal buffer habitat during food shortages in the preferred white spruce stands.

Analysis of Old White Spruce Seed

Although approximately 31% of the old white spruce seed sample consisted of potentially viable (filled) seed (Table 7), only 14 of 1,000 seeds (1.4%) germinated. Brink (1964) found approximately 46% filled seed in a sample taken from squirrel-cached cones of the current year. MacGillivary (1955) found very reduced rates of germination for spruce seed after stratification in moist sand at 0^{o} to 2^{o} C for 27 months. Considering that these old cones may have been cached for at least two or three years in middens, it is not surprising that viability was so low.

Table 7. Number of filled seed in 10-seed samples taken from each of 100 randomly selected old white spruce cones.

	Numbers of filled seed											Totals
	0	1	2	3	4	5	6	7	8	9	10	
Frequency (No. of cones)	28	7	9	11	10	13	11	6	3	2	0	100
Total filled seed	0	7	18	33	40	65	66	42	24	18	0	313

Calorimetric Determinations

Table 8 contains the caloric values obtained from the three squirrel foods tested. While only two samples each of white spruce seed and buds were tested, they do provide some indication of approximate caloric values.

Table 8. Caloric values of three red squirrel foods.

Food	n	Average cal/g	S.D.
Mushrooms (mixture of pilei from six species)	4	4,552	36
Old White Spruce Seed (minus seed coat)	2	5,976	54
White Spruce Buds (undifferentiated meristematic tissue)	2	4,986	46

The average value for the old white spruce seed (minus seed coat) was 5,976 cal/g. Brink (1964) reported a value of 6,615 cal/g for white spruce seed (with coat) taken from squirrel middens near Fairbanks in 1962. Smith (1965) found values ranging from 6,738 to 7,558 cal/g for 10 species of conifer seed (minus coat), with a value for Engelmann spruce (Picea engelmanii) seed of 7,107 cal/g (minus coat). Kendeigh and West (1965) found higher values for hulled seed in the four instances where samples were tested both with and without the seed coats. The consistently high caloric values obtained by Smith for conifer seed minus the coat, and the higher values for hulled seed found by Kendeigh and West, lead me to conclude that the value for white spruce seed (minus coat) should fall between 6,800 and 7,200 cal/g. Since many of the old spruce cones had been cached for from one to three or four years in middens before the seed samples were taken, the low caloric values obtained for the white spruce seed in this study were probably due to energy loss through respiration. Temperatures recorded at a depth of 50 cm in a riverbottom stand of white spruce in interior Alaska show that between early July and early November, the temperatures are above 0^{o} C (32^{o} F), reaching a maximum of 8^{o} C (46.4^{o} F) in August (Leslie Viereck, personal communication). Temperatures in a spruce stand on a south-facing slope, such as the Bonanza Creek study area, may be even higher. The majority of cached cones exhumed during the study were buried within the upper 50 cm of the middens and would therefore be subjected to temperatures above freezing long enough to lose energy by respiration. Over a three- or four-year period, this loss might account for the low caloric value found for the old spruce seed.

The caloric value of 4,986 cal/g found for the white spruce buds shows that they can provide a relatively high-energy food source in the absence of a cone supply. However, large numbers of buds would have to be consumed to meet the daily energy requirements.

The four samples of a mixture of pilei from six species of mushrooms averaged 4,552 cal/g. Smith (1965) found values for fungi ranging from 3,980 to 5,200 cal/g with the average for four samples of a mixture of Ascomycetes and Basidiomycetes surface fungi being 4,320 cal/g. Since mushrooms may contain well over 85% water by weight, a relatively large quantity of fresh mushrooms must be eaten to ingest the equivalent of 1 g of dry weight. While these values range from 2,000 to 3,000 cal/g below those of various species of conifer seed commonly eaten by red squirrels, mushrooms nevertheless provide a relatively dependable alternate food source in interior Alaska.

Feeding Trials

Group I. *Control*--The five squirrels (three males, two females) which remained on a laboratory chow diet and acted as controls had an average initial weight of 273 g (standard error = 18.8 g). The average maximum individual weight change recorded during the trial was 6.3% of initial weight (s.e. = 2.1%). The maximum weight change recorded for any individual was 11.5% (Table 9; Figs. 3, 7). These fluctuations are within the limits of normal

Table 9. Response of red squirrels to constant diet of laboratory chow.

Squirrel No.	Sex	Weight in Grams and Percent Change from Initial Weight: Days into Experiment 0	2	4	6	8	10	12	14	16
2	M	333	333	337	334	328	335	340	344	330
		0	0	+1.2	+0.3	-1.5	+0.6	+2.1	+ 3.3	-0.9
7	M	287	285	291	286	290	283	283	283	289
		0	-0.7	+1.4	-0.4	+1.0	-1.4	-1.4	- 1.4	+0.7
9	M	270	274	282	292	291	295	295	301	278
		0	+1.5	+4.4	+8.2	+7.8	+9.3	+9.3	+11.5	+3.0
12	F	258	258	263	261	261	253	269	268	265
		0	0	+1.9	+1.2	+1.2	-1.9	+4.3	+ 3.9	+2.7
13	F	218	227	233	228	224	226	231	235	240
		0	+4.1	+6.9	+4.6	+2.8	+3.7	+6.0	+ 7.8	+10.9
Average Percent Change from Initial Weight		0	+1.0	+3.2	+2.8	+2.2	+2.0	+2.3	+ 5.0	+3.3
Standard Error of Average Percent Weight Change		0	1.0	1.1	1.5	1.3	1.6	1.4	1.8	1.9

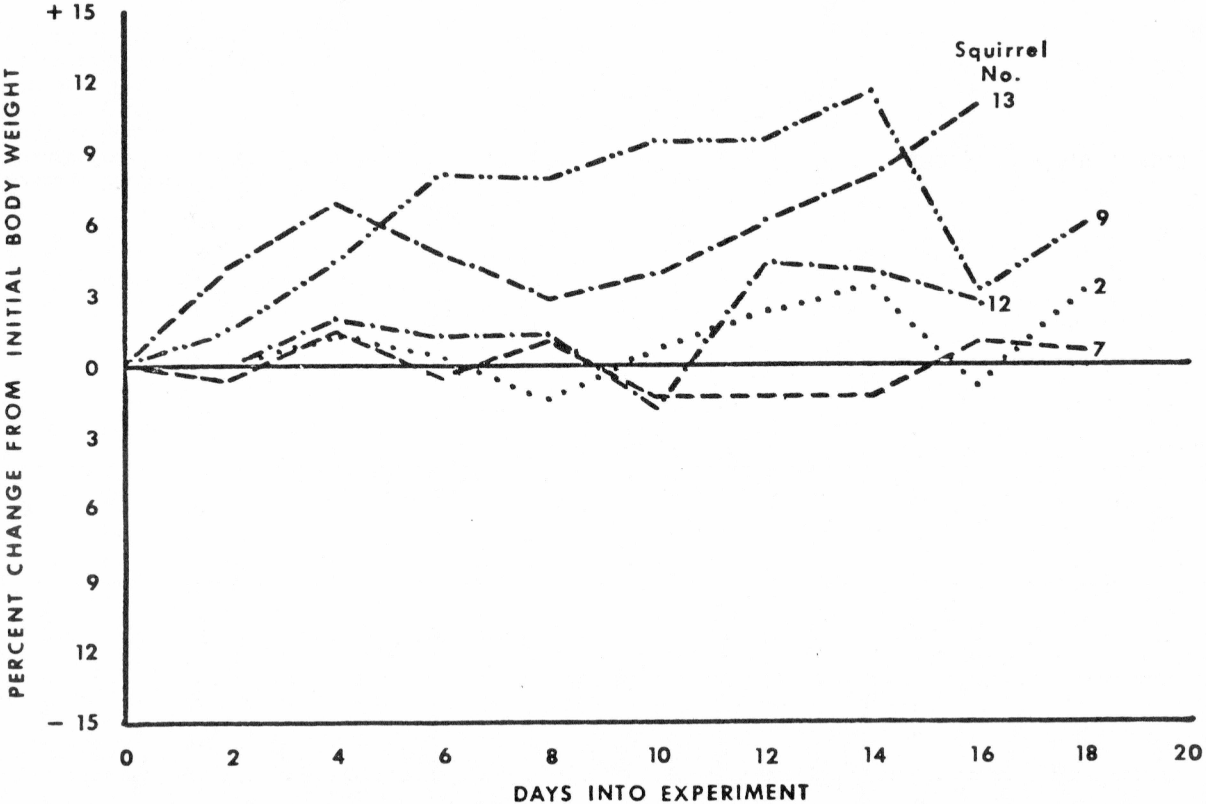

Fig. 3. Response of red squirrels to constant diet of laboratory chow.

daily variation and agree closely with Brink (1964).

Group II. Sudden change to old cones--The five squirrels (three males, two females) which made the sudden change in diet from laboratory chow to old white spruce cones had an average initial weight of 262 g (s.e. = 3.0 g). All five squirrels showed an immediate and sharp loss in weight, reaching an average of 11.5% below initial weight after the first day and 15.0% after the third day (Table 10; Figs. 4, 7). The weights then increased steadily, reaching an average of 5.8% below initial weight on the 11th day when the squirrels were returned to a laboratory chow diet. All five squirrels demonstrated an ability to increase body weight after the initial drop. One female, no. 17, had regained her original body weight while still on the spruce cone diet.

In attempting to make these results comparable with those of Brink (1964), certain assumptions were made. Since the cones were stored in the middens for from one to possibly three or four years, a large number of these old cones were rotten, mildewed, or insect-infested, with many cones containing no filled seed at all. Since Brink (1964) encountered few rotten cones and counted all partially stripped cones as half-stripped, it was necessary in this case to determine whether a partially stripped cone had been dropped because the squirrel was receiving no filled seed, or whether it had simply eaten only part of the available sound seed (see appendix for detailed discussion).

The male squirrels in this group consumed an average of 196 cones per squirrel per day (s.e. of the mean of individual daily

Table 10. Response of red squirrels to sudden change of diet to old white spruce seed following constant diet of laboratory chow.

		Weight in Grams and Percent Change from Initial Weight*									
		White Spruce Seed Diet							Laboratory Chow Diet		
		Days into Experiment									
Squirrel No.	Sex	0	1	3	5	7	9	11	13	15	17
6	M	274	250	242	243	248	254	251	267	271	276
		0	8.4	11.7	11.3	9.5	7.3	8.4	2.6	1.1	+ 0.7
15	M	292	251	245	253	253	262	269	288	285	292
		0	14.0	16.1	13.4	13.4	10.3	7.9	1.4	2.4	0
17	F	248	225	213	224	227	241	249	256	268	264
		0	9.3	14.1	9.7	8.5	2.9	+0.4	+3.2	+8.1	+ 6.4
21	M	238	206	198	202	197	208	219	248	255	269
		0	13.4	16.8	15.1	17.2	12.6	8.0	+4.2	+7.1	+13.0
22	F	260	228	217	228	233	239	249	273	277	266
		0	12.3	16.5	12.3	10.4	8.1	4.2	+5.0	+6.5	+ 2.3
Average Percent Change from Initial Weight		0	11.5	15.0	12.4	11.8	8.2	5.8	+1.7	+3.6	+ 4.5
Standard Error of Average Percent Weight Change		0	1.1	1.0	0.9	1.6	1.6	1.6	0.6	1.4	2.8

*Percent values negative unless otherwise indicated.

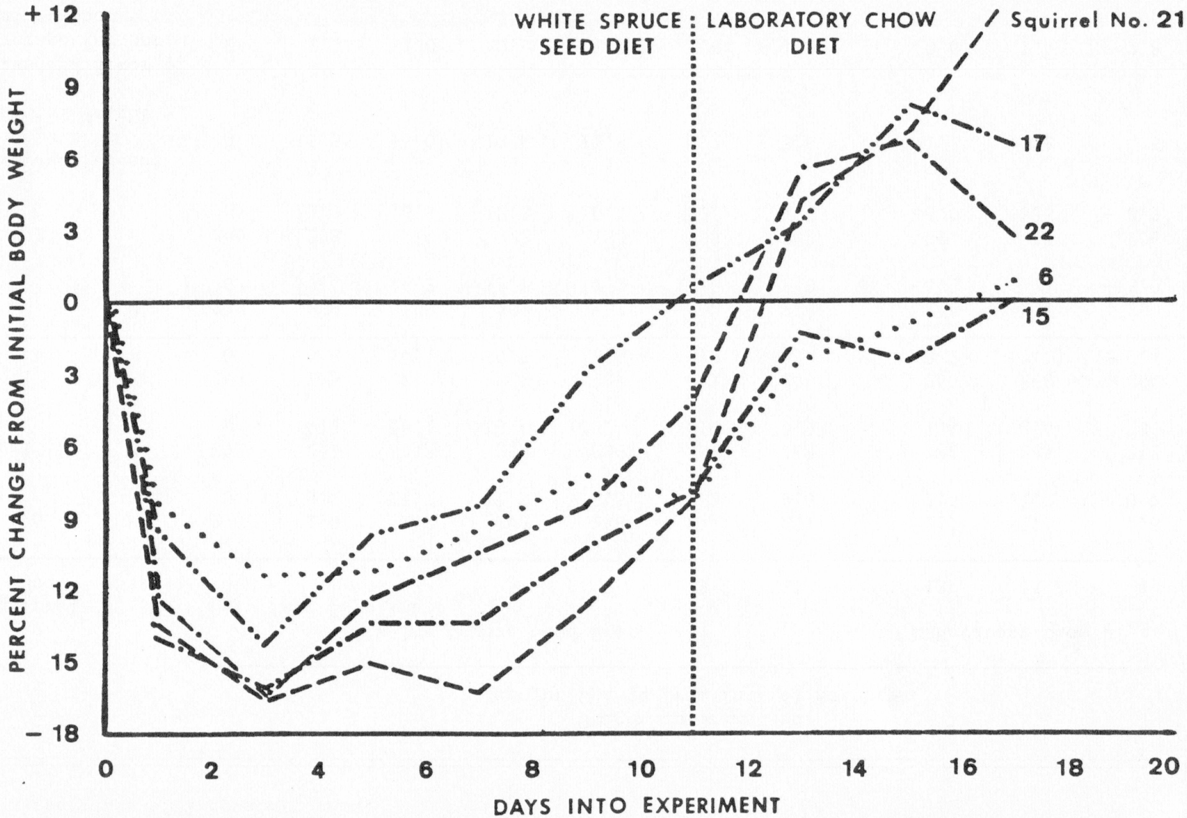

Fig. 4. Response of red squirrels to sudden change of diet to old white spruce seed following constant diet of laboratory chow.

averages = 1.3) while the females averaged 192 cones per day (s.e. = 0.7). A "t" test indicated the mean cone consumptions of the two sexes were different at the 84% level. Brink's (1964) data, however, indicates a highly significant ($P<0.01$) difference on the basis of sex with respect to daily consumption of cones. The reason for the failure to obtain such a high significance level in this study is not known.

During the experiment the squirrels as a group consumed an average of 194 old cones per squirrel per day (s.e. = 1.2). Brink (1964) found that red squirrels consumed an average of 144 new cones per squirrel per day (s.e. = 4.4) under similar conditions. The mean for male daily consumption of old cones found in this study, and the mean for male daily consumption of new cones found by Brink, showed a significant difference at the 0.02 level. A similar test made between the female means also showed a significant difference at the 0.02 level. The very poor condition of a large portion of the old cones and the lower caloric value of the seed presumably necessitated this 35% increase in cone consumption to allow the squirrels to receive sufficient nourishment.

Group III. Gradual change to old cones--The five squirrels (two males, three females) which made the gradual change from laboratory chow to a white spruce cone diet had an average initial weight of 259 g (s.e. = 13.1 g). When first presented with both foods, all five squirrels showed an immediate average weight loss of 5.9% of initial weight after the first day (Table 11; Figs. 5, 7). The average weight then increased to 2.7% below initial weight on the

Table 11. Response of red squirrels to gradual change of diet to old white spruce seed following constant diet of laboratory chow.

		Weight in Grams and Percent Change from Initial Weight*									
		White Spruce Seed Diet								Laboratory Chow Diet	
		Days into Experiment									
Squirrel No.	Sex	0	1	3	5	7	9	11	13	15	17
3	F	269	263	266	269	265	261	259	263	269	276
		0	2.2	1.1	0	1.5	3.0	3.7	2.2	0	+2.6
5	M	261	246	250	256	244	241	229	237	259	254
		0	5.8	4.2	1.9	6.5	7.7	12.3	9.2	0.8	2.9
10	M	280	256	267	262	263	250	255	262	271	275
		0	8.6	4.6	6.4	6.1	10.7	8.9	6.4	3.2	1.8
11	F	207	196	205	202	201	195	193	198	205	210
		0	5.3	1.0	2.4	2.9	5.8	6.7	4.4	1.0	+1.4
18	F	276	255	262	268	251	235	244	259	268	276
		0	7.6	5.1	2.9	9.1	14.9	11.6	6.2	2.9	0
Average Percent Change from Initial Weight		0	5.9	3.2	2.7	5.2	8.4	8.6	5.7	1.6	0.1
Standard Error of Average Percent Weight Change		0	1.1	0.9	0.9	1.3	2.0	1.3	1.2	0.6	0.4

*Percent values negative unless otherwise indicated.

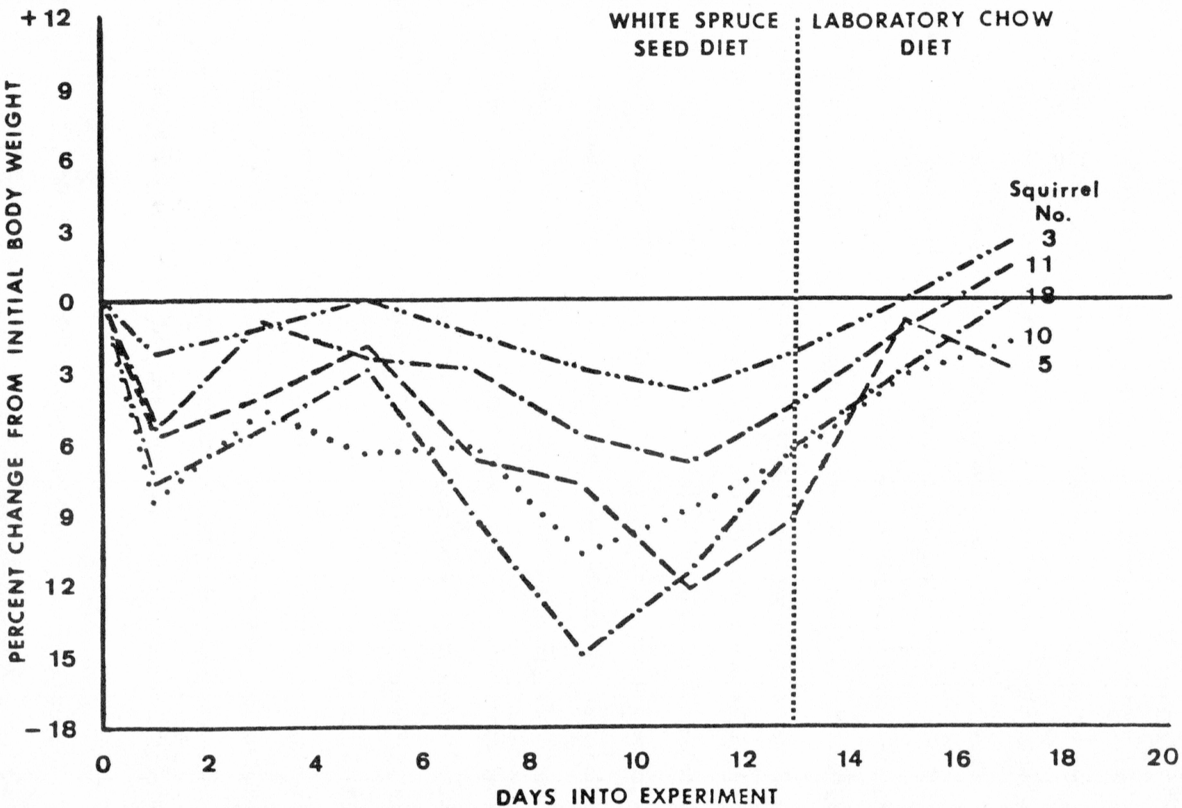

Fig. 5. Response of red squirrels to gradual change of diet to old white spruce seed following constant diet of laboratory chow.

fifth day. From this level the average weight decreased to a point that was 8.6% below initial weight after 11 days. On the 13th day, when the squirrels were returned to a laboratory chow diet, their average weight had increased to a point 5.7% below initial weight.

The gradual change of diet was used to determine if the initial sharp drop in weight recorded by Brink (1964) could be eliminated during future trials, thus causing less strain upon the animals. Figure 7 shows the average percentage weight change for each group of squirrels participating in the trials. After two days, the squirrels Brink suddenly changed to a spruce cone diet had an average weight of 6.5% below initial weight. The average weight then increased almost steadily to 4.4% below initial weight on the 10th day when the females were returned to a laboratory chow diet. The squirrels making the sudden change to old spruce cones in the present study showed a much sharper and more drastic average drop of 11.5% after the first day, reaching a maximum average loss of 15.0% of initial weight on the third day. The average weight then increased steadily, reaching 5.6% below initial weight on the 11th day when the squirrels were returned to a laboratory chow diet. The maximum average weight loss recorded by the latter group was 131% greater than recorded by Brink. This difference may be attributed to the very poor condition of the old cones as most other factors were equal.

The initial weight loss and subsequent increase recorded for the squirrels making a gradual change in diet is probably attributable to the availability of both foods simultaneously and possibly to some physiological reaction related to digestion. Although more than enough laboratory chow was available to maintain body weight during the first four days, all squirrels stripped some portion of the cones each day. The decrease in average body weight after the fifth day was undoubtedly due to the progressively smaller amounts of laboratory chow being fed and the greater dependence upon the spruce cones. The maximum average weight loss of 8.6% of initial weight occurred on the 11th day and was only 57% as large as the maximum recorded for squirrels in Group II. Since even the new cones fed by Brink initially caused a sharp decrease in body weights, it seems that some physiological digestive acclimation must occur when a change in diet is made. A gradual transition in diet allows this change to occur more slowly, resulting in less strain upon the animals. Squirrels and other smaller mammals are undoubtedly capable of maintaining body weight on a number of foods usually available, but not ordinarily preferred. Feeding trials using such foods should employ a gradual change in diet lest the physiological strain of a sudden switch to such unpreferred foods result in drastic weight loss, possibly death, and spurious conclusions.

<u>Group IV. Gradual change to spruce buds</u>--The five squirrels (three males, two females) which made the gradual change from laboratory chow to white spruce buds had an average initial weight of 240 g (s.e. = 12.6 g). All five squirrels showed a very sharp drop in body weight beginning the second day, and reached a maximum average weight loss on the sixth day of 23.6% of initial weight (Table 12; Figs. 6, 7). Squirrel no. 26, a male, had lost 29.4% of

Table 12. Response of red squirrels to gradual change of diet to white spruce buds following constant diet of laboratory chow.

		Weight in Grams and Percent Change from Initial Weight*									
		White Spruce Bud Diet									
Squirrel No.	Sex	Days into Experiment 0	1	2	3	4	5	6	7	8	9
26	M	255	253	248	252	222	195	180	Squirrel		
		0	0.8	2.8	1.2	13.0	23.5	29.4	Died		
27	F	207	219	214	191	176	163	158	162	159	Squirrel
		0	+5.8	+3.4	7.7	15.0	21.3	23.7	21.7	23.2	Died
28	F	217	221	214	197	188	174	176	183	177	180
		0	+1.8	1.4	9.2	13.4	19.8	18.9	15.7	18.4	17.1
29	M	276	277	268	251	243	222	214	210	217	221
		0	+0.4	2.9	9.1	12.0	19.6	22.5	24.0	21.4	19.9
30	M	247	244	237	226	207	194	187	188	192	186
		0	1.2	4.0	8.5	11.2	21.5	23.5	23.9	22.3	24.7
Average Percent Change from Initial Weight		0	+1.2	1.5	7.1	13.9	21.1	23.6	21.3	21.3	20.6
Standard Error of Average Percent Weight Change		0	1.0	0.4	1.3	0.6	0.7	1.7	2.0	1.0	2.2

*Percent values negative unless otherwise indicated.

Table 12 (cont'd). Response of red squirrels to gradual change of diet to white spruce buds following constant diet of laboratory chow.

		Weight in Grams and Percent Change from Initial Weight*								
		White Spruce Bud Diet				Laboratory Chow Diet				
		Days into Experiment								
Squirrel No.	Sex	10	11	12	13	14	15	16	17	18
26	M	Dead								
27	F	Dead								
28	F	188 13.4	191 12.0	190 12.5	194 10.6	201 7.4	209 3.7	218 +0.5	229 +5.5	233 +7.4
29	M	229 17.0	234 15.2	230 16.7	227 17.8	238 13.8	249 9.8	262 5.1	276 0	274 0.8
30	M	184 25.5	188 23.9	191 22.7	187 24.3	198 19.9	216 12.6	230 6.9	243 1.6	251 +1.6
Average Percent Change from Initial Weight		18.6	17.0	17.3	17.6	13.7	8.7	3.8	+1.3	+2.8
Standard Error of Average Percent Weight Change		3.6	3.6	2.9	3.2	3.6	2.6	1.9	2.8	2.1

*Percent values negative unless otherwise indicated.

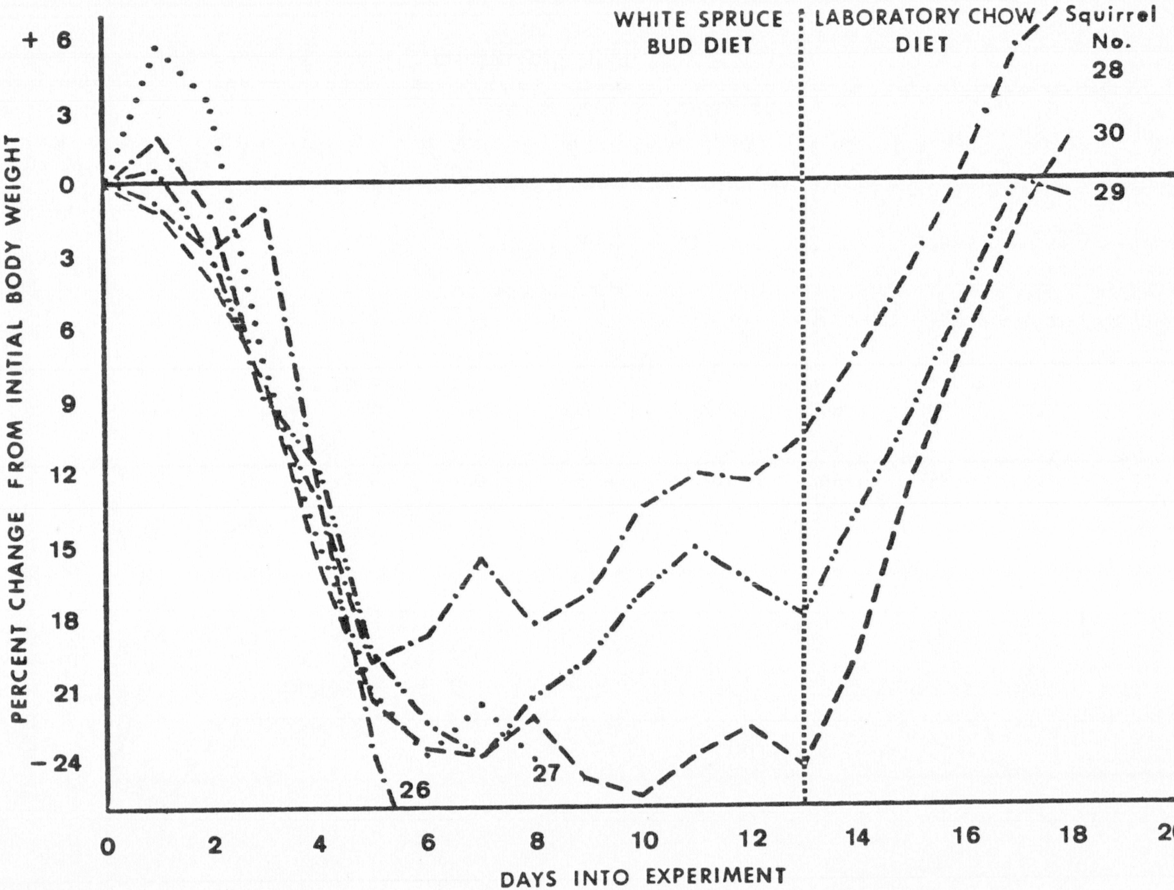

Fig. 6. Response of red squirrels to gradual change of diet to white spruce buds following constant diet of laboratory chow.

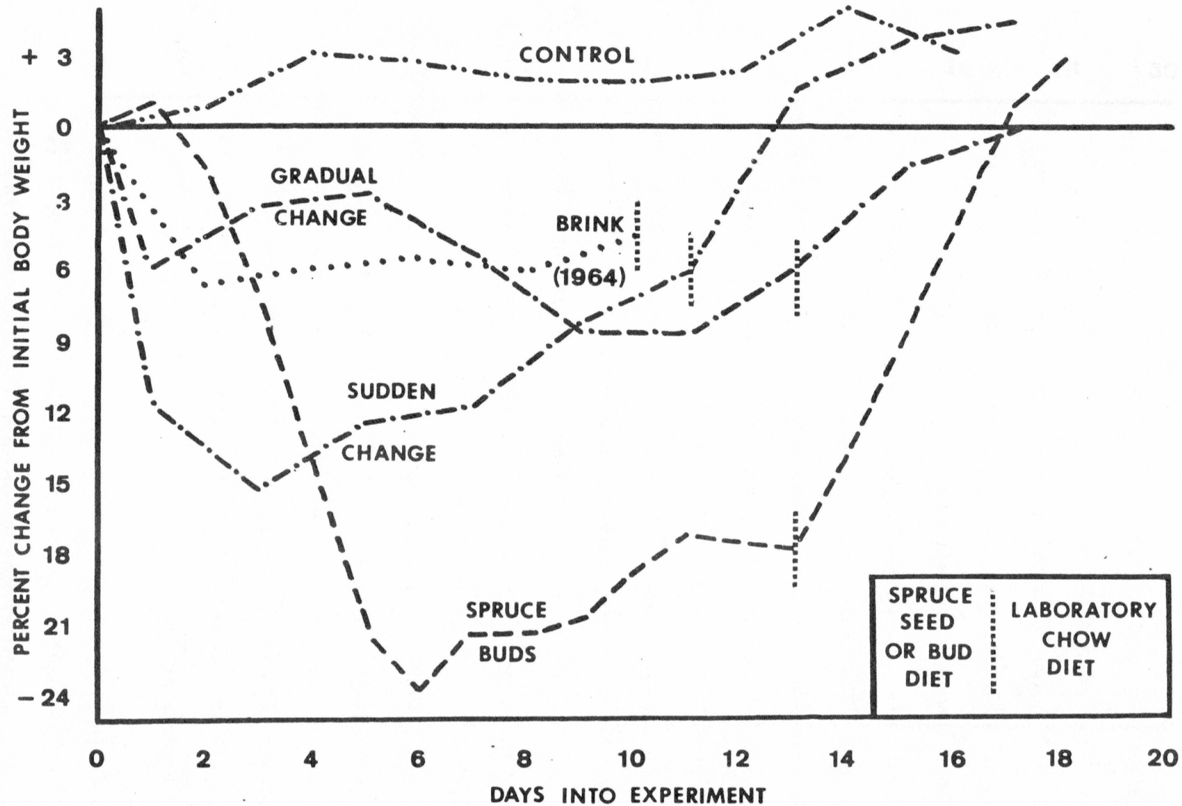

Fig. 7. Average percent weight change for individual feeding trials.

initial weight and was found dead in its nest box on that day. On the eighth day squirrel no. 27, a female, was also found dead after losing 23.2% of its initial body weight. The remaining three squirrels showed an increase in average weight for the next five days, reaching an average of 17.6% below initial weight on the 13th day when they were returned to a laboratory chow diet. Only two of the squirrels, no. 26 and 28, began eating buds as soon as they were available. The remaining three squirrels did not begin to eat buds until after the third day when only 14 g of laboratory chow were given. After the second day the five squirrels consumed all available laboratory chow whether or not they ate any buds.

The death of two of the squirrels during the trial does not necessarily mean they could not have survived on a spruce bud diet in the wild. Squirrel no. 27 managed to subsist on only buds for almost three days with no great additional loss of weight before it succumbed. It is doubtful that any of the squirrels would have survived a sudden change to the spruce bud diet, as discussed earlier. Even this gradual change in diet may have caused too great a strain upon nos. 26 and 27. The fact that three of the squirrels were able to survive for eight days on only white spruce buds shows that buds may serve as a food supply in the absence of preferred foods such as spruce cones or mushrooms.

Cone Consumption

Wagg (1964), using Yeager's (1937) assumption that red squirrels eat 2 g of Norway spruce (<u>Picea aibes</u>) seed per day, calculated that one bushel (35.2 liters) of white spruce cones could feed a squirrel for six months from November to April inclusive. Assuming 240,000 seed per 454 g (Anon. 1948), then 529 seeds equal 1 g. Wagg's estimate of 1,300 seeds consumed daily would equal approximately 2.5 g of seed per day. Assuming, as discussed earlier, an average value of 6,300 calories actually available to the squirrel for each gram of white spruce seed (weight of coat included) eaten, this would total approximately 16,000 cal/day. This estimate is far below the amount of spruce seed eaten by red squirrels in interior Alaska.

Smith (1965) did extensive calculations to determine the energy requirements of red and Douglas squirrels in the wild in southern British Columbia. By interpolating his data, values of approximately 78,000 and 74,000 cal/day are needed by male and female red squirrels respectively during the six colder months of the year when stored foods are used and a good deal of time is spent in the nest. Brink (1963) found that from 24 September to 12 October, 1963, 17 adult red squirrels (11 males, 6 females) in individual cages within an outdoor enclosure consumed an average of 35.1 g of laboratory chow (4,390 cal/g) daily, or 154,000 calories per squirrel per day. Data collected during the current study showed that from 11 to 21 March, 1965, five squirrels (three males, two females) consumed an average of 32.7 g of laboratory chow daily, or 143,000 calories per squirrel per day. The caged red squirrels in these studies consumed considerably more laboratory chow than dictated by their energy requirements, resulting in substantial weight increases.

The 154,000 and 143,000 cal/day values are therefore much higher than actually needed to maintain a squirrel at constant body weight. These figures show, however, that the average value of 76,000 cal/day calculated from Smith's data is not unreasonably high.

Brink's (1964) results from feeding trials conducted with eight male and eight female squirrels showed an average of 144 new cones consumed per squirrel per day. His analysis of these cones showed an average of 86.9 (s.e. = 2.0) seed in the productive zone of each cone with 46.1% (s.e. = 2.1%) of these being filled, giving a total of 40 sound seed per cone. Assuming 529 seed per gram by interpolation (Anon. 1948), approximately 13 cones were needed to supply 1 g of white spruce seed. Using the estimate of approximately 76,000 cal/day needed by an adult red squirrel and an average of 6,300 calories per gram of spruce seed (weight of coat included) consumed, a squirrel would have required approximately 12 g of seed per day. If 13 cones provided 1 g of seed, then 156 cones would have supplied the daily requirement. This figure is not unreasonably higher than the total of 144 found by Brink. Thus, it would appear that red squirrels require approximately 11 to 12 g of sound white spruce seed per day during the colder months of the year if spruce cones are the only source of food.

The number of white spruce cones a red squirrel is capable of cutting and caching in one year is not known. Tripp and Hedlin (1956) found that 25 white spruce in a heavy cone year had an average of 8,000 cones per tree and Roe (1952) estimated a total of 11,874 cones on a mature white spruce during a heavy crop year in northern Manitoba. Even in years of light to medium cone production, the majority of trees would be expected to bear an average of at least 500 to 1,000 cones per tree. Two 30 X 30 m sample plots on the study area had an average of 333 white spruce per hectare (135/acre) with a d.b.h. of over 30.5 cm (12 inches). Even with a squirrel density of one squirrel per 1.2 hectares (3 acres), it would appear that more than enough cones to maintain a squirrel for one year are available for the squirrels to cut and store during years of normal cone production.

Clarke (1939) reports a red squirrel picking and storing at least 1,000 red pine (Pinus resinosa) cones in one day, each cone representing a trip up and down the tree, or about one trip every 45 seconds during a 12 hour day. Red squirrels in interior Alaska cut and drop large numbers of cones at one time from the tops of white spruce and therefore save considerable amounts of time. Dice (1921), watching a red squirrel cutting cones near Tanana, Alaska, stated, "During fifteen minutes he worked continuously, dropping cones sometimes one per second...." During the period of cone harvesting by red squirrels in interior Alaska, approximately 1 August to 15 September, day length decreases from 18.5 to 12.5 hours respectively. It would seem, therefore, that if enough cones are available, a red squirrel would have more than ample time to cut and cache a large supply of cones.

The actual numbers of cones needed to sustain a squirrel between cone crops will vary with the amount of sound seed per cone. This value may fluctuate widely. Werner's (1964) data show that in five annual cone samples sound seed constituted 74, 37, 53, 10, and 22% of the total seed in the productive zone of white spruce cones in interior Alaska. Thus, depending upon the year and the individual area or spruce stand, the number of cones needed to sustain a particular squirrel through the winter will vary considerably. The fact that approximately 35% more old spruce cones were needed to maintain the squirrels in this study than was found by Brink for new cones is a good example.

The number of cones needed to sustain a squirrel between cone crops, however, is not necessarily related to the number of cones it will cut and store. Assuming that the number of cones cut and cached by a squirrel is directly proportional to the size of the cone crop, up to a physical limit, the two major variables which will determine the number of cones remaining in a midden, if any, when the next cone crop matures are the size of the previous cone crop and the amount of sound seed per cone. In a poor crop year, a high percentage of sound seed might be enough to sustain a squirrel while in a year with a low percentage of sound seed per cone, sheer numbers of cones eaten might suffice. Therefore, the number of cones eaten would be expected to vary considerably.

The "average" number of cones a squirrel may strip in a year is very hard to estimate. Despite his findings that an average of 144 cones per day were needed to maintain squirrels in captivity, Brink (1964) estimated that squirrels in the wild probably utilize an average of only 40 to 50 white spruce cones per day during the winter. This was based upon his estimate of 8,000 cones being the maximum number of cones cached by any of the 15 squirrels whose middens he excavated in the fall of 1962, a year of normal cone production. In the present study, a search of middens C1 and C2 yielded over 8,500 and 6,000 cones respectively in a year of almost total cone crop failure, yet these squirrels still possessed enough additional cones to form large bract piles throughout the winter. In the absence of a new crop, these cones were only part of a much larger supply which must have been available in those middens in the fall of 1963. Assuming a minimum of only 40 cones per day were eaten on these middens from October, 1963, until the cone supply became depleted in April, 1965, approximately 30,000 cones must have been available in each of those middens in the fall of 1963. Results of the feeding trials, observations in the wild, and the numbers of cones excavated from middens after the cone crop failure of 1964, make it appear that in normal to heavy cone crop years, red squirrels may cut and cache at least 12,000 to 16,000 white spruce cones. It is not hard to imagine that red squirrels in such years cache many more cones than are necessary to sustain them until the next cone crop. Over a period of years with normal cone crops, this excess would accrue until enough cones remained buried in the middens to successfully maintain the squirrels through the winter following a light cone crop or one with a very low percentage of sound seed. This was apparently the situation on the Bonanza Creek study area during the winter following the cone crop failure of 1964.

APPENDIX

Calculation of Numbers of Old Spruce Cones Consumed During Feeding Trials

In attempting to make the results of these trials comparable to those obtained by Brink (1964), I had to make certain assumptions since his feeding trials were conducted with new cones which, on the whole, were in good condition. Because a high percentage of the old cones were rotten, mildewed, or insect-infested, and usually contained little filled seed, a squirrel would often reject such cones after stripping only three to six whorls of bracts. Since the purpose of the feeding trials was to determine the total number of old cones which a squirrel had to handle in order to receive enough daily nourishment, those cones which had been rejected had to be counted as part of the total number of cones handled. I had to decide, therefore, whether a partially stripped cone had been rejected by the squirrel because it did not yield good seed, or whether the squirrel had merely stopped eating a cone for some unknown reason as they occasionally do. Observations in the wild and during the feeding trials resulted in the following assumptions:

1. All cones showing no bracts removed were counted as not stripped.

2. Cones stripped greater than halfway, but not entirely stripped, were counted as half-stripped, whether they contained filled or unfilled seed. Almost all cones greater than half-stripped

contained filled seed. Those few cones showing some unfilled seed were counted as half-stripped under the assumption that they had yielded enough filled seed from the stripped portions for the squirrel to have proceeded that far. Brink counted all cones partially stripped as half-stripped.

3. The remaining partially stripped cones, those stripped less than halfway, were broken down into two groups as follows:

A. Those which contained a majority of filled seed.

B. Those which contained a majority of unfilled seed.

The large majority of cones stripped less than halfway were obviously in poor condition and filled with unsound seed. Those cones had therefore been handled by the squirrel and rejected. In calculating the total number of cones handled, these were counted as completely stripped. When a squirrel began to strip a rotten cone, it seldom proceeded to strip it more than halfway before completely abandoning it and beginning a new cone.

Those cones not obviously insect-infested or in poor condition were further examined by removing the next few whorls of bracts and determining whether they contained empty or filled seed. If the majority of seed was filled, the cone was counted as half-stripped, otherwise it was recorded as completely stripped.

For example, squirrel no. 6 (Table I) was fed a total of 2,750 old cones. Of this total 547 were unstripped. Ninty-six cones were greater than half-stripped, but less than completely stripped, and were counted as half-stripped. A total of 264 cones were less than

Table I. Numbers of old white spruce cones consumed by Group II during feeding trials.

Sq. No.	Sex	Cones Fed	Total Cones Un-stripped	Cones <Entire>½ Stripped	Cones<½ Stripped: Sound Seed	Cones<½ Stripped: Empty Seed	Adjusted Total Un-stripped	Total Cones Handled	Daily Average (11 Days)
6	M	2,750	547	96	17	247		2,147	195
			(547)*	(48)	(8)	(0)	603		
15	M	2,750	549	133	13	184		2,128	193
			(549)	(66)	(7)	(0)	622		
17	F	2,750	491	268	49	266		2,100	191
			(491)	(134)	(25)	(0)	650		
21	M	2,750	463	172	46	303		2,178	198
			(463)	(86)	(23)	(0)	572		
22	F	2,750	505	231	28	327		2,115	192
			(505)	(116)	(14)	(0)	635		
Average Values		2,750	511	180	31	264		2,134	194
			(511)	(90)	(15)	(0)	616		

*Numbers in parenthesis represent those used in calculations (see text).

half-stripped. Only 17 of these contained sound seed, and these were counted as being half-stripped. The remaining 247 cones contained rotten or unfilled seed. Since they had been handled and rejected by the squirrel, they were counted as being completely stripped. This assumed that the squirrel had begun to strip the cone, but because it did not yield good seed it was then totally discarded. As cones with rotten or unfilled seed did not constitute more than 30 to 50% of the total cones fed, the great difference in numbers between the two groups of half-stripped cones shows that there was a definite tendency to reject cones which contained bad seed. Table II shows the method of counting cones for squirrel no. 6.

Table II. Method used in counting cones for squirrel no. 6.

		Actual Number	Counted as
Total cones fed		2,750	2,750
Unstripped cones		547	- 547
<entirely>½ stripped		96	- 48
<½ stripped:	Filled seed	17	- 8
	Unfilled seed	247	- 0
		Total cones utilized	2,147

Table III. Climatological data recorded during feeding trials (U. S. Coast and Geodetic Survey, College, Alaska).

	Temperature				Precipitation (mm)	
	Max.		Min.		Rain, Melted	Snow, Sleet,
Date	° C	° F	° C	° F	Snow, Etc.	Hail
Mar. 1965						
5	5.5	42	- 7.5	18		
6	5.5	42	- 6.0	21		
7	6.0	43	- 4.5	24	3.6	17.8
8	4.5	40	- 3.5	26	T*	T
9	8.0	47	0	32	T	
10	10.5	51	1.5	35	1.3	
11	5.0	41	1.5	35		
12	6.5	44	- 1.0	30		
13	1.5	35	-10.0	14		T
14	- 4.5	24	-12.0	10		
15	- 7.5	18	-20.5	- 5		
16	- 9.0	16	-22.0	- 8		
17	- 5.0	23	-16.5	2		
18	- 2.0	28	-12.5	9		
19	2.0	36	-11.5	11		
20	3.5	38	- 2.0	28		
21	9.0	48	- 1.0	30		
22	5.5	42	- 2.0	28		
23	7.5	46	1.5	35	2.3	
24	6.0	43	0	32		
25	9.5	49	0.5	33		
26	2.0	36	- 0.5	31	T	T
27	1.5	35	0	32		
28	6.5	44	1.0	34		
29	1.5	35	0	32	2.3	12.7
30	2.0	36	0	32	1.3	T
31	4.0	39	- 2.5	27	.8	
Apr. 1965						
1	4.0	39	- 2.0	28		
2	4.0	39	- 1.0	30		
3	5.0	41	- 2.0	28		
4	10.5	51	- 2.5	27		T

*T = Trace

Table III (cont'd). Climatological data recorded during feeding trials (U. S. Coast and Geodetic Survey, College, Alaska).

	Temperature				Precipitation (mm)	
	Max.		Min.		Rain, Melted Snow, Etc.	Snow, Sleet, Hail
Date	° C	° F	° C	° F		
Mar. 1966						
20	16.0	3	-23.0	-10		
21	- 0.5	31	-18.0	- 1		
22	2.5	37	- 6.0	21		
23	4.5	40	- 8.0	17		
24	4.0	39	- 6.5	20		
25	2.5	37	- 5.0	23		
26	4.0	39	- 6.5	20		
27	6.0	43	- 3.5	26		
28	7.0	45	0	32		
29	10.0	50	- 3.5	26		
30	10.0	50	- 3.0	27		
31	6.0	43	- 7.0	19		
Apr. 1966						
1	6.0	43	- 4.5	24		
2	8.0	47	- 4.5	24		
3	9.5	49	- 4.5	24		
4	3.5	38	- 6.5	20		
5	1.5	35	- 6.0	21		
6	7.0	45	- 4.5	24		
7	4.5	40	- 4.0	25		
8	4.0	39	- 6.5	20		
9	4.0	39	- 4.0	25		
10	6.0	43	- 4.0	25	1.0	12.7
11	- 3.5	26	- 8.0	17	1.3	20.3
12	0	32	-12.0	10		
13	- 2.5	27	-15.5	4		
14	- 3.5	26	-14.5	6		
15	1.0	34	-10.0	14		
16	7.5	46	- 2.0	28		
17	9.0	48	2.0	36	2.3	
18	2.5	37	- 2.5	27	6.1	
19	0	32	-11.0	12		

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