ASPECTS OF RED SQUIRREL (*TAMIASCIURUS HUDSONICUS*) POPULATION ECOLOGY IN INTERIOR ALASKA

A

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Paul Vincent Krasnowski, B.S.
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ASPECTS OF RED SQUIRREL (TAMIASCIURUS HUDSONICUS)

POPULATION ECOLOGY IN INTERIOR ALASKA

APPROVED:

Frederick C. Dean

Peter C. Lent

Samuel J. Harbo Jr.
Chairman

Samuel J. Harbo Jr.
Department Head

APPROVED: Brina Kessel DATE: 9 May 1969
Dean of the College of Biological Sciences and Renewable Resources

Vice President for Research and Advanced Study

ABSTRACT

Red squirrel (Tamiasciurus hudsonicus preblei) population ecology was investigated in a field study conducted between 21 September 1967 and 30 October 1968 near College, Alaska. Population density on the 21 ha study area was one squirrel per 1.1 ha during the spring 1968 and one per 1.2 ha during the fall 1968. Territoriality appears to be somewhat relaxed during the spring, and there are non-territorial squirrels present at that time.

Young of the year squirrels can be distinguished from adults, at least through October, according to the degree of closure of the epiphyses of the radius and ulna. Immature males can be distinguished from adults on the basis of testis weight during the fall.

Immature squirrels constituted 57.1% of the population sample during the fall 1967 and 51.3% during the fall 1968. Males formed 66.7% of the sample of adults and 64.0% of the sample of immature squirrels. Males were not significantly heavier or larger than females. Mean tail length of immature squirrels exceeded that of adults.

Fall molt commences for all red squirrels during late August and September. The spring molt commences for females during March, whereas males do not molt until May.

Testes measurements and female reproductive condition indicate that there is a single annual reproductive season, from late February through April. Squirrels breed during their first spring at about 10 to 11 months of age. Estimated mean litter size was 4.20 based on embryo counts and 3.92 based on placental scars. The most frequent litter size was four.

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INTRODUCTION

This study is the fourth in a series of projects designed to examine the ecology of the red squirrel, *Tamiasciurus hudsonicus preblei*[1], in interior Alaska. The three previous studies (Brink, 1964, M. C. Smith, 1967, and Streubel, 1968) emphasized the ecological relationships of the red squirrel to its primary food source, white spruce (*Picea glauca*) seed.

The purpose of this project was to determine the age distribution, sex ratio, density, and dynamics of the red squirrel population in interior Alaska; and to determine the length and timing of the reproductive cycles and the litter size.

Field work was conducted from 21 September 1967 to 30 October 1968. Behavioral observations, based primarily on live-trapping and tagging, were conducted on the Bonanza Creek study area established by M. C. Smith. Information about the population was derived from red squirrel specimens collected in stands of white spruce near College, Alaska.

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[1]Scientific names of mammals follow Hall and Kelson (1959), those of plants follow Hulten (1968), and those of birds follow the 1957 check-list of the American Ornithologists' Union.

STUDY AREAS

Bonanza Creek Study Area

The study area is located within the Bonanza Creek Experimental Forest about 25 km southwest of College, Alaska. A permanent grid system 457 m square (21 ha) was established by M. C. Smith. The study area has been subdivided into 25 sections, each 91 m square; the corners have been permanently marked. Each section has been further subdivided into nine subsections, and the corners of each subsection have also been marked.

On the basis of the homogeneity and density of the forest cover, Streubel (1968) showed that white spruce (*Picea glauca*) is the dominant species on the study area. Quaking aspen (*Populus tremuloides*), alder (*Alnus crispa*), and paper birch (*Betula papyrifera*) are interspersed with the spruce.

A detailed description of the study area and lists of the major plant, bird, and mammal species occurring on the study area can be found in M. C. Smith (1967).

Field work on the Bonanza Creek study area was limited to live-trapping, tagging, and observation in order to maintain, as much as possible, natural conditions.

Sampling Areas

Red squirrel specimens were collected regularly in areas near College, Alaska, where the habitat was similar to that of the Bonanza Creek study area. Some squirrels were collected along the Nenana

Road near the Bonanza Creek Experimental Forest. Others were taken along the Chena Hot Springs Road, northeast of College. Most of the specimens were collected in white spruce stands within a few kilometers of the University of Alaska campus.

METHODS

Population Sample

Sampling of the red squirrel population was limited to areas where white spruce was the dominant species. Red squirrels inhabit black spruce (*Picea mariana*) as well as white spruce, but Brink and Dean (1966) found that black spruce seed has significantly lower nutritional value than white spruce seed. Since this nutritional difference might affect some of the population characteristics of interest to this study, squirrels were not collected from black spruce stands.

Squirrels were hunted with shotguns, usually .410 gauge with either number 7-1/2 or number 9 shot. The hunter would walk slowly through a white spruce stand, or wait near a red squirrel midden. Middens are large accumulations of spruce cone bracts and stalks, stripped by squirrels. A midden is usually located near the center of a squirrel's territory, close to the base of a spruce or under old windfalls.

Many squirrels betrayed their location by giving territorial or alarm calls. If the approximate position of a squirrel could be determined from a call, the squirrel's movements would often give away its exact position. Locality, habitat description, time, behavior, and general conditions were recorded for each squirrel collected. These specimens were used to provide data about certain characteristics of the red squirrel population, i.e., age structure, sex ratio, measurements, and reproductive condition.

Specimen Preparation

Squirrels were weighed to the nearest 0.1 g on an Ohaus triple beam balance, and the four standard measurements (total length, tail length, hind foot, ear) were taken. Flat skins were prepared and dried with salt. Crown-rump length and weight were recorded for any embryos present.

One testis, the left unless damaged, was removed from each male. Greatest length and greatest diameter were measured with vernier calipers, and the weight was calculated to the nearest 0.1 mg on a Mettler H6 analytic balance.

Reproductive tracts were removed from females, examined for embryos and placental scars, and classified according to reproductive condition. Ovaries were sectioned by hand, and the corpora lutea were counted with the aid of a dissecting microscope.

One foreleg from each specimen was removed, tagged, and frozen. The forelegs were mounted on cardboard sheets, which were then x-rayed at the Fairbanks Medical Center, Fairbanks, Alaska. These x-ray plates were examined to determine the degree of epiphyseal closure in the distal end of the radius and ulna of each foreleg. The proximal end of the humerus was also examined, but did not yield as clear a picture as the radius and ulna. Information derived from the degree of closure was used to separate young of the year from adult squirrels collected in late summer and fall.

Captive Litter

On 14 April 1968 a pregnant female red squirrel was captured on the University of Alaska campus. It was placed in a wire cage in the animal pens northeast of the Biological Sciences Building on the campus. Sometime between the evening of 26 April and the morning of 28 April, she gave birth to a litter of four young: two males, two females.

A heavy rainstorm on 4 June soaked the nest box, and, subsequently, both mother and offspring died. However, three sets of measurements were obtained. These measurements provide some information concerning nestling growth rates.

Population Density

Population estimates for the 21 ha (50 acres) Bonanza Creek study area are available for the fall 1964 and 1965 (M. C. Smith, 1967), and fall 1967 (Streubel, 1968). These estimates were based on the assumption that red squirrels in Alaska occupy mutually exclusive territories, each of which contains one actively used midden. Therefore, the number of squirrels present in a given area can be estimated by counting the number of such middens in that area.

A population estimate using the time-area count method (Flyger, 1959) was conducted in the fall 1967. Subsequent estimates in the spring and fall 1968 were based on the number of active middens on the study area.

Live-trapping and Tagging

In May 1968 a live-trapping and tagging program was begun in order to determine the validity of the squirrel-midden relationships set forth by M. C. Smith (1968). National live traps were placed on or near the middens and baited with peanut butter. On two occasions during the initial trapping, a squirrel was found dead in a trap after a sudden rain shower. Subsequently, traps were covered with cellophane, and no other losses occurred. Traps were checked in the early morning and late evening, and were left set overnight.

Squirrels were restrained in a wire cone during handling. Number one monel fingerling tags were attached to one ear. The other ear was tagged with a loop of colored polyvinyl chloride plastic tubing, utilizing a procedure perfected by Curtis Halvorsen (Bureau of Sport Fisheries and Wildlife, personal communication). A 14 gauge hypodermic needle was inserted through the pinna of the squirrel, and the tubing was inserted through the needle. Then the needle was withdrawn leaving the tubing in the hole. An overhand knot was made in one end; the other end was drawn through the knot, which was then tightened forming a loop about 1 cm in diameter. The knot was sealed with a drop of acetone.

RESULTS AND DISCUSSION

Bonanza Creek Population Estimation

During October 1967 I conducted a time-area count on the study area based on the method described by Flyger (1959). Each of the 225 subsections was assigned a number. Twenty numbers were selected from a random number table, and the center of the subsection corresponding to each number was designated as an observation point. Each observation area was watched for 15 minutes, and the distance from the observer to each squirrel sighted was measured. The population estimate was calculated using the formula:

$$\hat{P} = \frac{A \cdot Z}{\pi S y^2}$$

where:
A = total area of the study area
Z = the number of squirrels observed
S = the number of observation periods
y = mean distance from observer to squirrels sighted

Use of this method yielded an estimated population size of 50 squirrels. The data were then used with a modification of this formula that utilized the mean area within which a squirrel was observed:

$$\hat{P} = \frac{A \cdot Z^2}{S\pi(\Sigma y_i^2)}$$

where:
y_i = the distance from the observer to the i^{th} squirrel sighted

This formula yielded an estimated population size of 46 squirrels.

Based on my observations and those of Streubel (personal communication), the fall 1967 population estimates based on my time-area count are considered to be much higher than the actual population size. Similarly, Brink (1964) conducted a time-area count of the red squirrel population on an island in the Tanana River southwest of College and found that his estimate of 24 squirrels was considerably higher than a subsequent estimate of 16 squirrels that was based on an attempted total kill.

Since red squirrel activity patterns may vary widely with day-length and weather, estimates based on observation of individual squirrels may vary greatly.

Both M. C. Smith (1967) and Streubel (1968) estimated red squirrel population density on the Bonanza Creek study area on the basis that one active midden represents one squirrel (Table 1). Streubel (1968:35) found that, "at no time during the study was more than one squirrel caching cones on more than one midden." M. C. Smith (1968) noted only one occurrence when more than one squirrel was observed on a midden, and he concluded that a single red squirrel occupies one midden. Gordon (1936:171) found a similar situation in _T. h. fremonti_: "Each [bract] pile was the center of an area an acre or two in extent which was guarded jealously by a single squirrel." C. C. Smith (1968) found that in the genus _Tamiasciurus_, territories are occupied and defended throughout the year by one squirrel of either sex.

Three types of middens were recognized in this study: active, auxiliary, and inactive. An active midden is one which was determined to be the center of activity for one squirrel. Degree of activity of a midden can easily be determined by the amount of freshly stripped cone bracts laying on the midden, numerous entrance tunnels, the general activity of the squirrel that defends it, and the presence of fresh digging and tracks in the snow. Streubel (1968) used similar criteria to determine the degree of activity of a midden.

Several smaller middens are also present on the study area. By all indications these lack the degree of activity observed for the active middens. These are called auxiliary middens because the squirrels utilizing them are probably dependent upon another, larger, active midden.

Old, currently unused middens are called inactive. They can be recognized by the lack of any fresh sign of activity. Cone bracts from past years can be distinguished from bracts of recently stripped cones by their darker color.

Population estimates on the Bonanza Creek study area for spring and fall 1968 were again based on the assumption that one active midden represents one red squirrel. Results of a live-trapping and tagging program conducted concurrently with the spring 1968 population estimation indicate that there might be some squirrels present on the study area in the spring that do not have established territories. Therefore, the estimated population size for spring 1968 should be considered a minimum estimate.

The presence of these non-territorial squirrels may have been partly responsible for the high population estimate obtained from the time-area count during the fall 1967. Table 1 gives the estimated population size for the study area.

Population Density

The spring 1968 population on the study area was estimated to be

19 squirrels (Table 1), representing a density of one squirrel per 1.1 ha (2.7 acres). In the fall the population was estimated to be 18 squirrels, or one squirrel per 1.2 ha (2.9 acres). Streubel (1968) estimated a density of one squirrel per 0.9 ha (2.2 acres) on the study area during the fall 1967. During two successive years of spruce cone failure, 1964 and 1965, fall densities of one squirrel per 2.1 ha (5.2 acres) and one squirrel per 5.25 ha (13.0 acres), respectively, were reported (M. C. Smith, 1967).

Hatt (1929) found a population density of one squirrel per 0.73 ha (1.8 acres) in mature red spruce (*Picea rubens*) in New York. Klugh (1927) observed a density of one squirrel per 0.42 ha (1.0 acre) in spruce forests in New Brunswick. Hatt (1943) and Gordon (1936) estimated

Table 1. Estimated population size and density of the Bonanza Creek study area based on the number of active middens.

Season and Year	Estimated Population Size	Estimated Population Density One Squirrel Per (acres	(hectares)
Fall 1964	10 [a]	5.2	2.1
Fall 1965	4 [a]	13.0	5.25
Fall 1966	no data	----	----
Fall 1967	23 [b]	2.2	0.9
Spring 1968	19	2.7	1.1
Fall 1968	18	2.9	1.2

[a] Derived from M. C. Smith (1967)
[b] Streubel (1968)

one per 0.84 ha (2 acres) and one per 0.21 ha (0.5 acres), respectively, for *T. h. fremonti*. C. C. Smith (1968) suggested that red squirrel behavior regulates territory size in response to food supply. The population density of the Bonanza Creek study area may fluctuate in response to changing availability of white spruce cones (Streubel, 1968).

Territoriality

Figure 1 shows the location of all the middens found on the study area. All middens located on the study area will be referred to according to the subsection in which they occur, e.g., midden 1SW is that midden found in the southwest subsection of section one. Only one midden that was used in this aspect of the study is located outside the boundaries of the study area. It is located just north of subsection 3N and will be designated as midden A.

The only previously unreported midden found during this study was 7N. This midden was active in the spring 1968. The lack of weathered cone bracts indicated that it was a new midden, probably first used during the previous fall. During the fall census in October 1968 it was reclassified as inactive because no cones had been cached on the midden; there were few tracks in the snow and no fresh cone cuttings in the vicinity of the midden.

Between 27 May and 26 June 1968, 56.7 trap-days (one trap-day = one trap set for 24 hr) were spent in an attempt to determine the relationship of the number of squirrels to the number of middens found on the study area. Trapping effort was concentrated in the northwest half of the study area. Squirrels were tagged with colored plastic ear loops, and recognition of individuals was possible. Squirrels will be designated by the location of the first midden on which they were trapped, prefixed by "S-". For example, that squirrel trapped for the first time on midden 1SW will be referred to as S-1SW.

Nine red squirrels were tagged; four were subsequently observed defending the midden on which they were tagged. Six of the squirrels tagged were never recaptured, but three others were recaptured one or more times. These recaptures all occurred on middens other than the one on which the squirrel was first caught and tagged. Squirrel S-7W, tagged on 1 June, was found dead in the trap on midden A two days later. Squirrel S-6NW was observed defending midden 6NW, but was later recaptured on midden 7N and on 7W. In September 1968 it was observed caching cones on 6NW. Squirrel S-A was recaptured four times. On the morning of 10 June, it was caught in the trap on 3S. That evening S-A was again captured, this time on 7N. On the evening of 24 June it was recaptured on 7N, and the following morning it was caught on 3S.

Several breakdowns in the normally strict territorial behavior of red squirrels were observed on the study area during the trapping. On 2 June a squirrel was caught in the trap on midden 7W. Another, unmarked squirrel was giving an aggressive call from a tree 2 m from the trapped squirrel. The trapped squirrel (S-7W) was tagged, and when released it quickly headed north away from the midden. The following day S-7W was found dead in the trap on midden A. At the same time another squirrel was giving an aggressive call from a spruce near the trap.

In subsequent trapping on midden A, an unmarked squirrel was trapped, tagged, and released. This was the squirrel that was recap-

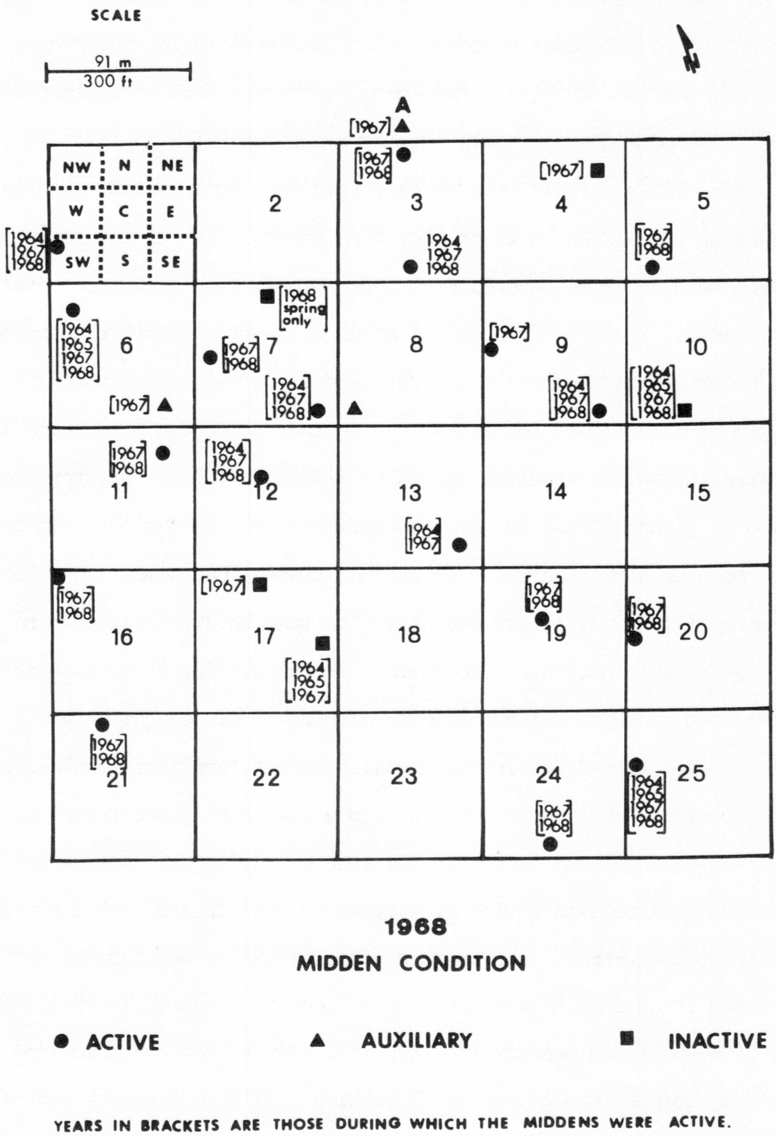

Figure 1. Location and classification of all middens found on the Bonanza Creek study area.

tured four times, as has already been described. Its fourth recapture was on midden 3S. As I released S-A from the trap, an unmarked squirrel began calling from a tree 10 m away. S-A ran away from the midden, and the unmarked squirrel went to the midden and began to feed.

On 9 June when I found a dead lactating female in the trap on midden 11NE, another unmarked squirrel was active on that midden. In another instance, a squirrel was observed feeding on midden 12C within 1 m of the trap that held another squirrel. Upon the approach of the observer, the free squirrel ran down a burrow in the midden. The trapped squirrel escaped during tagging and ran away from the midden.

Squirrel S-6NW clearly controlled the territory surrounding midden 6NW. The fact that S-6NW was also captured on other active middens indicates that squirrels may make occasional forays into neighboring territories. In those cases involving a trapped squirrel and a free squirrel observed near the midden at the same time, it is not clear whether one of the squirrels controlled the territory on which the trap was located, and whether the other squirrel also controlled a territory.

C. C. Smith (1963) cited similar cases in which a trapped squirrel and a free squirrel were together on a midden. He found that there were squirrels present, which he called vagrants, that did not possess a territory. They are solitary and compete for area in which they can establish a territory. In some instances, a territory owner could be driven from part or all of its territory by a vagrant squirrel (C. C. Smith, 1968). He further suggests that vagrant squirrels can determine when a territory owner is not actively defending his territory, for example, when he is confined in a trap. He cites two examples in which the vagrant squirrel successfully defended the territory against the original owner that had been held in a trap for several hours.

Differences in the trapability of individual red squirrels must also be considered when examining the results of this trapping. Although Layne (1954) felt that there was no tendency for squirrels to become trap-shy or trap-prone, C. C. Smith (1963 and 1968) found distinct differences in the responses of different squirrels to trapping. Balph (1968), studying trap responses in Uinta ground squirrels, felt that an animal's response to a trap after it had once been captured depended on its previous experiences with the trap. Capture and confinement could be a punishing stimulus, while eating bait could be a rewarding stimulus. This suggests the possibility that the four squirrels on the Bonanza Creek study area that were neither recaptured nor observed after tagging might still have been present on the territory on which they were first caught, but afterwards avoided the trap.

Balph (1968) also believed that an animal was more likely to show avoidance of the particular trap in which it was captured, but might still be attracted by the novelty of a similar trap in another area. C. C. Smith (1968) stated that red squirrels were more susceptible to capture on areas other than their own territory. Therefore, a trap may be more likely to catch a vagrant or a squirrel with a neighboring territory than the squirrel that controls the midden on which the trap is located. If this situation exists on the Bonanza Creek study area, a squirrel, for example S-7W, that is believed to be a vagrant, may actually be a territory owner that was never caught on his own midden.

Streubel (1968) found that territorial structure was most rigid during caching, after which territoriality lessened somewhat. C. C.

Smith (1963) believed that territorial behavior broke down when conifer seed was not the major food source. This is probably the case on the Bonanza Creek study area during late spring and early summer. Although the relationship between the number of squirrels to the number of middens, and the interactions between squirrels are still not clear, two factors are evident: territoriality does relax somewhat in the spring, and there are probably vagrant squirrels present in the population at that time of year.

Predation and Competition

On 22 April 1968 I heard two simultaneous alarm calls, apparently originating from the same location. Although it took at least five minutes traveling through deep snow to locate the squirrels, the calling never stopped. As I approached a clump of spruce where the squirrels were located, a great horned owl (Bubo virginianus) flew from a tree less than 10 m from one of the squirrels. The first squirrel, a male, was shot; the other, located in a spruce tree 5 m away, still had not stopped calling. It was shot and was later classified as a pregnant female.

C. C. Smith (1968) felt that squirrels may become tolerant toward each other in the spring when feeding on the male cones at the extremities of tree branches because they would be particularly susceptible to avian predation and, "could warn each other of predators when feeding together" (C. C. Smith, 1968:36). This conclusion is based on his observation of seven different pairs of squirrels that were feeding on male Douglas fir (Pseudotsuga menziesii) cones in the spring. M. C. Smith (1967) reported that red squirrels in Alaska occasionally eat white spruce buds during February through April. However, the stomachs of the squirrels I collected were not examined. Since it is not known if they had been feeding on spruce buds, the reasons for the occurrence of these two squirrels so close together remain unclear.

A marsh hawk (Circus cyaneus) was observed capturing a red squirrel that was crossing a road northeast of College of 16 October 1968 (Carl McIlroy, personal communication). C. C. Smith (1965) observed a great horned owl that was attempting to catch a red squirrel. M. C. Smith (1967) attributed at least one red squirrel loss on the Bonanza Creek study area to predation by a goshawk (Accipiter gentilis). However, no indications of predation were observed on the study area during the present study.

While live-trapping red squirrels at Bonanza Creek, two flying squirrels (Glaucomys sabrinus) were captured. The first, caught on 6SE, an auxiliary midden, was removed from the study area. The second flying squirrel was captured on 3S, an active midden. It was ear-tagged and released, but never recaptured. Midden 6SE continued to show signs of limited activity after removal of the flying squirrel, probably due to occasional red squirrel use.

Although flying squirrels may be almost as numerous as red squirrels in interior Alaska (Brink, 1964), it is doubtful that they are active food competitors of the red squirrel. Brink and Dean (1966) found that whereas white spruce seed was the staple food of red squirrels, flying squirrels appeared unable to survive on a diet of white spruce seed alone. C. C. Smith (1968) felt that since northern flying squirrels were mainly bud and foliage feeders, and exhibited a nocturnal activity pattern, there would be relatively little competition with red squirrels. Hazard (1960) observed flying squirrels caching food in captivity.

While flying squirrels may utilize red squirrel middens, the two captured at Bonanza Creek may have actually been attracted by the peanut butter bait or the trap itself. Balph (1968) found that Uinta ground squirrels are easily captured because of their tendency to approach strange objects such as unbaited traps.

Traps on several middens were often found sprung but empty. Teeth marks on the bait indicated that mice might be raiding the traps. After the first snowfall many tracks and runways of mice were found on several middens. These mice may live near the middens or perhaps in burrows within the middens themselves.

Hatt (1929) suggested that the white-footed mouse (*Peromyscus leucopus*) may be a competitor of the red squirrel in New York. Kangur (1954) found that shrews (*Sorex* sp.) both in the wild and in captivity will consume large amounts of Douglas fir seed. Although the extent to which these species utilize white spruce cones is not known, mice, shrews, and flying squirrels probably lack the dexterity of the red squirrel in stripping a cone quickly to obtain the seeds.

Age Ratio

Three age classes, based on those described by Hanson (1963), are utilized in this study: (i) juveniles are young of the year that have not yet reached full growth; (ii) subadults are young of the year that have reached adult size, but have not yet participated in a breeding season; (iii) adults are fully grown animals that have completed one or more breeding season. Juvenile and subadult animals may be lumped together as immature.

All of the red squirrel specimens collected were classified as adult or immature (young of the year) according to the degree of closure of the epiphyseal cartilage of the radius and ulna. The exact age at which this suture closes in T. hudsonicus is unknown. Five of the six squirrels shot during November 1967 had open epiphyses. In 1968 several of the squirrels collected in late October had sutures that were nearly closed. Since most red squirrel litters are probably born in April, it was assumed that the epiphyses remained open for six to seven months. It is possible that some squirrels born in early litters may have closed epiphyseal sutures in October, and might be mistaken for adults. However, measurements of male testes indicate that my age determination by epiphyseal closure was accurate (see section on male reproductive cycle). Young of the year squirrels could not be distinguished from adults after November.

Layne (1954), working with T. h. loquax in New York, found that the distal epiphyseal suture of the humerus was distinct until approximately 11 weeks of age, while the proximal suture remained open for 18 to 19 weeks. Carson (1961) used a similar technique to separate young of the year and adult fox squirrels (Sciurus niger) and gray squirrels (S. carolinensis). Maximum cartilage width in the distal end of the radius and ulna persists in these species until they are about 18 weeks old. Immature gray squirrels can be identified and age ratios determined, at least through October, with this method (Petrides, 1951).

Age ratios for the monthly samples are shown in Table 2. In 1968 juveniles were first collected during June and July when they constituted 30.7% and 29.4% of the sample, respectively. By August young of the year, some of which had reached adult size, composed 56.3% of the sample. The percentages of immature squirrels present in September (54.5%) and October (56.2%) vary slightly from the figure for August.

Sample data were grouped into subjectively chosen seasons to facilitate statistical comparison (Table 3). During June and July the young are still smaller than adult size, have not been weaned, and are not actively competing for territory. They are considerably less active than adults and are probably less susceptible to hunting. Therefore, the figures for June and July are probably lower than the actual percentage of young squirrels present during those months. For this reason, data from squirrels collected during June and July have been grouped, and will be considered as the summer season data. Cone caching begins in August, and the increased proportion of immature squirrels collected is probably a result of the increased amount of activity necessary to establish and defend a territory, and harvest cones for a winter food supply. The fall, August through November, is designated as those months during which young of the year are adult size, but can still be distinguished from adults on the basis of epiphyseal closure.

This grouping also allows comparison with data from two other sources. Marilyn Modafferi supplied data for red squirrels she collected near College during September and October 1968. Additional data, derived from a project executed by an undergraduate class in the Department of Wildlife Management at the University of Alaska during the fall, 1966, is also shown.

There is no significant difference between the total proportion of young in the samples (Table 2) and any of the seasonal totals in Table

Table 2. Percentages of immature red squirrels collected in the monthly population samples.

	September 1967			October 1967			November 1967			June 1968			July 1968		
	M	F	Total	M	F	Total	M	F	Total	M	F	Total	M	F	Total
Number in sample	5	7	12	17	7	24	5	1	6	8	5	13	11	6	17
Number immature	1	3	4	10	5	15	5	0	5	3	1	4	1	4	5
Per cent immature	20.0	42.8	33.3	58.8	71.4	62.5	100.0	0.0	83.3	37.5	20.0	30.7	9.1	66.7	29.4

	August 1968			September 1968			October 1968			Sample Total		
	M	F	Total	M	F	Total	M	F	Total	M	F	Total
Number in sample	9	7	16	9	2	11	8	4	12	72	39	111
Number immature	5	4	9	6	0	6	2	3	5	33	20	53
Per cent immature	55.5	57.1	56.3	66.7	0.0	54.5	25.0	75.0	56.2	45.8	51.3	47.7

Table 3. Percentages of immature red squirrels in the population samples grouped by season.

	Fall 1967 (Sept-Nov)			Summer 1968 (June-July)			Fall 1968 (Aug-Oct)			Modafferi Fall 1968			Wildlife Course		
	M	F	Total	M	F	Total	M	F	Total	M	F	Total	M	F	Total
Number in sample	27	15	42	19	11	30	26	13	39	20	22	42	22	22	44
Number immature	16	8	24	4	5	9	13	7	20	6	9	15	15	11	26
Per cent immature	59.3	53.3	57.1	21.1	45.4	30.0	50.0	53.8	51.3	30.0	40.9	35.7	68.2	50.0	59.1

3 ($p > 0.05$). The data from the fall 1966 (59.1% immature) do not differ significantly from my data from the fall 1968 (51.3%). However, the 1966 data are significantly different ($p < 0.05$) from that of Modafferi.

Data from Modafferi indicate a smaller percentage of immature squirrels present (35.7%) than my data from the fall 1968 (51.3%). This difference is not significant at the 5% level. However, Modafferi's data do differ significantly from my data from the fall 1967 (57.1%).

Population estimates at the Bonanza Creek study area (Table 1) indicate that the population has remained relatively constant for the past two years. Thus the fall 1967 and fall 1968 age ratios of 57.1% and 51.3%, respectively, may be indicative of a relatively stable population size. In comparison, Allen (1943) calculated that for the fox squirrel, which, similar to the red squirrel in Alaska, produces four young per year, a fall population composed of 60% young squirrels represents a population level that is not changing.

Sex Ratio

Table 4 shows the sex ratio by age class of each monthly sample. The data are also grouped by season (Table 5). The period of reproductive activity, February through May, is included in the sex ratio analysis and will be referred to as the spring season. Prolonged cold resulted in reduced squirrel activity in January and prevented any squirrels from being collected. The winter sample is, therefore, composed of only six specimens shot during December and is insufficient to allow statistical comparison with other seasonal data. Data from Modafferi and from the Department of Wildlife Management class project,

Table 4. Sex ratios of the monthly population samples according to age class.

		Sept 1967	Oct 1967	Nov 1967	Dec 1967	Feb 1968	Mar 1968	Apr 1968	May 1968	June 1968	July 1968	Aug 1968	Sept 1968	Oct 1968	Total
ADULT	M:F	3:4	7:2	0:1	3:3	9:1*	3:4	14:6	8:4	4:4	10:2*	4:3	3:2	6:1	74:37**
	%M	42.8	77.7	0.0	50.0	90.0	42.8	70.0	75.0	50.0	83.3	47.1	60.0	85.7	66.7
IMMAT.	M:F	1:3	10:4	5:0	----	----	----	----	----	3:1	1:4	4:3	6:0*	2:3	32:18*
	%M	25.0	71.4	100.0	----	----	----	----	----	75.0	20.0	57.1	100.0	40.0	64.0

* significantly different from 50:50 ratio ($p < 0.05$)
** significantly different from 50:50 ratio ($p < 0.01$)

Table 5. Sex ratios of the population samples grouped by season and age class.

		Fall 1967 (Sep-Nov)	Winter 1967 (Dec)	Spring 1968 (Feb-May)	Summer 1968 (June-Jul)	Fall 1968 (Aug-Oct)	Modafferi (Sep-Oct 68)	Wildlife Course (Fall 1968)
ADULT	M:F	10:7	3:3	34:15*	14:6	13:6	14:13	7:11
	%M	58.8	50.0	69.3	70.0	68.4	51.8	38.8
IMMAT.	M:F	16:7	----	----	4:5	12:6	6:9	15:11
	%M	69.5	----	----	44.4	66.7	40.0	57.6

* significantly different from 50:50 ratio ($p < 0.05$)
** significantly different from 50:50 ratio ($p < 0.01$)

fall 1966, are again provided for comparison.

There was considerable variation in the sex ratio of the monthly samples of adult squirrels. Eight of the 13 samples exceeded 50% male, but only two were significantly different from a 50:50 sex ratio ($p < 0.05$): February (90.0% male) and July (83.3% male). The sex ratio of the total adult sample was 66.7% male and differed very significantly from an even sex ratio ($p < 0.01$). None of the seasonal sex ratios of adults differed significantly from that of the total sample of adults.

The immature sex ratio, 64.0% male, also differed significantly from a 50:50 ratio ($p < 0.05$). All six immature squirrels collected during September were male, and this was the only month during which the sex ratio was significantly different from an even sex ratio. Seasonal grouping showed similarity between data from the fall 1967 and the fall 1968, 69.5% and 66.7% male, respectively. Data from Modafferi showed a considerably lower proportion of males present in her sample, but this did not differ significantly from my data ($p > 0.05$).

It was initially assumed that the adult sex ratio for red squirrels in interior Alaska would show an equal proportion of males and females in the population, or, because the red squirrel is polygamous, perhaps a higher proportion of females.

The unexpected abundance of males in the sample of adults suggested the possibility that an unknown factor was influencing the collection technique causing males to be more susceptible to hunting than females, thereby giving a biased estimate of the sex ratio in the population.

C. C. Smith (1968), after studying territoriality in T. douglasii and T. hudsonicus, stated that there was no behavioral dimorphism in the method or intensity of defense of territory. However, he also found that during the breeding season males may wander from their territories more often than females (C. C. Smith, 1968). This increased activity of the males during the spring may make them more vulnerable than females. Therefore, female adults may not be adequately represented in the spring sample in my data. However, the sex ratio of my population sample, excluding those specimens collected during the spring months, still differs significantly from the expected 50:50 sex ratio ($p < 0.05$). Except during the spring breeding season, no behavioral differences in adults have been reported, and none were observed during this study. Therefore, I have assumed that, except during breeding season, both sexes are equally vulnerable to hunting, and that my sample does represent the actual sex ratio in the population. Lampio (1965) felt that the hunting of European red squirrels (Sciurus vulgaris) in Finland yielded an unbiased sample of the population.

The sex ratio of the total sample of immature squirrels was 64.0% male. Layne (1954) calculated a sex ratio of 55% male in nine litters of nestling young. C. C. Smith (1968) observed a sex ratio of 71% male among five litters. Lampio (1965 and 1967) found sex ratios of 58.3% male in nestlings and 57.1% male in juveniles in the European red squirrel.

Lampio (1967) believed that male squirrels suffer a higher natural mortality rate due to migration, diseases, predation, and accidents than do females. C. C. Smith (1968) found that female young are more likely to obtain the territory left by their mother because the male offspring, more involved in sexual play, are less aggressive in territorial competition. Thus, male young might have a lower survival rate than females because they are less successful in establishing territories. In both of the above situations it might be a selective advantage to have a higher proportion of males than females at birth in order to offset the higher mortality rate of male young and therefore have approximately equal proportions of male and female adults at the time of breeding. Hence, adult sex ratios following years of good survival and high reproduction probably would have high proportions of males.

Measurements

Means, confidence intervals, and standard deviations for the weight, total length, tail length, hind food, and ear length are shown in Table 6 and Table 7 from the samples of adult and immature squirrels, respectively. Adult males sampled are heavier ($\bar{x}$ = 233.9 ± 3.7 g) than adult females sampled ($\bar{x}$ = 227.5 ± 8.1 g); however, the difference is not significant ($p > 0.05$).

Means of total length and ear length measurements were slightly greater for males than females, whereas females were larger than the males in tail length and hind foot. However, none of the differences in the mean measurements for males and females were significant ($p > 0.05$).

Measurements of the immature squirrels in the sample showed similar trends. Mean immature male weight was 206.9 ± 11.2 g and exceeded

Table 6. Means, confidence intervals, and standard deviations for the measurements of adult squirrels.

Measurement	Adult Males		Adult Females		Total	
	Mean and CI*	S.D.	Mean and CI	S.D.	Mean and CI	S.D.
Weight (g)	233.9 ± 3.7	15.7	227.5 ± 8.1	21.2	232.4 ± 3.3	17.4
Total Length (mm)	319.8 ± 3.4	10.7	316.6 ± 5.5	9.0	318.9 ± 2.1	10.3
Tail Length	120.2 ± 1.3	6.7	120.9 ± 2.5	6.1	120.4 ± 1.3	6.5
Hind Foot	49.9 ± 0.1	2.1	50.0 ± 0.2	1.9	49.9 ± 0.5	1.9
Ear	26.2 ± 0.1	2.3	25.6 ± 0.2	1.8	26.0 ± 0.3	1.6

* ($p < 0.05$)

Table 7. Means, confidence intervals, and standard deviations for the measurements of immature squirrels.

Measurement	Immature Males		Immature Females		Total	
	Mean and CI*	S.D.	Mean and CI	S.D.	Mean and CI	S.D.
Weight	206.9 ± 11.2	29.9	195.6 ± 13.6	27.3	203.3 ± 8.6	29.1
Total Length	316.4 ± 25.4	17.6	313.7 ± 22.9	13.5	317.6 ± 4.1	13.2
Tail Length	125.5 ± 5.7	8.4	124.9 ± 6.1	7.0	125.3 ± 2.4	7.7
Hind Foot	50.3 ± 0.4	2.2	48.8 ± 0.6	2.1	49.7 ± 0.7	2.3
Ear	25.1 ± 0.2	1.8	25.7 ± 0.5	2.0	25.3 ± 0.6	1.9

* ($p < 0.05$)

the mean immature female weight of 195.6 ± 13.6 g. Immature males averaged slightly larger than immature females in all measurements except ear length. None of the differences between the means for immature males and females were significant.

Layne (1954) found that in _T. h. loquax_ in New York females were slightly larger in all measurements except hind foot than males. However, males were slightly heavier than females. Comparison with data from interior Alaska indicates that _T. h. preblei_ is larger and considerably heavier than _T. h. loquax_. Mean monthly weights from Layne's (1954) sample vary from 180 g to 205 g and are consistently lighter than those shown in Figure 2 for my samples.

Other measurements for red squirrels from New York recorded by Hamilton (1939) similarly indicate that female adults are heavier than males, but that males are longer. Weights for his sample ($\bar{x}$ = 182 g for adult males, $\bar{x}$ = 187 g for adult females) are considerably less than weights for adult squirrels collected in interior Alaska.

Weights and measurements for red squirrels collected in Washington and southern British Columbia (C. C. Smith, 1965) are slightly larger than those of the squirrels collected in this study.

In my sample adults were heavier and longer than immature adults, although the differences were not significant. However, mean tail length of immature squirrels is longer than that of adults. This difference is significant for females ($p < 0.05$) and highly significant ($p < 0.01$) for males. Several squirrels were missing the tip of their tail when collected, and the wound appeared fresh. I assumed that the damage was due to gunshot, and these individuals were not included in the measurements of tail length. Of 70 adult males collected whose tails had not been damaged by shot, 54 (77%) had tail lengths less than the mean tail length of immature males. Among the females 59% of the 29 adults had tail lengths shorter than the mean tail length for immature females.

Layne (1954) found that deformity of the tail was common, occurring in 20.2% of his sample. Layne (1954), C. C. Smith (1968), and Streubel (1968) report that chasing occurs between squirrels during defense of territory and in normal breeding behavior. Loss of the tip of the tail due to the infliction of a wound could result from these chases. Since juvenile squirrels do not defend territories or participate in breeding chases, they might be far less susceptible to this type of injury. During breeding season two or more males may compete for an estrus female and chasing occurs (C. C. Smith, 1968). This might increase the occurrence of tail injury among males and be responsible for the higher frequency of tail injury among males than among females.

Figure 2 shows the mean weights of the monthly samples of adult males and females. Both male and female adults show a gradual increase in mean weight during winter and early spring. Mean male adult weight reached 239.6 g during March, the beginning of breeding season, then declined gradually during June to 214.4 g. Mean female adult weight increased from 202.1 g in December to 241.2 g in May, then declined to 229.2 g in June. Mean monthly weights of both male and female adults then rose to their highest peak during September, at the time when cone caching had been completed and food was abundant.

The weight changes shown in Figure 2 may not necessarily reflect actual seasonal fluctuations in mean weight, but could be the result of

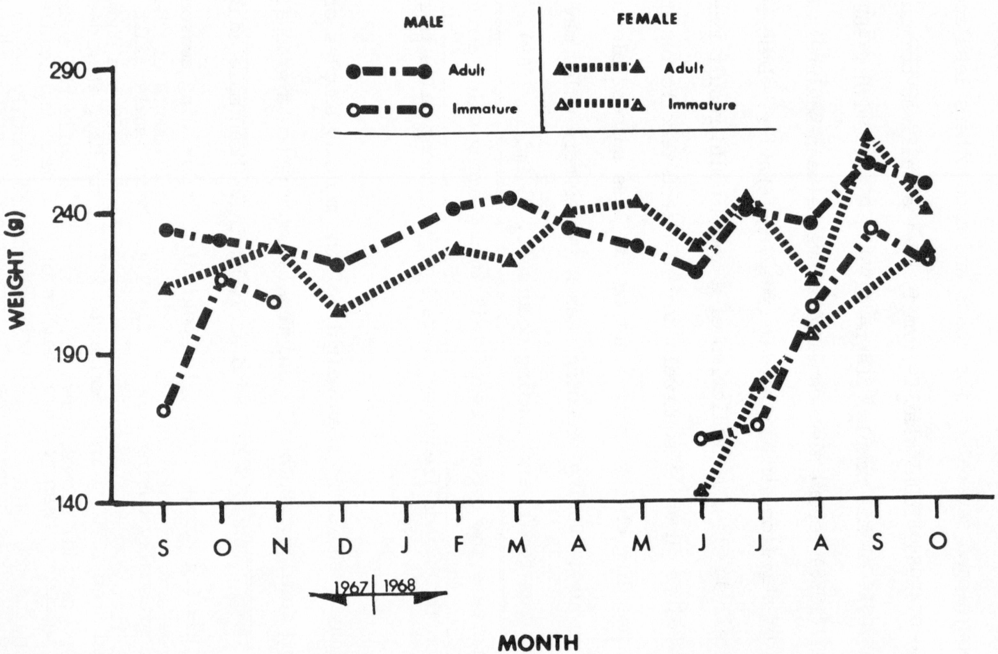

Figure 2. Fluctuations in mean weights for male and female, adult and immature squirrels in the monthly population samples.

samples taken from different local populations during different times of year. Sometimes an area would be hunted during the course of a few weeks or a month, and then another area would be used. For example, when snow closed several of the roads and made others less accessible, suitable stands of white spruce nearer College were sought. Therefore, I cannot determine to what degree the variation in mean weight was influenced by seasonal changes or by my sampling technique. Layne (1954) thought his data suggested some seasonal fluctuation in weight, whereas C. C. Smith (1965) found no similar trends in red squirrel weight changes in Washington and British Columbia.

Table 8. Data from measurements of the litter of four red squirrels born in captivity.

	7 Days		14 Days		28 Days	
Measurement	Mean and CI	S.D.	Mean and CI	S.D.	Mean and CI	S.D.
Weight (grams)	23.4 ± 7.5	4.0	26.6 ± 3.2	2.1	45.8 ± 6.7	4.1
Total Length	118.3 ± 5.7	3.6	133.0 ±11.8	7.4	168.3 ±10.0	5.0
Tail	33.0 ±10.0	5.0	41.3 ± 3.2	2.1	53.3 ± 3.2	2.1
Hind Foot	19.9 ± 0.3	0.3	24.8 ± 2.2	1.6	34.3 ± 2.2	1.5

Three sets of data for the weight and measurements of the red squirrel litter born in captivity about 27 April 1968 are shown in Table 8. A hypothetical growth curve (Fig. 3) for juvenile red squirrels was plotted using the data from this litter and the monthly means of the weight and total lengths of juvenile squirrels shot during the summer and fall.

The graph indicates that the highest rate of growth, both absolute and relative, in juveniles probably occurs during late May and June. Layne (1954) found a similar period of rapid juvenile growth in red squirrels in New York; spring young in his sample had a mean weight of 79.6 g in May and 121.0 g in June.

According to Hamilton (1939), red squirrels in New York weigh approximately 47 g at 27 days. This is similar to the mean weight of 45.8 g obtained at 28 days for my captive litter.

By July the young of the year in my population sample had reached adult length, but the mean weight (175 g) was still considerably lower than that of adults (239 g). Although the mean immature weight in September is still lower than the mean adult weight, the difference is not significant, and there is overlap of ranges. Layne (1954) found that on the basis of weight young of the year were virtually indistinguishable from adult squirrels in September.

Pelage Characteristics

Pelage coloration and the molt sequence of the red squirrel have been described in detail by Layne (1954) and Nelson (1945). Pelage coloration of _T. hudsonicus_ in interior Alaska was found to be similar to that described for more southerly populations. The outstanding characteristics of red squirrel summer pelage are the distinct black lateral stripes and the white ventral fur. Winter pelage is characterized by dull, grayish ventral fur and the lack of the distinct lateral stripes. There are other, more subtle differences between summer and winter pelage coloration, but these vary between individuals and are not as easily recognized as the lateral stripes and the color of the ventrum.

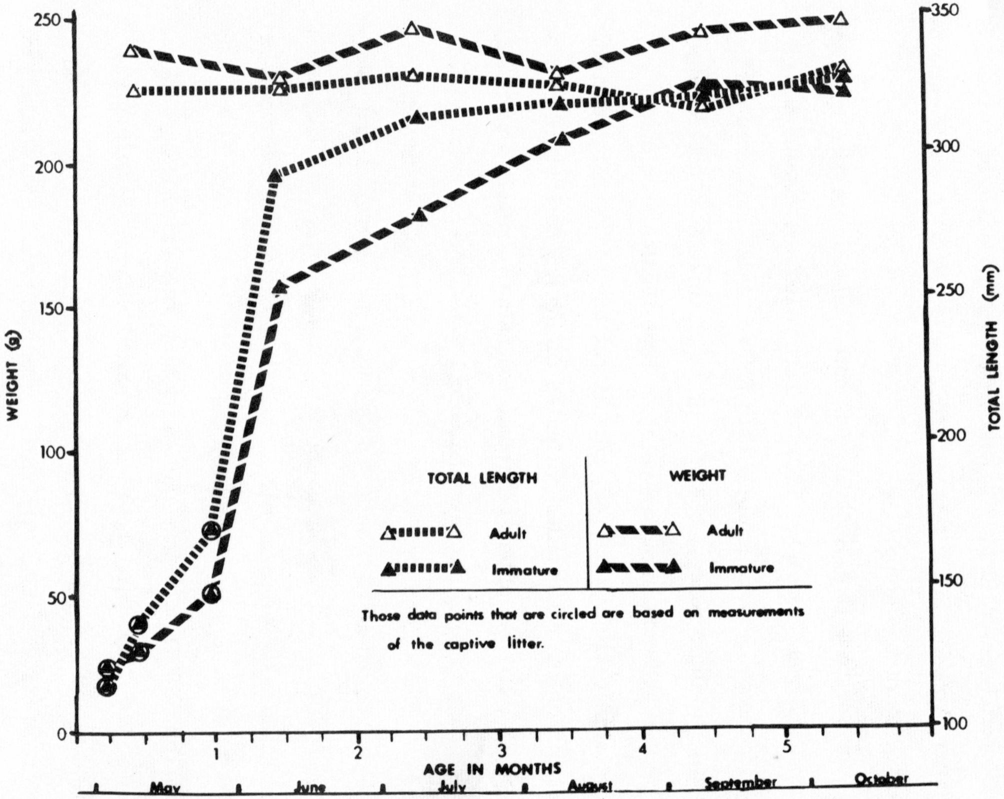

Figure 3. Hypothetical growth curves for juvenile red squirrels based on data from a captive litter and monthly means from the population samples.

In Alaska the red squirrel molts twice each year. The fall molt commences for both adults and juveniles alike during late August and September. By late October several specimens were in winter pelage, and all others were molting. The exact date of the onset of the fall molt appears to vary widely between individuals and does not seem to be related to sex or age group.

In the spring molt a disparity was noted between the time of onset of molt in males and females. In March both males and females showed typical winter pelage characteristics. Fifteen males collected during April were in winter pelage, but four of the five females collected at that time were already in summer pelage. Four females shot during May all had distinct lateral stripes, and all but one had a white ventrum. However, six of the eight males collected during May were still in winter pelage, and two others were just beginning to molt. In the sample for June five of the seven males collected were in summer pelage.

Nelson (1945) found that the beginning spring molt of red squirrels in Minnesota varied as much as 40 to 50 days; the earliest found was 6 April, and the latest was about 29 May. Summer pelage was complete early in August. However, he made no distinction between the sexes in regard to the time of pelage change.

Hamilton (1939) felt that the spring molt began during May and June in New York, and that there was no sexual difference indicated in the molt. Layne (1954) found that while both sexes began the spring molt at about the same time, the males seemed to be in a more advanced stage during the latter part of the molt.

The reasons for this dimorphism in the time of onset of spring molt in interior Alaska are not clear. C. C. Smith (1965:93) found no evidence that, "color or color pattern are functional in intraspecific or interspecific displays or recognition signals." The difference in the time of molt may be related to energy requirements. In May, when male squirrels are beginning to molt, the females are still nursing their young. Since both molt and lactation are energy-expensive processes, the female molt may be displaced to an earlier date to reduce the energy requirements during lactation. However, this answer is not entirely satisfactory because pregnancy and molt occur at the same time, thereby causing a potential conflict in energy requirements.

Male Reproductive Cycle

One testis from each male squirrel collected was weighed to the nearest 0.1 mg. Testis weights for all specimens are given in Appendix B. For statistical comparison gross testis weights were adjusted by dividing by the body weight and multiplying by 100, yielding testis weight per 100 g body weight. Table 9 gives the mean monthly values for testis weight for adult and immature male squirrels.

Greatest length and greatest width were recorded for each testis. The length multiplied by the square of the width was used as an estimate of testis volume. This showed a very high degree of correlation with testis weight ($r = 0.978$ for adults, $r = 0.508$ for immatures).

Data for the winter months is unavailable. However, it was noted in field observations that during December the testes of all males collected were much enlarged over the fall condition, and in every male the scrotum was pendant and very conspicuous. Mean testis weight for February (468.6 ± 38.8 mg) was considerably heavier than that of the

Table 9. Mean testis weights for adult and immature red squirrels in the monthly population samples.

		Sep 67	Oct 67	Feb 68	Mar 68	Apr 68	May 68	Jun 68	Jul 68	Aug 68	Sep 68	Oct 68
ADULT	n	3	1	9	3	9	7	5	9	4	3	6
	Mean	31.66	18.48	468.64	422.07	337.16	307.30	57.81	32.95	32.65	26.87	33.23
	± CI	±0.47	-----	±38.82	±203.8	±47.50	±69.45	±25.62	±8.19	±15.72	±9.94	±8.95
	S.D.	0.19	-----	50.65	82.11	61.96	56.77	20.65	10.66	9.88	3.99	8.53
IMMATURE	n	0	4	0	0	0	0	2	1	4	5	2
	Mean		13.44					21.98	18.15	10.57	11.20	12.59
	± CI		±4.26					±27.06	-----	±0.54	±1.55	±6.48
	S.D.		2.28					3.01	-----	0.34	1.25	0.72

previous September (31.6 ± 0.5 mg) or October (18.48 mg). Mean testis weight and mean estimated testis volume declined after February, and the sharpest drop occurred during May and June.

Layne (1954) found that the presence of sperm in the cauda epididymides was closely related with testis weight and length. Hoopes (unpublished; data on file in the Department of Wildlife Management, University of Alaska) first found sperm present in epididymal smears from squirrels collected near College, Alaska, during early March. This corresponds to the time of year during which testis measurements of squirrels in my sample were near their peak. On the basis of the information from Layne (1954) and Hoopes, my monthly data for testis weight and volume should be indicative of male reproductive condition.

Figure 4 shows the annual fluctuations in mean testis weight and estimated volume for red squirrels in interior Alaska. The single peak in the data and the abrupt drop-off in both weight and estimated volume indicate that there is only a single annual breeding season. In addition, none of the males collected during the summer or fall were judged to be in reproductive condition on the basis of testis weight or estimated volume.

Layne (1954) found that testis weight in *T. h. loquax* began to increase during November and December and reached a peak of about 1,500 mg (gross weight) in February. Testis weights remained above 1,000 mg throughout the summer with only a slight dip in April, which he felt indicated a lull between the two breeding seasons. Testis weight then fell sharply during September (Layne, 1954). Hamilton (1939) found enlarged testes during February through April with a subsequent decline in size through June; testes were enlarged again during July through

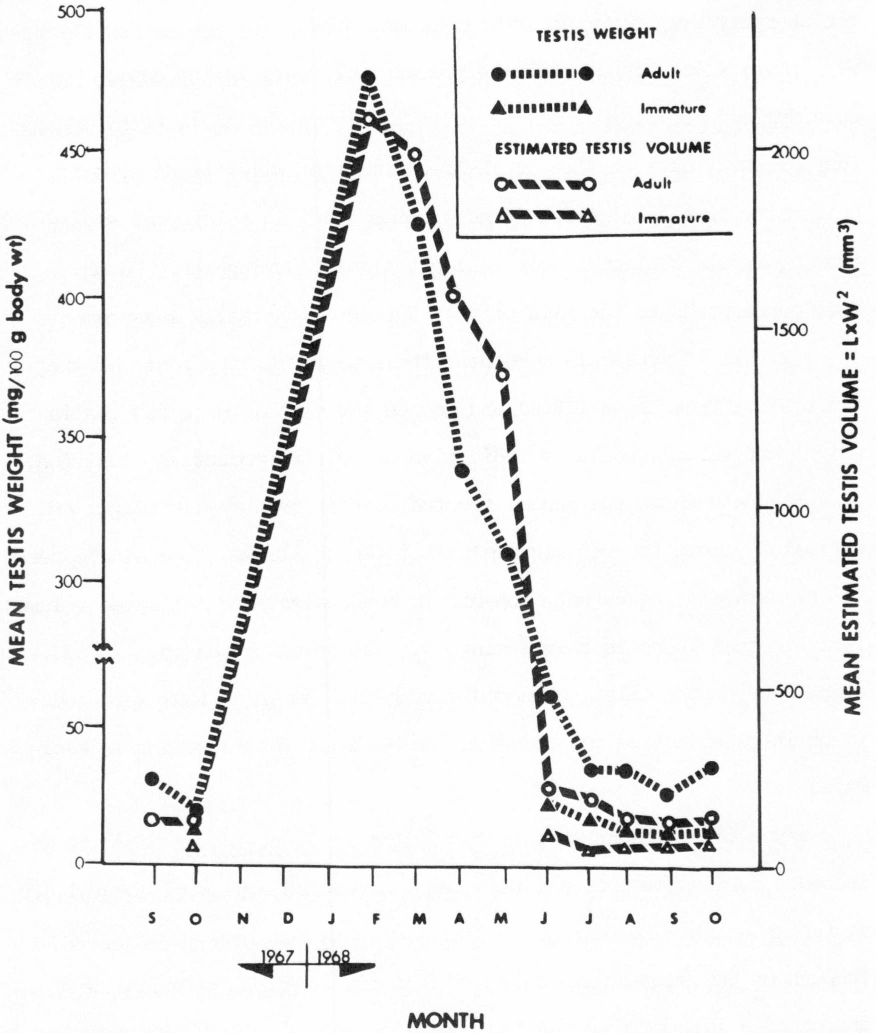

Figure 4. Mean testis weights and mean estimated testis volumes of adult and immature red squirrels collected in the monthly population samples.

September, which he believed indicated the existence of two breeding seasons.

Because all male squirrels collected during the spring had enlarged testes, it is believed that young of the year males are sexually mature and breed during their first spring; that is, at about 10 to 11 months of age. Similarly, gray squirrels born in the spring reach sexual maturity at about 11 months of age and remain sexually active throughout the breeding season (Kirkpatrick and Hoffman, 1960).

Figure 5 shows the means and ranges of testis weights for adult and immature squirrels collected during August, September, and October. The difference between the mean adult testis weight (30.0 mg) and the mean subadult testis weight (11.8 mg) was highly significant ($p < 0.01$), and there is no overlap of ranges.

Although mean juvenile body weight was significantly less than mean adult body weight during June and July ($p < 0.001$), by August some young have reached adult size. Testis weight provides a clear, convenient method for segregating adult from subadult male red squirrels during the fall when body weight is no longer useful for this purpose.

Female Reproductive Cycle

The reproductive cycle for female red squirrels was determined by the condition of the reproductive tracts of the specimens collected. The nulliparous reproductive tract is characteristically small, slender, and opaque white; whereas an anestrous adult reproductive tract is larger, more flaccid, and translucent (Layne, 1954). An estrous female can be recognized readily by the condition of the reproductive tract, which becomes greatly enlarged. Also, the coiled nature of the vagina

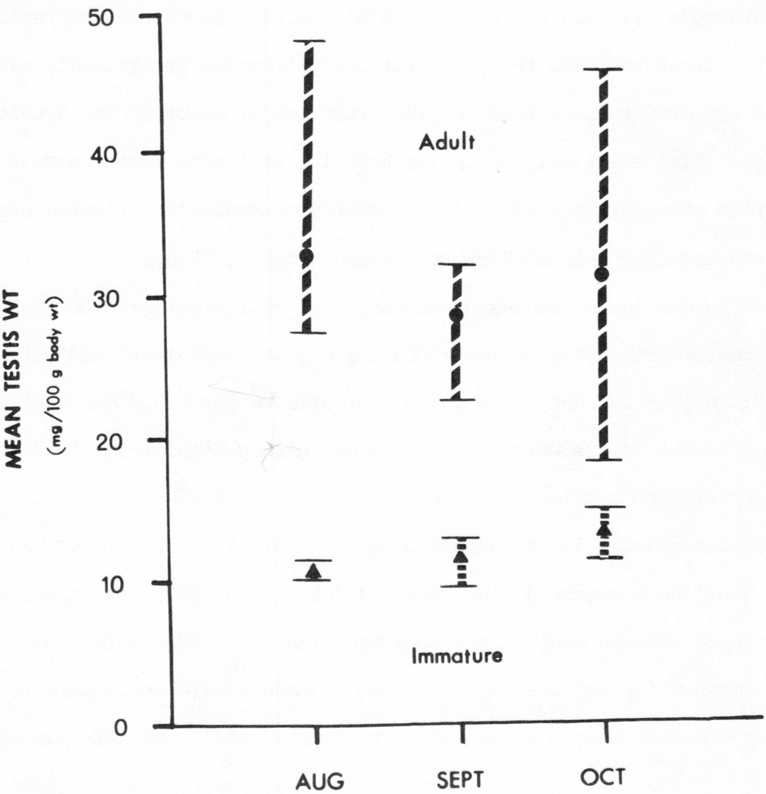

Figure 5. Means and ranges for testis weights of adult and immature red squirrels collected during August, September, and October.

becomes apparent (Layne, 1954). Females were considered to be lactating when milk could be forced from the teats. Post-partum females had enlarged, flaccid uteri. Placental scars appeared as dark patches on the uterus and were readily discernible through October. The uterine walls appeared heavier and the mesentary more vascular in the area of the placental scars. These characteristics were more pronounced in recently post-partum females and became less noticeable in specimens collected during the late summer and fall. Reproductive condition of all adult females collected during 1968 is recorded in Appendix C.

Figure 6 shows the reproductive condition of all adult females collected from February through July 1968. The single estrous female collected during February was shot on the 28th. Two other estrous females were collected on 2 March. All other females collected in March and April were pregnant.

The first pregnant female was collected on 27 March and had 5 embryos present that had a mean weight of 6.8 g. Since weight at birth is approximately 7.5 g (Hamilton, 1939), these embryos were probably almost fully developed. The last pregnant females collected were shot on 22 April. Two were in the early stages of pregnancy, while the third had almost full term embryos. Lactating females were collected during May and June; the last was shot on 12 June.

Only two of the 23 females collected after 2 February 1968 were classified as barren. The first was collected on 31 May, five weeks after the last pregnant female had been collected. The other was shot on 17 October. Both were classified as adults on the basis of epiphyseal closure. Both individuals had reproductive tracts that appeared similar to those of juveniles, and there were no corpora lutea present

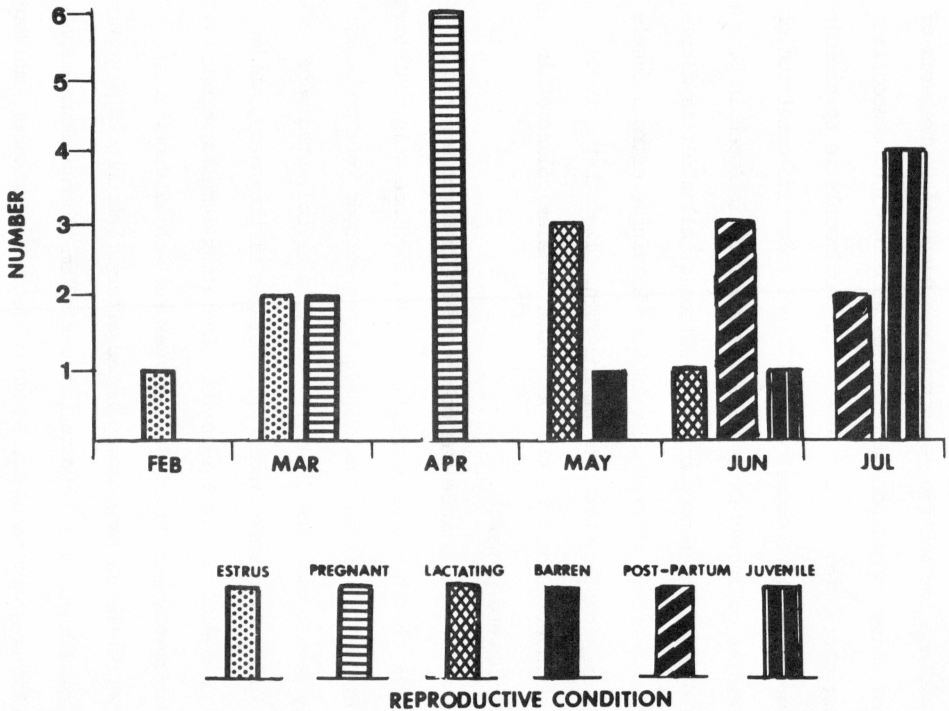

Figure 6. Reproductive condition of the females collected during February through July 1968.

in the ovaries.

The high percentage of fecund females in the sample (91%) suggests that female red squirrels, like the males, breed during their first spring, at about 10 to 11 months of age.

The limits of the breeding season were estimated on the basis of female reproductive condition using the 40 day gestation period estimated by Hamilton (1939) to calculate the approximate time of breeding. On this basis the female collected on 27 March that had almost fully developed embryos must have bred approximately the last week in February. This corresponds with the occurrence of estrous females in the samples on 28 February and 2 March. The peaks of male testis weight and estimated testis volume also occur during February.

If it is assumed that the last lactating female collected had just recently given birth, she would have bred by the last week in April. In addition, no pregnant females were collected after 22 April. It appears, therefore, that red squirrels in interior Alaska breed from late February until the end of April.

Hoopes first found signs of reproductive activity on 9 March, when a pregnant female was collected. Pregnant females were collected during late March and throughout April. Five of the 24 adult females he collected showed no signs of having bred and were classified as barren. Soper (1942) observed that there was only one litter per year, in late spring, in northern Alberta and the District of Mackenzie. C. C. Smith (1968) observed breeding activity in March, April, and May in red squirrels in Washington and British Columbia, but felt that the time of breeding varies in response to cone abundance. In that portion of their range red squirrels have a single breeding season, while

Douglas squirrels (_T. douglasii_) have two potential breeding seasons (C. C. Smith, 1968).

Hatt (1943) observed nursing females in a population of _T. h. fremonti_ in Colorado between 18 June and 17 July. In Alaska the frequency of lactating females dropped from 75% of the sample in May to 20% during June, suggesting a somewhat earlier breeding season than that in Colorado.

Hamilton (1939) observed two distinct breeding periods in New York: February through May, and July through September. Information from Layne (1954) similarly indicates that peak breeding occurs during February and March, and during June and July. However, the spring breeding season accounted for 71% of the young produced each year. Klugh (1927) and Hatt (1929) believed that second litters were exceptional.

In interior Alaska, it is doubtful that any breeding after April would produce a litter than could survive the winter. Cutting and caching of white spruce cones begins between August 1 and 15 (M. C. Smith, 1967). Streubel (1968) found that red squirrels were actively territorial during caching. Since young of the year are independent during their first winter, they must either have established their own territory and have harvested a winter cone supply or be able to displace a squirrel that controls a territory. White spruce cones open, and seed begins to fall in early September. Any cones remaining on the trees after mid-September would be of little food value. Therefore, harvesting of white spruce cones must be nearly completed by that time.

A female that bred in early May would have her young during the second week in June. The young are weaned at about 78 days of age

(C. C. Smith, 1968). For this hypothetical litter, this would be approximately the first of September. Thus, while most squirrels were completing their cone-caching, these late-born young would not yet have established a territory or stored any cones, and would have to compete with squirrels of adult size. Without a cone supply it is doubtful that they could survive the winter.

Litter Size

Litter size was estimated on the basis of the number of placental site scars, embryos, or corpora lutea present. Table 10 shows the mean litter size based on each of these three methods of estimation. Information from Hoopes and from Marilyn Modafferi is also shown.

The mean number of corpora lutea per female was 5.58. The mean number of embryos, based on five specimens, was 4.20. The mean litter size based on placental scars was 3.92. Data collected by Hoopes showed a mean of 4.17 embryos per pregnant female. Marilyn Modafferi collected eight squirrels in September and October 1968 that had a mean of 4.5 placental scars. This is considerably higher than the mean of 3.92 found in this study; however, the difference is not statistically significant ($p > 0.05$) and may be due to the small sample size.

The difference between the means of my samples for corpora lutea and embryos suggests a rate of implantation of about 75%. Layne (1954) found a 95% rate of implantation based on the ratio of corpora lutea to placental scars in red squirrels in New York. Corpora lutea may yield estimates of litter size that are higher than those based on counts of embryos or placental scars because of the loss of ova which are not fertilized or do not implant (Layne, 1954). In one specimen I counted

13 corpora lutea and in another 15 in a pair of ovaries. These most likely represent two or more sets of ova that have been shed. If a female fails to breed successfully, more follicles may mature, and a second set of ova may be shed. If the squirrel is then successful in breeding, the corpora lutea from both cycles will be maintained (Robert L. Rausch, personal communication).

Table 10. Litter size and uterine distribution.

Method	Sample Size	Litter Size $\bar{x}$	Litter Size SD	Uterine Distribution Left $\bar{x}$	Left SD	Right $\bar{x}$	Right SD
corpora lutea	36*	5.58	---	3.00	2.21	2.58	1.77
embryos	5	4.20	0.5	1.60	1.14	2.60	1.14
	19 [a]	4.17	---	1.54	----	2.63	----
placental site scars	12 [b]	3.92	0.7	2.25	0.75	1.67	0.65
	8	4.50	1.6	1.75	1.28	2.75	0.89

[a] Hoopes, 1957 (unpublished)
[b] data provided by M. Modafferi
* number of ovaries

C. C. Smith (1968) stated that during breeding season a female is in heat for one day only. Poor weather or other ecological conditions may inhibit normal breeding activity causing loss of ova. However, only two of the 21 parous females examined had more than seven corpora lutea present in the ovaries. Since litters of six have been reported in the red squirrel (Hatt, 1929), the pairs of ovaries that contained seven or fewer corpora lutea probably represent a single estrous cycle. This indicates that most female red squirrels are successful in breeding during their first estrous cycle.

Comparison of the mean litter size estimation based on embryos to that based on placental scars indicates that about 93% of the embryos continue development until birth. However, it is possible that some of the placental scars were the result of embryos that were resorbed. Therefore, the above percentage should be considered a maximum estimate. Comparison of the data derived from corpora lutea to that based on placental scars indicates that less than 70% of the ova that are shed successfully implant and develop.

Frequency of occurrence of each litter size is shown in Figure 7. On the basis of embryo counts and placental scar counts, the most frequent litter size was four young per female (80% and 57%, respectively). Litters of three occurred in 25% of the sample based on placental scars. Litters of five young were indicated in 20% of the sample based on embryos, and 16% based on placental scars.

Litter size estimates of less than three or more than five young per female were not found based on either embryos or placental scars. However, 2, 6, 7, 13, and 15 corpora lutea per pair of ovaries were found, each occurring in about 6% of the sample of ovaries.

C. C. Smith (1965) estimated litter size to be 2.75, 2.85, and 3.75 in successive years in Washington and British Columbia. Litters contained only two or three young in 1963, whereas in 1964 three to five young were common (C. C. Smith, 1965). He believes that litter size is related to Douglas fir cone abundance.

Lampio (1967) suggests that reproduction in Finnish red squirrels (Sciurus vulgaris) may be affected by periods of unfavorable weather in winter, which lower the physical condition of the animals, leading to

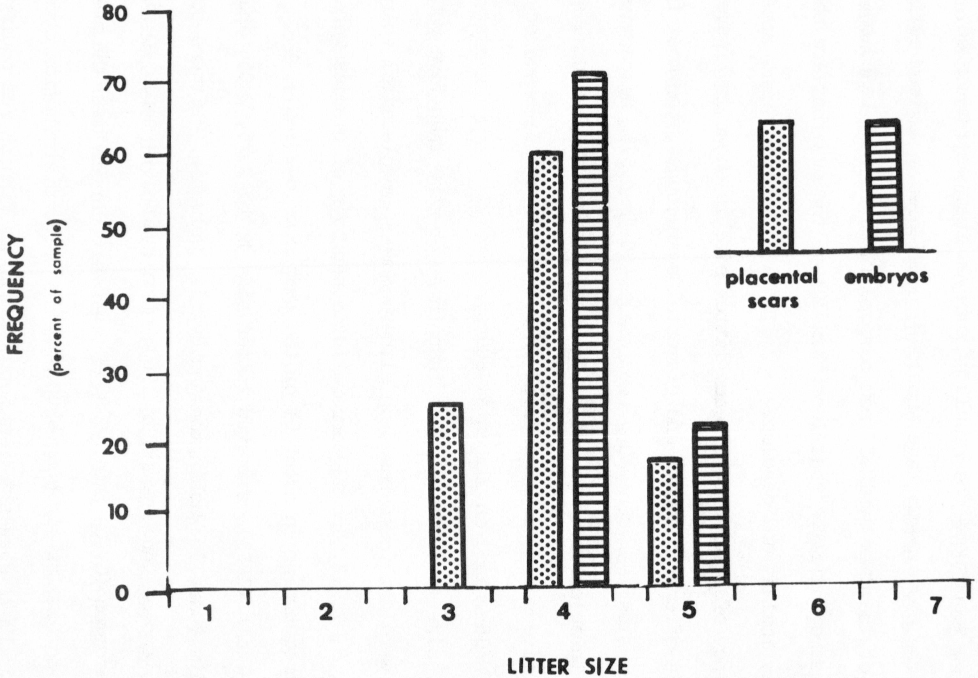

Figure 7. Frequency of litter sizes based on the numbers of embryos or placental scars present in adult females collected during February through October 1968.

fewer and smaller litters the following summer.

Hatt (1929) thought that six young per litter was the most common for red squirrels in New York. Data from Hamilton (1939) showed a mean of 4.2 embryos in the 38 squirrels he collected, with a range of three to five young per litter. Layne (1954) found a mean litter size of 4.2 based on counts of nestling young. Estimates based on embryo counts gave a mean of 4.2 per female, and placental scars yielded an average of 4.7 per female (Layne, 1954).

Layne (1954) found that corpora lutea and placental scars appeared to be randomly distributed with regard to left and right side. Hoopes found a significant difference in uterine distribution in his sample: the left uterine horn had a mean of 1.54 embryos, whereas the right horn had a mean of 2.63. This differs significantly ($p < 0.05$) from the expected 50:50 distribution. My data based on five pregnant females is very similar: the mean of the left horn was 1.60 embryos, and the mean of the right was 2.60. This was not, however, significantly different from the expected distribution, perhaps due to the small sample size. Data derived from placental scars of the eight females collected by Modafferi showed a similar distribution (left = 1.75, right = 2.75), but the difference was not significant. However, my data derived from corpora lutea (left = 3.00, right = 2.58) and from placental scars (left = 2.25, right = 1.67) showed the opposite trend; that is, the means of the left horn were **larger** than the means of the right. Again the departure from the 50:50 distribution observed by Layne (1954) was not significant ($p > 0.05$).

Recommendations

The data presented and discussed in this thesis constitute a preliminary study of red squirrel population ecology in Alaska. Further research is needed in order to clarify some of the concepts presented in this study. In addition, many of the characteristics of red squirrel population ecology that were discussed may vary in response to long-term fluctuations of environmental factors such as spruce cone production or weather. Continued research is necessary to assess the degree to which these factors may affect the red squirrel population. For further research, I recommend:

1. That the midden count method of population estimation be studied to determine more precisely the relationship between the number of squirrels and the number and classification of middens present in a given area. The proportions of non-territorial squirrels present in the population during different seasons must be determined. These objectives would require a comprehensive study of territoriality in the red squirrel.

2. That various methods of collecting red squirrel specimens be evaluated to determine which provide random samples. Sampling of the population must take into account possible differences between territorial and vagrant squirrels in both population structure and behavior.

3. That red squirrel behavior be studied, especially during winter and the breeding season. Much of the interpretation of data derived from population samples is dependent upon a comprehensive knowledge of red squirrel behavior.

4. That long-term studies of red squirrel population ecology be continued with increased emphasis on changes in population density and composition, behavior, and reproductive biology in relation to fluctuations in food supply and other environmental factors.

APPENDIX A

MEASUREMENTS

ADULTS

	Spec. No.	Date	Wgt. (g)	Total Length	Tail Length	Hind Foot	Ear from Notch
September 1967							
Males	2	21 Sept.	238.1	323	114	47	25
	3	21 Sept.	224.9	307	113	49	23
	12	24 Sept.	239.6	287	88*	48	27
Females	1	21 Sept.	213.8	---	---	--	--
	7	24 Sept.	232.4	---	---	--	--
	8	24 Sept.	210.0	319	115	49	25
	9	24 Sept.	193.4	315	126	47	23
October 1967							
Males	18	5 Oct.	228.1	332	123	49	24
	19	5 Oct.	251.6	---	---	--	--
	22	5 Oct.	235.4	---	---	--	--
	24	7 Oct.	230.4	321	120	48	26
	26	7 Oct.	226.8	327	129	50	28
	33	28 Oct.	207.8	339	129	47	26
	37	28 Oct.	-----	318	125	50	26
Females	23	7 Oct.	251.3	---	---	--	--
	34	28 Oct.	-----	305	118	45	22
November 1967							
Females	41	4 Nov.	238.8	308	100*	52	21
December 1967							
Males	45	26 Dec.	213.0	318	122	50	28
	47	26 Dec.	225.8	315	114	48	27
	48	26 Dec.	220.1	322	126	45	28
Females	46	26 Dec.	208.4	308	115	51	26
	49	26 Dec.	184.6	298	117	48	23
	50	26 Dec.	213.3	302	129	50	24
February 1968							
Males	51	12 Feb.	249.0	338	132	50	31
	52	12 Feb.	262.8	336	115	51	28
	53	14 Feb.	233.4	318	110	49	27
	54	18 Feb.	240.6	306	109	47	26
	55	26 Feb.	229.9	335	124	47	26
	56	26 Feb.	238.2	331	124	49	24
	57	26 Feb.	232.2	331	124	52	27
	58	26 Feb.	212.6	329	112	48	26
	59	29 Feb.	229.8	325	119	50	28

	Spec. No.	Date	Wgt. (g)	Total Length	Tail Length	Hind Foot	Ear from Notch
Females	60	28 Feb.	224.9	328	127	52	27
March 1968							
Males	63	2 Mar.	241.5	325	112	52	28
	65	30 Mar.	239.3	325	121	52	27
	67	30 Mar.	238.1	302	113	51	27
Females	61	2 Mar.	219.0	317	115	51	28
	62	2 Mar.	222.7	323	116	50	28
	64	27 Mar.	298.3p	313	118	49	28
	66	30 Mar.	226.0p	312	115	50	28
April 1968							
Males	68	6 Apr.	227.6	282	78*	51	26
	69	6 Apr.	233.1	312	104	48	27
	71	6 Apr.	243.5	318	123	50	26
	73	6 Apr.	232.0	306	116	49	26
	74	6 Apr.	214.0	310	118	49	23
	75a	14 Apr.	-----	305	102	48	24
	77	22 Apr.	243.8	317	125	48	25
	79	22 Apr.	247.6	319	124	48	28
	80	22 Apr.	223.0	312	123	50	25
	82	28 Apr.	219.8	308	122	51	26
	83	28 Apr.	240.7	312	108	53	28
	84	28 Apr.	236.4	323	113	50	26
	85	28 Apr.	216.3	314	116	51	27
	86	28 Apr.	240.5	312	122	51	27
Females	70	6 Apr.	244.1p	292	117	50	26
	72	6 Apr.	232.5p	319	126	48	26
	75	6 Apr.	233.4p	280	76*	49	26
	76	22 Apr.	------	---	---	--	--
	78	22 Apr.	221.7p	322	132	50	26
	81	22 Apr.	251.3p	289	92*	51	26
May 1968							
Males	87	10 May	225.5	331	131	51	24
	88	13 May	220.6	325	124	50	24
	89	13 May	229.1	323	116	51	26
	90	13 May	234.7	319	123	49	25
	92	13 May	247.9	325	123	52	27
	94	25 May	233.9	318	121	50	26
	95	25 May	214.9	301	124	49	--
	97	29 May	213.9	296	122	51	27
Females	91	13 May	257.2	329	127	51	25
	93	13 May	257.9	320	118	49	24
	96	29 May	229.5	319	123	50	27
	98	31 May	220.0	325	125	51	25

	Spec. No.	Date	Wgt. (g)	Total Length	Tail Length	Hind Foot	Ear from Notch
June 1968							
Males	100	9 June	232.8	330	126	52	25
	102	10 June	206.7	330	122	48	27
	106	25 June	205.3	275	98*	47	23
	109	29 June	210.9	308	120	52	27
	110	29 June	216.5	321	123	51	26
Females	99	9 June	251.4	321	125	48	25
	101	9 June	-----	312	120	47	25
	105	12 June	207.9	312	132	49	26
	111	29 June	229.8	320	114	51	27
July 1968							
Males	112	2 July	224.8	321	126	51	27
	114	2 July	274.3	337	133	53	26
	115	2 July	259.9	326	121	53	25
	116	2 July	234.2	321	112	49	26
	117	2 July	232.3	333	128	50	27
	120	20 July	218.5	314	121	50	25
	122	21 July	236.8	289	88*	45	24
	123	21 July	266.2	313	117	49	25
	124	27 July	231.2	321	130	47	24
	125	27 July	221.2	309	116	49	24
Females	113	2 July	228.7	321	117	52	26
August 1968							
Males	131	13 Aug.	225.7	291	106*	50	28
	132	19 Aug.	229.0	312	114	49	25
	135	19 Aug.	223.1	313	115	47	27
	143	30 Aug.	244.0	328	128	51	27
Females	137	19 Aug.	228.1	327	124	51	26
	138	19 Aug.	199.3	322	128	50	24
	144	30 Aug.	214.0	320	126	50	26
September 1968							
Males	149	17 Sept.	239.8	307	120	53	27
	150	17 Sept.	255.5	291	88*	53	27
	151	17 Sept.	240.7	310	116	49	27
	152	27 Sept.	277.9	319	122	55	28
Females	147	15 Sept.	280.9	327	116	53	26
	156	27 Sept.	248.2	322	112	53	27
October 1968							
Males	157	15 Oct.	244.4	337	128	52	28
	158	15 Oct.	268.9	333	116	55	29
	159	15 Oct.	243.7	313	126	49	25
	160	17 Oct.	240.1	303	113	50	27
	164	25 Oct.	218.2	---	---	50	25
	165	29 Oct.	263.2	347	129	52	27

	Spec. No.	Date	Wgt. (g)	Total Length	Tail Length	Hind Foot	Ear from Notch
Females	162	17 Oct.	231.8	---	125	53	26
IMMATURE							
September 1967							
Males	6	21 Sept.	170.3	308	117	50	24
Females	5	21 Sept.	241.8	340	125	50	26
	10	24 Sept.	204.8	317	115	48	27
	11	24 Sept.	191.4	314	126	48	24
October 1967							
Males	15	1 Oct.	207.1	304	124	49	24
	16	1 Oct.	216.8	---	---	--	--
	17	1 Oct.	256.9	364	146	49	24
	20	5 Oct.	224.2	---	---	--	--
	21	5 Oct.	203.3	---	---	--	--
	27	7 Oct.	195.7	321	124	48	28
	29	12 Oct.	207.8	---	---	--	--
	30	12 Oct.	205.6	315	124	47	24
	32	27 Oct.	215.1	329	125	48	26
	35	28 Oct.	-----	---	---	49	23
Females	14	1 Oct.	206.9	---	---	--	--
	25	7 Oct.	192.1	---	---	--	--
	28	12 Oct.	171.2	---	---	--	--
	36	28 Oct.	-----	303	126	47	24
	38	28 Oct.	-----	300	125	47	26
November 1967							
Males	39	1 Nov.	199.7	326	128	50	24
	40	4 Nov.	226.1	316	124	50	23
	42	4 Nov.	241.0	329	131	49	21
	43	2 Nov.	183.3	320	133	53	24
	44	3 Nov.	201.9	322	127	51	24
June 1968							
Males	103	12 June	187.9	314	129	51	26
	104	12 June	104.4	258	104	46	26
	108	25 June	174.2	304	129	50	26
Females	107	25 June	140.8	297	118	52	25
July 1968							
Males	127	27 July	163.0	307	121	48	23

	Spec. No.	Date	Wgt. (g)	Total Length	Tail Length	Hind Foot	Ear from Notch
Females	118	20 July	199.4	309	126	48	26
	119	20 July	201.6	326	138	46	24
	128	27 July	144.4	306	128	48	24
	129	27 July	172.4	306	128	48	24
August 1968							
Males	139	19 Aug.	187.5	303	106	50	24
	140	30 Aug.	217.6	323	131	52	26
	141	30 Aug.	210.6	324	126	52	26
	145	30 Aug.	208.4	319	128	53	27
Females	130	13 Aug.	183.8	307	125	50	26
	133	19 Aug.	200.9	314	120	51	27
	136	19 Aug.	208.9	315	137	46	27
	142	30 Aug.	190.2	299	115	49	25
September 1968							
Males	146	15 Sept.	265.4	333	128	55	28
	148	15 Sept.	227.0	307	125	50	25
	153	27 Sept.	218.9	316	119	52	25
	154	27 Sept.	224.4	324	125	51	27
	155	27 Sept.	219.7	314	135	49	27
October 1968							
Males	163	25 Oct.	222.0	300	95*	52	24
	166	29 Oct.	221.0	310	129	55	28
Females	161	17 Oct.	239.1	328	116	50	31
	167	29 Oct.	201.2	308	122	49	23
	168	29 Oct.	229.8	343	134	54	28

* -- Tail damaged during collection
p -- Pregnant

APPENDIX B

TESTES MEASUREMENTS

	Date	Spec. No.	Testis Wgt. (mg)	Greatest Length (mm)	Greatest Width (mm)
ADULT					
1967	21 Sept.	2	75.4	8.0	4.7
	21 Sept.	3	71.4	6.2	3.3
	24 Sept.	12	75.2	9.0	4.1
	7 Oct.	24	42.6	7.4	4.1
1968	12 Feb.	51	1138.5	----	----
	12 Feb.	52	1058.9	----	----
	14 Feb.	53	914.9	----	----
	18 Feb.	54	1213.2	19.5	10.4
	26 Feb.	55	1094.9	20.0	10.0
	26 Feb.	56	1040.7	20.0	11.0
	26 Feb.	57	1177.4	20.2	11.3
	26 Feb.	58	1059.6	19.0	10.5
	29 Feb.	59	1247.4	----	----
	2 Mar.	63	1018.6	19.0	11.0
	30 Mar.	65	813.9	17.5	8.9
	30 Mar.	67	1200.8	20.7	11.3
	6 Apr.	68	835.6	16.6	8.8
	6 Apr.	69	900.0	18.0	9.4
	14 Apr.	75a	1105.2	18.5	10.2
	22 Apr.	77	648.1	17.6	8.3
	22 Apr.	80	943.5	17.2	9.9
	28 Apr.	82	745.2	18.7	10.2
	28 Apr.	83	553.2	14.6	9.2
	28 Apr.	84	854.0	18.2	10.1
	28 Apr.	85	835.5	17.2	10.7
	28 Apr.	86	707.0	19.7	9.4
	10 May	87	623.6	15.8	8.2
	13 May	88	862.7	18.3	10.2
	13 May	89	671.5	15.6	9.3
	13 May	90	630.2	16.2	9.0
	13 May	92	684.0	16.1	9.5
	25 May	94	672.3	17.2	9.4
	29 May	97	670.5	15.5	9.2

	Date	Spec. No.	Testis Wgt. (mg)	Greatest Length (mm)	Greatest Width (mm)
1968	9 June	100	92.7	10.8	4.5
	10 June	102	124.2	11.2	4.7
	25 June	106	144.0	11.0	5.0
	29 June	109	73.5	8.0	4.0
	29 June	110	182.3	11.0	5.5
	2 July	112	77.1	9.1	5.0
	2 July	114	68.8	8.9	4.1
	2 July	115	81.1	9.0	4.9
	2 July	116	88.0	10.0	5.1
	2 July	117	95.7	9.0	5.0
	20 July	120	116.3	11.1	5.6
	21 July	122	39.8	7.3	3.5
	27 July	124	55.9	8.2	4.3
	27 July	125	73.6	9.5	4.5
	13 Aug.	131	106.2	10.7	4.7
	19 Aug.	132	57.4	7.3	4.2
	19 Aug.	135	68.7	8.0	4.3
	30 Aug.	143	62.1	7.4	4.6
	17 Sept.	149	65.8	8.9	4.3
	17 Sept.	150	57.8	8.5	4.1
	27 Sept.	152	84.9	9.5	4.2
	15 Oct.	157	82.1	8.0	4.5
	15 Oct.	158	75.4	5.3	4.0
	15 Oct.	159	98.4	10.0	5.1
	17 Oct.	160	108.5	9.3	5.2
	25 Oct.	164	47.1	6.2	3.9
	29 Oct.	165	80.5	8.6	4.5
IMMATURE					
1967	1 Oct.	15	24.3	5.3	2.5
	1 Oct.	17	29.2	6.3	3.2
	12 Oct.	30	30.0	5.3	3.1
	27 Oct.	32	34.6	6.5	3.0
	28 Oct.	35	34.4	6.3	3.2
1968	12 June	103	37.3	6.4	3.4
	25 June	108	42.0	6.0	4.1
	27 July	127	29.6	4.8	3.0

	Date	Spec. No.	Testis Wgt. (mg)	Greatest Length (mm)	Greatest Width (mm)
1968	19 Aug.	134	27.4	5.0	3.4
	19 Aug.	139	20.3	5.0	3.0
	30 Aug.	140	23.3	4.8	2.8
	30 Aug.	141	22.5	5.7	2.5
	30 Aug.	145	21.0	5.0	3.7
	15 Sept.	146	29.4	5.5	3.1
	15 Sept.	148	21.0	5.0	3.1
	27 Sept.	153	26.8	6.1	3.7
	27 Sept.	154	25.0	5.8	2.4
	27 Sept.	155	27.2	5.7	3.1
	25 Oct.	163	29.1	5.6	3.2
	25 Oct.	166	26.7	6.5	3.2

APPENDIX C

FEMALE REPRODUCTIVE CONDITION

Date	Spec. No.	Reproductive Condition	Est. Litter Size	Embryos Left	Embryos Right	Plac. Scars Left	Plac. Scars Right	Corpora Lutea Left	Corpora Lutea Right
28 Feb.	60	Estrus							
2 Mar.	61	Estrus							
2 Mar.	62	Estrus							
27 Mar.	64	Pregnant	5	2	3				
30 Mar.	66	Pregnant						3	2
6 Apr.	70	Pregnant	4	3	1				
6 Apr.	72	Pregnant	4	2	2			?	2
6 Apr.	75	Pregnant	4	0	4			0	4
22 Apr.	76	Pregnant	2+	1	1+*			2	3
22 Apr.	78	Pregnant						3	0
22 Apr.	81	Pregnant	4	1	3			7	6
13 May	91	Lactating	4			2	2	2	2
13 May	96	Lactating	4			3	1	3	?
31 May	98	Barren	0					0	0
9 June	99	Post-partum	4+			1+*	3	?	5
9 June	101	Post-partum	4			2	2	8	7
12 June	105	Lactating						2	2
29 June	111	Post-partum	4			3	1	5	?
2 July	113	Post-partum	3			2	1	2	1
20 July	121	Post-partum	5			3	2	4	2
19 Aug.	137	Post-partum	4			1	3	-	-
30 Aug.	144	Post-partum	3			1	2	1	2
15 Sept.	147	Post-partum	4			3	1	3	2
27 Sept.	156	Post-partum	3			2	1	?	1
17 Oct.	161	Barren						0	0
17 Oct.	162	Post-partum	4			2	2	2	2

* reproductive tract damaged by gunshot

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