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PROJECT CHARIOT -- FINAL REPORT

MASTER

TERRESTRIAL MAMMALS INVESTIGATION,
OGOTORUK CREEK -- CAPE THOMPSON AND VICINITY

PART B

ECOLOGY OF THE ARCTIC GROUND SQUIRREL

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June 1962

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TERRESTRIAL MAMMALS INVESTIGATION

PART B

ECOLOGY OF THE ARCTIC GROUND SQUIRREL

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by

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INTRODUCTION

In 1959, under Contract No. AT(04-3)-310 between the U.S. Atomic Energy Commission and the University of Alaska, an ecological study of the flora and fauna of the Cape Thompson-Ogotoruk Creek Region of Alaska was initiated. The Terrestrial Mammals Investigation, with Dr. W. O. Pruitt, Jr. as Senior Scientist, was one aspect of this study. This investigation was subdivided into four main categories: (1) General studies, including winter observations, (2) Small mammal biology, (3) Ecological investigations of the Arctic Ground Squirrel, and (4) Caribou investigations. This current report (Part B) includes the ecological investigations of the Arctic Ground Squirrel.

The studies of the Arctic Ground Squirrel (Citellus parryi barrowensis = Spermophilus undulatus kennicottii; see Hall and Kelson [1959] for synonymies) were initiated by Ernest A. Carl in June, 1960. Carl was in the study area until 24 August and from 28 September until 18 October, 1960, and from 18 April until 13 October, 1961.

The general research plan was to establish a study plot and to conduct a trapping, marking, and retrapping program thereon to develop data on population size and dynamics, sex and age structure, and territoriality and home range. Observations were made with the aid of binoculars and a telescope in a descriptive study of individual and social behavior, feeding, and burrow selection, construction, and maintenance. Squirrels inhabiting areas remote from the study area, but in the same valley, were collected from time to time to gain information on reproductive condition, embryo development, stomach content, and parasite infestation. Burrows outside the study plot were excavated and mapped. The existence and movements of larger predators in the valley were noted; and scats, pellets, and droppings were collected. Eskimos in surrounding villages were interviewed and observed relative to their utilization of squirrels. Detailed methods will be given under appropriate sections.

DESCRIPTION OF STUDY AREA

An irregular-shaped, 72-acre study plot was selected one-half mile west northwest of the mouth of Ogotoruk Creek at Lat. $68^{\circ} 6' 3''$ to $24''$ North; Long. $165^{\circ} 46' 33''$ to $53''$ West. Although located in the Ogotoruk Creek Valley, the entire plot drains directly into the Chukchi Sea, not into Ogotoruk Creek. The center of the plot lies $1 \frac{1}{4}$ miles west southwest of the proposed ground zero point for the 280 kiloton Chariot explosion.

The study plot is situated on the lower part of the east south-east facing slope of Sahligvik (Crowbill) Ridge between 15 and 250 feet above mean sea level. In the center of the plot, and superimposed upon the general slope, is a small hill ("The Ogotoruk") composed of an anticline which strikes both north and south thus having a sort of "canoe shape." The soil is mostly rocky shale and Lisburne Limestone, with many shale and limestone outcrops and occasional boulders strewn about the surface. At higher elevations the particle size is larger, becoming a talus slide in places. The extreme lower edge of the plot is flat, with standing water on it through much of the frost-free season. This lower edge is not utilized by squirrels. One intermittent creek, which forms the major drainage of the plot, runs its entire course within the confines of the plot and exhausts directly into the Chukchi Sea. Sahligvik Ridge rises just west of the plot to a maximum elevation of about 850 feet.

Botanically, the plot is a complicated mosaic of plant communities. The plant types used here are those described in Project Chariot Botanical Progress Reports. About 70 per cent of the plot area is occupied by Dryas mat types. Of this, half is Dryas Fellfield, a type dominated by Dryas octopetala interspersed with lichens and other mat plants. Bare ground, consisting largely of a pavement of small stones covered by crustose lichens, occupies about half the area in this type. The patches of mat are of variable size, but generally run some 2 or 3 yards in diameter. Bare ground tends to be the continuous phase.

About 25 per cent of the Dryas mat is of the Dryas Steps type. This type is dominated by Dryas intergrifolia; however, quite a variety of other plants also occur, including Salix arctica, Parrya

nudicaulis, Polygonum bistortum, Carex scirpodea, C. bigelowii, Allium schoenoprasum, Phlox sibirica, Pedicularis oederi, P. capitata, and Antennaria arctica. All are low-growing species and are incorporated into the mat.

The most striking aspect of the Dryas Steps type is that it occurs in narrow strips oriented at right angles to the slope and having a step-like appearance such that the tread of the step is bare ground (mostly a pavement of stones) and the mat itself occupies the riser of the step. The type generally occurs on slopes of between 5 and 10 degrees, but this is variable.

The remaining 25 per cent of the Dryas mat is of the Dryas Stripes type. This type is most like the Dryas Fellfield and is dominated by Dryas octopetala; however, the mats are laid out in long narrow tongues oriented in the same direction as the slope, which usually exceeds 10 degrees. The space between the mats is bare ground, in some places talus, and accounts for about half of the surface area.

The flat top of Sahligvik Ridge above the plot tends to be occupied by Dryas Fellfield. At the shoulder this gives way to Dryas Stripes, which continue downward into the upper edge of the plot itself. As the slope begins to flatten at an elevation of about 150 to 200 feet, the Dryas Stripes give way to Dryas Steps which in turn continue to an elevation of about 60 feet where the slope becomes quite gentle and Dryas Fellfield again becomes dominant. The remaining plant types, described below, are superimposed upon this general backdrop where special conditions of drainage and surface irregularities exist. All the non-Dryas types together occupy about 30 per cent of the surface area of the study area.

The Ericaceous Snow-bed Community is represented by scattered patches throughout the plot; some occupy several thousand square feet, but most occupy less than ten square feet. This community is limited to depressions and the sides of embankments that collect snow during the winter. The snowdrifts melt during the last week in May or the first two weeks in June; if the snow disappears much before or after this time, other vegetation types seem to develop. The type is dominated by a dense mat of ericaceous shrubs including Ledum decumbens,

Vaccinium uliginosum, V. vitis-idaea, Cassiope tetragona, and Arctostaphylos alpina. Bare ground is generally absent.

The Eriophorum-Carex Wet Meadow type occurs in several poorly drained pockets on the plot and forms the boundary of the plot on the north and east. These areas contain standing surface water through much of the frost-free season, and they are dominated by a dense cover of Eriophorum vaginatum and Carex aquatilis. Sphagnum mosses form a heavy mat under these sedges, sometimes to a considerable depth.

The Mixed Meadow Community occupies a rather large "field" in the southwest corner of the plot and occurs in pockets elsewhere. This type appears distinctive to the eye, but it is ecotonal and is actually a hodge-podge of vegetation that defies easy description. It is drier than a Wet Meadow, although small puddles of standing water do occur. Eriophorum vaginatum "tussocks" are scattered about, with Eriophorum angustifolium, Carex sp., and Dryas sp. making up a large part of the mat-like ground cover. The tussocks are often invaded by Dryas, forming peculiar "Dryas tussocks." Ericaceous shrubs are also present, especially on frost ridges.

Other plant communities occur on the squirrel mounds themselves. These communities are discussed in some detail by Melchior (Part B, June 1961 Botanical Progress Report).

The plot is generally well drained, except for the small areas of Wet Meadow; small puddles do persist in most of the types, however. The small creek which drains the plot flows at least a little through all but a few days of the frost-free season, and during the heavier rains it becomes a minor torrent. During these rains, sheet runoff blankets most of the Dryas areas; however, the runoff remains channeled through the Ericaceous Snow-bed Communities.

Before the spring thaw in 1961, about 70 per cent of the plot was free of snow, due to the high and frequent North winds in Ogotoruk Valley. A large volume of snow was present--concentrated into drifts in the depressions of the undulating Dryas areas, on the southern exposure of boulders, rock outcroppings, and solifluction slumps, and in the creek. Drifts 15 to 30 feet deep and 200 feet long extended from the leeward side of Ogotoruk Hill and did not melt until mid-June. Most of the other snow cover of the plot had disappeared by mid-May.

GENERAL SQUIRREL PHENOLOGY

In the spring of 1961 the first squirrels were observed above ground on 20 April. Between 20 and 28 April all specimens taken were males. The first females were observed on 29 April. The number of squirrels seen active on the study area increased steadily until about 4 May, at which time the entire population apparently had emerged from hibernation.

Active territorial defense, consisting of boundary disputes between neighboring males, began on 25 April. Territorial boundaries began to solidify by the first week in May, and most territories were firmly established by the 15th of May. Territorial defense then began to decrease and became virtually non-existent by late June. The territories themselves, however, endured until at least the 1st of August.

Sexually oriented behavior was first observed on 1 May, with the first actual copulation being observed on the 10th. Sexual activities began to taper off about 15 May and were not observed after 20 May. Although squirrels may be seen gathering and transporting nesting material at any time during their active season, a sudden increase in this behavior was observed on the same day as the first copulation was seen, and a sudden drop occurred during the first few days of June.

Assuming a gestation period of 25 days, as determined for captive C. parryi by Mayer (1954), the first young should have been born on 4 June, with births tapering off until 14 June. The first young of the year appeared above ground on 28 June in both 1960 and 1961.

The young squirrels operated in an ever-expanding home range centered around the natal burrow from emergence until the first week in August. By early August the sexual, male dominated, territories had disintegrated and a new rash of territory formation broke out, resulting in the establishment of the fall territories. The latter became solidified by the middle of September.

The population began to disappear into hibernation during the first week of October. No squirrels were observed above ground after 1 November during either 1960 or 1961.

POPULATION DYNAMICS

Methods

A system of live-trapping, marking, and re-trapping was initiated on the study area on 15 June 1960 and continued intermittently until 16 October 1960 and then again from 1 May 1961 until 10 October 1961. During the 1960 program, 53 National Live-trap Company wire mesh live-traps measuring 9 x 9 x 30 inches were rotated over 115 permanent trapping sites. The sites were located at places likely to catch squirrels--near burrows, trails, and prominences--and were marked with colored flags or numbers painted on rocks; they were located on a map by means of triangulation with a Brunton compass. The traps were baited with slices of fresh apple and operated at each site for about ten days before being moved to the next site; thus, each trapping site was trapped about fifteen days per month. Traps were checked three times a day: once near mid-day, once around 1700 hours and once between 2200 and 2400 hours. As the nights began to darken in August, the last check was moved up to 2000. Since the squirrels are not active at night, even when the sun shines all night, this checking schedule limited the maximum holding time to about six hours. Traps were closed with the onset of rain and on calm days when the temperature rose above about 20° C in order to minimize trapping mortality. Even so, 11 squirrels died of exposure to either heat or wet cold in the traps.

During 1961 the same general approach was used, except that 140 traps were used on 125 trapping sites (including the 115 used in 1960) and it was not necessary to rotate traps. The traps were operated for the first ten rain-free days of each month.

Squirrels in 1960 were marked by clipping off one toe from each hind foot and punching holes in either ear in various combinations. In 1961 the ear-punching was abandoned since identification of squirrels so marked the previous year required good light and was time consuming. All squirrels were then re-marked using various toe-clipping combinations of all four feet, a method which proved very satisfactory. After each snowfall squirrels could be identified by their tracks as well as by recapture in the traps.

Individual squirrels varied a great deal in their response to traps; however, most entered the traps quite readily and did not seem to become trap-shy. In fact, some individuals became so "trap-prone" that a few trap sites had to be closed prior to the completion of the normal ten day run in order to avoid upsetting the social order of their districts.

Each captured squirrel was checked for age (young of the year or adult) and sex, and was then marked with a distinct toe-clip combination and released at the site of capture. On subsequent captures its location and pelage condition were noted. In 1961 the squirrels were also weighed with a hand-held spring balance when high winds did not prevail. At first only the sex of the adults could be determined; however, by 1961 the author had gained sufficient experience to also sex the young of the year.

Breeding Season

The squirrels of the study area were observed to have one, sharply delimited breeding season per year. All observed copulations took place between 10 and 20 May during 1961. Of over thirty female specimens autopsied during 1961, only those collected during the last half of May were found to be pregnant, and those collected during the first half of June showed evidence of recent parturition (see Table 1). Young squirrels with juvenile pelage and with body weights below 200 grams entered the trapping records exclusively between 29 June and 15 July (see Table 2).

Breeding Population

The existence of a single, short breeding season precluded young squirrels from breeding during their first season. These young do, however, breed the following spring, when they are just less than one year old. There was no evidence for the existence of a non-breeding age class or "sub-adult" group during the breeding season, as occurs in species which require more than one year to mature. There is a group of males which appear to be non-breeders--the satellite males, animals which lose out in the formation of sexual territories. These males are of all age groups and constitute about half the male population of the study area. No non-breeding females were observed.

TABLE 1. Number of implantation sites, developing embryos, and functional pairs of mammae in pregnant or recently postpartum females collected at Ogotoruk Creek during 1961.

Specimen Number	Number of Implantations	Number of Embryos	Pairs of Mammae
61-6 (12 May)	6	---	---
61-9 (19 May)	7	6	6
61-11 (22 May)	8	8	6
61-12 (24 May)	6	6	6
61-15 (24 May)	8	8	6
61-19 (10 Jun)	9	(8)*	7
61-20 (10 Jun)	7	(7)*	6
61-24 (15 Jun)	11	(9)*	6 + 1
61-25 (15 Jun)	6	(6)*	6
Average	7.6	7.2	---

*Post-parturition

TABLE 2. Actual number of squirrels present on study area as determined by trap records. Listed by month and age class.

Date	Remnant of 1959 Population	Young of 1960	Young of 1961
June 1960	41	---	---
July 1960	36	141	---
August 1960	25	109	---
September 1960	21	99	---
October 1960	21	91	---
May 1961	12	64	---
June 1961	11	38	---
July 1961	10	30	180
August 1961	10	18	103
September 1961	10	15	57
October 1961	9	13	43

Number of Young per Litter

No good data on the number of ova produced per female were obtained from this study. Corpora haemorrhagica and corpora lutea could be observed macroscopically, but they were massed together in bunches, confounding accurate counting. Ripe follicles were present in pregnant females, but no evidence of superfoetation was observed. Implantation sites which survived long enough to develop a maternal blood supply were found to average 7.6 per female in the nine specimens examined. Some specimens contained embryos in various states of resorption. Embryo or parturition scars in eight squirrels examined averaged 7.2 embryos per female (Table 1).

Counts made between 1 and 9 July 1961 of 13 newly emerged litters on the study area showed an average of 5.9 young per litter (Table 3). These counts must be considered minimal as only the highest number seen simultaneously during a one to two hour observation time were used. All counts were, however, made on very young litters and on days of favorable weather when squirrel activity in general was high.

Trapping data for 1960 indicated an average of 6.1 young per female and for 1961 an average of 5.5. These figures represent those young which survived an average of 15 days following first emergence from their natal burrow.

Population Levels

The study area population, as reflected by live-trapping records, is shown in Table 2 and graphically in Figure 1 for the period June 1960 to October 1961. Statistical analysis of the rate of capture of new (unmarked) animals indicates that we may reject with great confidence the existence of unmarked animals in the study area after late July. Young animals which may have moved into the area during the summer were treated as though they had emerged from natal burrows on the area and so tend to raise the July total. Young emerging on the area but dying before their first capture naturally escape detection and tend to lower the July total unrealistically. Field observations tend to indicate the latter is the larger error. The study area was judged to be better habitat for squirrels than the surrounding country and to act as a center of dispersal rather than a zone of immigration. A few squirrels were known to have immigrated to the area, however.

TABLE 3. Number of young squirrels in litters observed soon after emergence from the natal burrow between 1 and 9 July 1961. Further explanation in text.

Mound Number	Number of Young in Litter
81	5
63	5
92	3
93	4
33	6
94	5
95	7
96	5
98	7
70	3
1	7
80	2
29	6
Average	5.9

Figure 1. The squirrel population levels on the study area during 1960 and 1961 by age classes.

Sex Ratios

Sex ratios by month and age class as indicated by trapping records are shown in Table 2. Among adults, the sex ratio upon emergence from hibernation in late April was very nearly 1:1. A higher immigration of males than females (4:1, total 7.1 per cent of population) shortly after emergence tipped the balance slightly in favor of the males (105 males per 100 females). During the formation of the sexual territories, however, the number of males dropped disproportionately, bringing the ratio to only 70 males per 100 females in June and 62 per 100 in July, 1961. Data for 1960 are similar. With the setting up of the small non-sexual fall territories, the loss of females rises as the females come into conflict with the males, bringing the end of the season sex ratio to 80 males to 100 females (average for both 1960 and 1961). It would appear that the females experience a higher overwintering mortality than the males, which is what one could expect with the males getting "first pick" of the hibernation sites (see Fall Territories). It must be noted that the number of animals utilized in calculating sex ratios here is very small, as the young were not segregated by sex during the 1960 season.

The young of 1961 appeared to have a sex ratio very close to 1:1, with a few more males than females early in the season and a few more females than males late in the season.

Age Structure

Trapping and marking operations allowed the squirrel population on the study area to be divided into three age groups: (1) those animals existing on the study area as of June 1960 and representing all age groups surviving from the 1959 population; (2) the young emerging from their natal burrows in July 1960; and (3) the young emerging from their natal burrows in July 1961. The size of these three groups throughout the time of the study are shown in Table 2 and Figure 1. In 1960 the study area produced a ratio of 290 young per 100 adults, and, in 1961, 278 young per 100 adults. By the end of the active season, the ratios stood at 434 to 100 and 308 to 100 in the respective years. This situation shows an interesting phenomenon where the adults have a higher attrition rate than the young. If predation was the major cause of removal from the population, one would expect the young, who should be the least clever at avoiding predators,

to have the highest percentage mortality. Even in 1961, when predator pressure was high, relatively more adults than young fell prey.

Within the adult group, age ratios between second year animals and the animals three or more years old show the same trend as the young to adult ratios above. During 1961 they rose from 534 second year animals per 100 third year animals to 692 second year animals per 100 third year animals through the course of the season. Between May and June, 1961, a short-term reversal of this trend took place when the age ratios went from 534 second year squirrels per 100 third year squirrels in May to 345 second year squirrels per 100 third year squirrels in June. If the small numbers here are reliable, it would seem that the animals facing their first breeding season are less effective than older animals in attempts to establish and defend their territories.

Judging from the data presented above, it seems doubtful that squirrels can be expected to survive their fourth year of life. The fact that squirrels show a higher rate of decline during their second year of life than during their first and a still higher rate during their third would indicate that either older animals are developing a belligerent attitude toward their predators, which proves to be their undoing, or that they are reaching "old age" as early as their second year. Especially during 1961, when nine foxes resided on the study area, many observations were made on the reactions of squirrels to these carnivores. No evidence for differential reaction to foxes between the age groups was observed.

Growth Rates

Mean body weights of squirrels examined from Ogotoruk Creek Valley are shown in Table 4 and in Figure 2. Specimens were either weighed alive in the field with a hand-held spring balance, calibrated to the nearest one-quarter ounce, or dead in the laboratory with a triple-beam balance. Many of the weights represent the same squirrels, retrapped from month to month.

Variation in weight by adults through the active season is interesting. Adult males, who have an over-all tendency to be larger and heavier than the females, emerge from hibernation about 8 days before the females and have gained considerable weight by the first weighing period, 1 to 15 May. They undergo a rapid drop in weight during the

TABLE 4. Semi-monthly mean and extreme body weights of squirrels at Ogotoruk Creek by age class and sex. Weights are in grams.

Period	Males			Females		
	Mean Weights	Range of Weights	Number Examined	Mean Weights	Range of Weights	Number Examined
	<u>Adults</u>			<u>Adults</u>		
1-15 May	911	741-1,197	7	545	382- 778	12
16-31 May	717	627- 882	11	830	401-1,066	25
1-15 June	875	738-1,039	14	829	396-1,008	22
16-30 June	971	805-1,150	9	708	365- 915	19
1-15 July	---	---	--	---	---	--
16-31 July	1,140	850-1,365	20	1,034	450-1,156	32
1-15 Aug	1,305	818-1,205	14	1,094	427-1,236	18
16-31 Aug	1,270	852-1,321	10	1,073	482-1,304	12
1-15 Sept	1,279	853-1,370	18	1,080	559-1,300	15
16-30 Sept	---	---	--	---	---	--
1-15 Oct	1,320	996-1,405	5	1,141	868-1,311	8
	<u>Young</u>			<u>Young</u>		
16-30 June	153	133- 171	5	127	117- 140	4
1-15 July	380	182- 477	8	304	115- 435	15
16-31 July	530	285- 605	35	428	296- 580	41
1-15 Aug	602	572- 910	23	630	560- 869	29
16-31 Aug	645	601- 957	25	668	560- 901	28
1-15 Sept	728	612-1,000	15	735	355- 889	17
16-30 Sept	---	---	--	---	---	--
1-15 Oct	845	551-1,025	12	806	492- 950	12

Figure 2. Semi-monthly mean body weights of squirrels by age class and sex during 1961.

establishment of sexual territories and the breeding season. During this time the females, who are still light in early May, are not involved in territory defense, and are pregnant, gain weight rapidly. Part of the gain is lost in June, however, with parturition and lactation. By the first half of August, both sexes have gained steadily and are near their seasonal high; this is also the time of the break-up of the sexual territories and the formation of fall territories. Since both sexes are involved in fall territory formation, both show a weight drop, though only a slight one--which is in keeping with the low intensity with which the fall territorial defense proceeds. After this brief set-back, weights rise to their seasonal high of 1,320 grams for males and 1,141 grams for females in October. One of the reasons for the low weight means for females seems to be the existence of a few runts on the study area. Possibly runt males are eliminated in the competition for sexual territories.

No data were obtained for birth weights of young squirrels. Mayer and Roche (1954) report 9.7 to 13.2 grams average for young of litters born in captivity. At about 30 days of age, when they emerged from the natal burrows on the study area and became free living, they weighed an average of 140 grams, the males outweighing the females in a small sample. Growth is rapid from this point and there is no significant difference in weight between the sexes. A small retardation in growth rate occurs when the fall territories are set up and the young, no longer given preferential treatment by the adults, begin shifting for themselves. By the end of the season, the young have grown into the weight range of the adults, but they still average lighter.

Mortality

For the purposes of this study, any phenomenon which removed individuals from the study area has been considered mortality, even though the squirrel involved might not have been lost from the species population. As suggested before (see Age Structure), old age may be a primary cause of death in many instances; however, the coup de grace would probably be delivered by some secondary mechanism before the animal actually died. The old age death rate is therefore highly disguised.

Disease

No observations of obviously "sick" animals were made. One young squirrel was picked up dead on the study area in August 1960. It had no wounds, broken bones, or evidence of saliva on its fur, and a gross autopsy gave no evidence as to the cause of death. The squirrel was fat and had a full stomach.

Starvation

Observations showed that an abundant food supply existed during all active seasons on the study area. Although squirrels lose weight during some parts of the season, this loss seems to be related to their preoccupation with activities other than food gathering and not to a shortage of food (see Growth Rates). No really emaciated squirrels were observed, even during periods of low average weights.

Parasites

Mayer (1953b) found that squirrels in the general vicinity of Point Barrow were largely free of ectoparasites. The squirrels in the Ogotoruk Creek region were found to be highly parasitized; all specimens examined possessed the louse, Neohaematopinus laeviusculus Grube, and most harbored the flea, Oropsylla alaskaensis (Baker 1904). (Determinations of external parasites were made by Dr. Cluff E. Hopla, University of Oklahoma.) Squirrels examined immediately upon emergence from hibernation were infested with both ectoparasites, as were the young upon their emergence from their natal burrows. In no case was a heavily infested squirrel seen to be grossly emaciated, and it appears that parasitization, although widespread, is not an important direct cause of mortality.

Gross autopsy failed to reveal any widespread endoparasitism. One large Ascaris laevis Leidy 1856 was found in the coelom of one specimen by workers from the Hanford Laboratories, and a single careful examination of the lower intestine of a squirrel produced a few small, unidentified nematodes.

Predation

The ground squirrel appears to be an important prey species on the tundra. Predators observed on the study area or in surrounding territory include large carnivores (Grizzly Bear, Wolf, Arctic

Fox, Red Fox, and Wolverine and predaceous birds (Golden Eagle, Gyrfalcon, Long-tailed Jaeger, Glaucous Gull, Snowy Owl, and Common Raven). The Ermine is present in and around squirrel burrows and may or may not prey on the squirrels. The occurrence of ground squirrel remains in predator scats and pellets is shown in Table 5.

Grizzly Bear (Ursus horribilis): Most of the large squirrel burrow systems on the study area show evidence of excavation by predators at some time. While some of these are certainly the work of bears, judging from the large boulders which have been disrupted, I was unable to distinguish between Grizzly Bear and Wolverine excavations at old sites. Bears were common in the Ogotoruk Valley both in 1960 and 1961.

During 1960 no bears were seen on the study area itself; however, on 19 July one specimen was observed about 1/4 mile north of the area, digging for ground squirrels and working its way southward. The intrusion of members of the field party caused the bear to reverse its course.

During 1961 evidence of fresh bear destruction and sign was observed on the study area on five days in late August and on three days in early September. On these eight occasions, ten squirrel mounds were over 50 per cent excavated and six others were molested to a lesser degree. The actual number of squirrels killed is unknown; however, two of the disturbed systems were not reoccupied by the end of the active season and seven were reoccupied by squirrels other than the ones known to be living there before the bear or bears appeared. If we assume that the squirrels did not move off the plot when their burrow systems were destroyed (see Burrowing Behavior), it would appear that the bear enjoyed a 56 per cent hunting success and eliminated 4.1 per cent of the squirrel population. (At the time of year when observed bear predation occurred there was only one squirrel per burrow.) During the same period many burrow systems near, but not on, the study area were also disturbed by bears.

It is of interest to note that observed bear predation during both years occurred between late July and early September--a time when the annual frost line lies below the deepest levels of the burrows. During the remainder of the year, the burrows extend into frozen

TABLE 5. Occurrence of ground squirrel remains in scats and pellets collected in the vicinity of Ogotoruk Creek during 1960.

Species	Number Examined	Number Containing Squirrel Remains
Grizzly Bear	7	3
Wolf	3	1
Red Fox	101	83
Ermine	1	0
Wolverine	1	0
Golden Eagle	2	0
Jaeger (sp.?)	14	0
Glaucous Gull	3	0
Snowy Owl	10	2

ground and are probably impregnable to bears, who hunt squirrels solely by excavation.

Wolf (Canis lupus): No wolves were seen directly on the study area at any time. They occur in the region of Ogotoruk Creek, but are never common and their predations on the squirrels were impossible to determine. Bee and Hall (1956) reported predation on squirrels by wolves and the presence of squirrel remains in wolf scats.

Arctic Fox (Alopex lagopus): The Arctic Fox, although not seen in the valley during the 1960 season, was prevalent in 1961. From over a hundred sightings of this species it was estimated that the population of the valley was about five or six animals. No individuals were seen actually on the study area and their effectiveness as squirrel predators could not be estimated.

Red Fox (Vulpes fulva): The observed Red Fox population of the study area is shown by months in Table 6. The resident foxes appropriated and reworked squirrel burrows for their dens; the displaced squirrels often moved to other parts of the same system. The foxes hunted over a range much larger than the study area. One female, who was observed through the entire 1961 field season and had a litter of four young on the study area, typically went on two hunting trips per day. She would rarely enter her den herself, but would drive the young into it before leaving the area. Although she was occasionally seen to depart along the ocean beach, usually she would leave the plot headed inland to the north. She usually returned in about two hours, carrying one to four squirrels in her mouth. On 18 days, when both morning and afternoon trips were observed, she returned with an average of 4.2 squirrels per day. These squirrels were rarely eaten when fresh, but were taken from the returning female by the young and buried within a 15 yard radius of the den by the young. At odd times during the day the young would unearth such buried squirrels, chew on them for awhile, and then rebury the remainder. Carcasses recovered from the feeding young were in all states of reduction from quite fresh to hard, dried mummies. Fortunately for the investigator, foxes do not eat the feet, tail, or skin of the squirrels; they usually leave the hind feet and tail, attached together by a strip of hide, lying

TABLE 6. Observed population of Red Fox, Vulpes fulva, on the study area.

Period	Resident		Transient
	Adults	Young	Adults
<u>1960</u>			
June	1	2	1
July	1	2	0
August	1	0	1
September	--	--	--
October	1	0	0
<u>1961</u>			
April	0	0	2
May	1	?	2
June	1	4	1
July	1	4	0
August	2	7	1
September	2	7	1
October	2	7	0

near their den. A continual check of these refuse piles was made during 1961 and indicated that 27 marked squirrels were eaten by the two litters of young foxes. The adult foxes were not observed to eat near the den.

As the young grew larger in August 1961, they began to hunt on their own in the vicinity of their dens (and hence on the study area), expanding their hunting range slowly during the rest of the season. The female would lie on the hillside above the den or on the slope of Ogotoruk Hill across a creek from the den and make no effort to join the young in their hunting activities. The success of these hunts by the young appeared to be very poor. Typically the young foxes would make the rounds of the local burrow systems, sniffing at most of the openings. If squirrels were seen on the open ground, they were rushed by the young foxes in a straightforward manner, but no captures were observed. A more rewarding strategy for the foxes was to lie in the taller vegetation of a burrow system and await the appearance of a squirrel. When a squirrel appeared, the fox would leap quickly into the air and would occasionally land on top of the squirrel. In nearly a hundred such attempts observed, only five squirrels were caught. The constant chorus of alarm calls (see Vocalizations) which issued from the surrounding burrow systems during the attempted ambush probably added nothing to the success of the hunt. Despite the apparent low level of success, it is probable that most of the 27 marked squirrels recovered from the den areas were caught by the young foxes. This catch represents 12.3 per cent of the study area population.

Ermine (Mustela erminea): Ermine are present in the vicinity of Ogotoruk Creek and appeared to be more numerous during 1961 than during 1960. In 1961 several sightings were made of this species in the campsite. One individual lived most of the summer in a squirrel burrow concurrently inhabited by one male squirrel. Both were quite bold in the face of human disturbance and entered buildings readily. The two species were seen to either ignore or avoid one another. Bee and Hall (1956) implicate the Ermine as an important, though elusive, predator of ground squirrels. The influence of Ermine on the study area is unknown.

Wolverine (Gulo luscus): Wolverines were seen occasionally in the Ogotoruk Valley, but no observations of this species were made on the study area. Wolverines excavate squirrel burrows in much the same tradition as grizzlies. Bee and Hall (1956) mention the Wolverine as a predator of ground squirrels, but it is doubtful that they contributed to the demise of squirrels on the study area during the present study.

Golden Eagle (Aquila chrysaëtas): One Golden Eagle was seen soaring over the study area on 10 May 1961, but it was not seen to attack the squirrels. Squirrels were active at the time and gave no indication of seeing the eagle. Bee and Hall (1956) list both this species and the Gyrfalcon as predators of the ground squirrel.

Gyrfalcon (Falco rusticolus): Gyrfalcons were seen occasionally in the vicinity of the study area; a pair had a nest on the cliffs nearby. They were never seen to attack the squirrels.

Long-tailed Jaeger (Stercorarius longicaudus): The Long-tailed Jaeger was commonly seen on the study area, and in 1960 one nested about 1/2 mile from the study area. No outright captures of squirrels were observed; however, on 22 June 1960 a jaeger was seen eating a marked squirrel known to have been alive on the preceding day. The Parasitic Jaeger (S. parasiticus) and occasionally the Pomarine Jaeger (S. pomarinus) occurred in Ogotoruk Valley and possibly took some squirrels as food; neither, however, was ever seen over the study area.

Glaucous Gull (Larus hyperboreus): This gull was the most common flesh-eating bird on the study area, there being a nesting colony on Crowbill Point less than 1/4 mile away. No evidence of predation by this species was observed. They were often seen eating squirrel carcasses on the study area, but out of ten such occurrences, at least six were known to involve squirrels already killed by some other agent.

Snowy Owl (Nyctea scandiaca): Snowy Owls were seen occasionally in the Ogotoruk Valley during the season of squirrel activity; however, none was seen directly on the study area. Snowy Owl pellets collected by Robert S. Spooner during 1960 contained squirrel remains.

Common Raven (Corvus corax): A family group of five ravens frequented the ocean beach ridge of the study area and occasionally rested on the crest of Ogotoruk Hill. When ravens were present, the squirrels became quite disturbed, uttering alarm calls and staying near places of refuge. No raven was seen either catching or eating a squirrel, though on two occasions they were seen to chase squirrels. The ravens ran along the ground in a peculiar striding gait, using their wings to balance themselves, but the squirrels easily outmaneuvered them by making quick turns which the ravens overshot. One of these encounters occurred on a rather steep slope, and the raven made up lost distance by periodic glides, but it landed short of the fleeing mammal and continued the chase on the ground. This episode ended when the squirrel made a safe entrance into a burrow. The other chase was terminated by the close proximity of the observers.

Artificial Mortality

During 1960, trapping mortality amounted to 11 squirrels, and predations by domestic dogs and human hunters accounted for an unknown number of squirrels lost to the population of the study area. In 1961 all these sources of mortality were eliminated.

Migrations

During 1960 immigrations of squirrels could not be determined since the population was not fully marked. In May 1961 five adult squirrels (four males and one female) moved onto the area from some unknown point of origin.

During the establishment of territories in the spring of 1961 (see Sexual Territories) widespread emigrations were observed. The migrants were largely adult male animals, and they spread out in all directions from the study area. The beach ridge, which extended from the study area 1/2 mile to near the mouth of Ogotoruk Creek, was populated by squirrels at this time, as were several areas along the course of Ogotoruk Creek itself where no squirrels had been observed to emerge from hibernation. The percentage of these emigrants that came from the study area is not known. Tracks of squirrels were seen as far as 2 1/2 miles out on the sea ice in May 1961. Twenty-seven squirrels were lost from the study area population during the time these emigrations were taking place. This loss must amount to something less than 12.2 per

cent of the maximum seasonal population, but it consisted of 35 per cent of the population that existed at the time of the movement.

Another series of changes in home range takes place in August as the fall territories are set up, but such movements are considerably shorter and do not seem to result in any significant loss to the study area as a whole, although the placement of squirrels within the area changes considerably (see Fall Territories).

BURROWING BEHAVIOR

Habitat Selection

In general, squirrels avoid any situation which impedes either vision or movements. As a result, they are rather effectively excluded from tall sedge and tussock vegetation types, which together constitute 63.5 per cent of the Ogotoruk Valley. Vision is impaired by vegetation exceeding about 20 centimeters in height, movements by vegetation exceeding 5 to 10 centimeters in height. In meadows where the obstruction heights fall between 5 and 10 centimeters, the squirrels maintain trails which allow rapid passage in comparative safety. Such trails evolve over a period of time. In the spring the sedges are low and dry, and as squirrels pass along the same route again and again, the blades of sedge are broken up and then are blown away by the wind. As the growing season progresses and the surrounding sedges gain in height, wandering from the usual route becomes less attractive to the squirrels and the trail receives a heavier traffic load, resulting in a beating back of all vegetative regrowth. In areas where the surrounding growth finally exceeded 20 to 25 centimeters later in the season, existing trails were abandoned, and they quickly grew in. An exception to this was observed in the trail between Burrow Systems 1 and 10 on the study area, where the trail was maintained despite tall sedges. This trail crossed a concave drainage bed, however, improving visibility considerably. Another exception was the trail between Burrow System 97 and Burrow Systems 126 and 104. This trail crossed a strip of sedge meadow only 5 yards wide. Squirrels avoided tarrying along this trail and seemed ill at ease while in the tall sedge area--an attitude that seemed to disappear as soon as clear ground was attained.

Movements into tussock areas were even more restricted than those into non-tussock sedge areas. Here, squirrels were occasionally seen resting on peripheral tussocks but they seldom penetrated deeper into these areas. In places where tracked vehicles had broken paths through tussock fields, the squirrels sometimes moved out along the track mark. In such excursions, squirrels moved progressively shorter distances between observation poses as they penetrated deeper into the tussocks; thus, forward progress became slower as the animal moved farther into

into the tussock field. At somewhere between 20 and 50 yards, apparently depending on the individual, all forward progress would give way to observation behavior; and, finally, the squirrel would bolt back down the track in the direction from which it had come. On several occasions squirrels were surprised by the observer on the track between Burrow Systems 81 and 115. Such squirrels would first run on down the track away from the observer; eventually, however, they would turn and attempt to cut back past the observer, even though the track was only about 15 inches wide. In no event could the squirrel be forced to turn off the track into the tussock area.

Squirrels readily enter small clumps of tall willows, but they remain near the edge of the clump where vision is not impaired through more than 180 degrees. Where willow clumps surround burrow systems, dirt piles are thrown up in the center of the clumps and are heavily used as observation posts.

Standing water and soupy mud are both avoided by squirrels. Here it is probably the impediment to rapid movements that the squirrels are avoiding, since they will readily forage in wet ericaceous shrub areas and even, to some extent, during rainstorms. If cornered, squirrels will enter water and swim with considerable agility, but they do not choose such avenues of travel unless under duress. When the creek on the study area was high, squirrels would go quite out of their way to apparently known narrow places in order to cross. During 1960 adult male number 4 held territory number 3 which straddled the creek. Normally he gained access to all parts of this territory by crossing the creek at several narrow places on the territory itself. During times of high water it became necessary for Male 4 to travel upstream to a more narrow crossing or to swim one of the pools that developed on his own territory. Even though he was able to swim these pools (the observer once cornered him just below Burrow System 50 and forced such action) he invariably chose to travel 250 feet upstream to the dry crossing. This choice was obtuse for two reasons: 1) it required a 500 foot side trip at a time when Male 4 was highly motivated to attack Male 431, who continually threatened his territory from the northeast, and 2) it required Male 4 to transgress onto Territory 4 (on which the better

crossing was situated) which was held by Male 24 who very often inflicted wounds on Male 4 during the transgression.

Squirrel 13, an adult male holding Territory 2 in late 1960, was also faced with the problem of a territory straddling the creek. At high water he would avoid swimming by traversing the ocean beach gravel ridge, a circuitous route which took him 150 feet out of his way and onto an area devoid of refuge from predators. During low water this animal avoided the beach gravel areas.

A long tongue of soft mud, about ten yards wide, existed in the northern end of the study area. Although firm mud in other sections of the study area was readily traversed by the squirrels, they avoided this soft area (see Figure 10. The mud shows as a light color running between Territories 6 and 12), and it formed an effective boundary during territory formation. Squirrels being pursued would cross the mud without hesitation, whereas pursuing squirrels would not. Foraging squirrels likewise did not cross the mud; those who were found on the wrong side had, in all cases where data are available, crossed by skirting the upper end of the formation. If not attacked while on the wrong side, they would eventually return home by the same route.

Sedge marshes, which combine standing water and soupy mud with an almost impenetrable tangle of sedges and near zero visibility are judiciously avoided by squirrels. The single observation of a squirrel entering this vegetation type was an individual who was pursued by a territorial male--until the chase was broken up by the appearance of a fox. The sudden appearance of the fox caused the luckless squirrel to veer abruptly into the marsh, where he was quickly caught by the fox.

Finally, squirrels usually avoid areas in which there are no burrows, either their own or those of another squirrel. If forced into burrowless areas by competition with other squirrels, they immediately move on or start digging.

Burrow Site Selection

There are, on the study area, at least 73 large and complex burrow systems which show evidence of perennial occupancy by squirrels (see Figure 3). Such systems may be taken over by foxes for a time, but the squirrels either move to other parts of the same system or re-invade

Figure 3. Map of ground squirrel study area, Ogotoruk Creek, northwestern Alaska, showing location of major permanent burrow systems. Fox dens are indicated by "X."

the site when the foxes move on. Many are excavated by grizzlies or Wolverine, but these are quickly rebuilt by the squirrels.

Of these 73 burrow systems, all are situated in well-drained situations on hillsides, creek or ocean beach banks, or raised mounds of porous material in flats. With the possible exception of the latter, all these locations have a comparatively deep permafrost level. During the heavy rains prevalent in August and September of 1960 and 1961, none of these systems were flooded even though much of the surface of the study area experienced sheet runoff or standing water.

Loose rocky soil prevailed at all sites; however, areas of highly compacted silt were also characterized by flooding during rains, causing squirrels to be excluded. Rock outcrops were well drained in most cases but were obviously impenetrable to the squirrels and were avoided. Most burrow sites on the study area showed a southeast exposure; however, the prevailing slope is also exposed in that direction. Burrow systems located on the other side of Ogotoruk Valley showed the opposite exposure.

During April 1961, before melting conditions began, a survey of snowdrifts revealed that all except eight burrow systems were located under drifts of snow, and all except four had some surface openings not covered by the drift. Thus 61 of the burrow systems were situated at the intersections of an interesting and irregular grid formed by the generally east-west drainage pattern and the north-south drift system. Since the deep-cut drainages, such as the creek on the study area, collect drifts regardless of their direction of flow, their banks form a continual intersection of the drift-drainage grid and support a great many burrow systems. The same conditions exist along the ocean beach bank. In these situations social pressures alone probably determine the spacing between squirrels, a spacing not stabilized by limited potential burrow sites, as is the case elsewhere. A survey of ocean beach banks revealed that almost every yard of bank showed some evidence of previous squirrel burrowing activities, though most of the sites were in some state of disrepair. None of the occupied sites showed the complexity of tunnels of the non-bank sites, except where a discontinuity in the bank allowed a drainage to cross the bank and destroyed the continuity of the habitat type.

The beach bank which extended east of the study area to the mouth of Ogotoruk Creek, as other banks, showed this changing burrow location. Here, however, the bank was only 1 to 3 feet in height, capped by tussock and wet meadow, and did not appear to support a stable squirrel population. Rather, it was apparently recolonized each spring during the formation of sexual territories elsewhere, and the new inhabitants failed to survive hibernation on the bank. Such a continual population flux could have been the reason for the apparent flux in burrow locations at this particular place.

Burrow Construction

Squirrels were found to be associated with five types of excavated structures: (1) rooting pits, (2) boundary pits, (3) duck holes, (4) burrow systems, and (5) adventitious burrows. The rooting pit is a shallow depression, wider than deep, resulting from root feeding behavior; it is always abandoned by the squirrel upon completion of feeding at the particular site (see Food Gathering). These pits do not appear to be important in the burrowing behavior of the animals. The boundary pits, duck holes, and burrow systems seem to be related to one another. Adventitious burrow systems exist in special situations.

Boundary Pits

During the formation of sexual territories in May 1961, the squirrels were observed to dig shallow pits in the vicinity of the termination of each encounter with a rival. Only the victorious males engaged in this behavior (see Sexual Territories). The resulting pits were from 5 to 8 centimeters in diameter at the rim and from 10 to 25 centimeters in depth, and thus were too shallow to serve as places of refuge. The deeper of these pits were the result of several periods of digging, one following each boundary dispute ending in the area of the pit. By the end of the formation of sexual territories, boundary pits occurred almost everywhere, but the highest concentrations were found along the boundaries of territories (or, the boundaries of territories were found along the highest concentrations of pits) and especially where heavily traveled routes crossed such boundaries. The vast majority of the pits were obliterated by rain, wind, or traffic during the ensuing season.

Duck Holes

Duck holes are small, relatively simple burrow systems which are not permanently occupied by squirrels; squirrels go into them occasionally, often during times of duress. Squirrels entering duck holes were never observed to remain there longer than 4 minutes, unless held at bay by a predator or observer (see Alarm Calls).

Typically, duck holes have one to four openings, interconnected by a simple tunnel system; they lack enlarged caverns or nests. A few duck holes were observed to have as many as 10 surface openings, but such extensive workings were rare. Excavated dirt was dumped at one, or at most two, of the openings; the other openings were excavated from below and were often difficult to locate. In 18 duck holes unearthed by the observer, the longest distance between surface openings was 2 meters; 1 meter or less was common. All these duck holes appeared to contain a basic element in common. From an entrance with a surface earth pile, they had a tunnel which angled downward at about 70 degrees to a depth of about 25 centimeters where it would fork. The left branch, turning from the first section of the tunnel at about 130 degrees in the horizontal plane, continued downward at about 40 degrees to a blind end at a depth of about 30 centimeters. The right branch turned at about 160 degrees and veered upward at about 10 to 25 degrees until it reached a depth of about 10 centimeters; it then turned upward at 90 degrees to an incaved surface opening.

In the eighteen cases observed, all were in uniform soil devoid of impenetrable obstacles and not on steeply sloped terrain. One mirror image of the above plan was observed, and six duck holes had extra tunnels branching off the basic system and leading to the surface. Four systems had only the first mentioned surface opening; the right-hand tunnel ended blindly, but angled upward as far as it went as per the basic plan.

Duck holes may be considered to be detached elements of the large perennial burrow systems. They surround these more permanent burrow systems in a series of rather haphazard concentric circles, but affiliation with a particular system is often difficult to assign. Duck holes are generally maintained by the squirrels of the nearest burrow system, though where the holes are located between two burrow systems,

both groups maintain them with considerable overlap. When squirrels emerge from their burrows after a new fall of snow, they immediately begin clearing the burrow entrances, starting with those of the main burrow system, then turning to the duck holes. The location of the duck holes is known or detected by the squirrels with great surety in spite of the even cover of snow. In several hundred repetitions of this behavior, no false starts were observed. Such clearing operations were used in an attempt by the investigator to assign ownership to duck holes, but it became apparent that a given hole was cleared by different squirrels at different times. Any passing squirrel will use any handy hole in time of need. Duck holes are not defended against transgressions as such, but if they are located within a particular territory, they are not available to stray males without a fight.

Burrow Systems

The large, complex, perennially occupied, burrow systems are the home bases and centers of squirrel activities. These structures, with their earth piles and special plant communities are a major edaphic feature in areas occupied by squirrels and thus render the locating of colonies a simple matter, even by aerial reconnaissance. Their permanence is such that they are useless as indirect indices to present squirrel population levels.

The plans of three systems excavated by the author were varied in detail, but quite similar in general. Figure 4 shows one of these. Mayer (1953b) shows a diagram of a burrow system near the Meade River, Alaska, which strongly resembles the adventitious systems found in Ogotoruk Valley. Quay (1951) gives a diagram of a burrow near Nome, Alaska, which compares closely with those excavated by the author. The existence of two separate complexes in close association seems to be the rule. In the burrow of Figure 4 the two complexes were in such close association that their separation was not apparent from the surface. On the study area 33 of the 73 burrow systems showed separation of the two complexes by distances of 8 to 15 feet such that they formed two distinct surface mounds. In their social organization, however, the squirrels treated the two mounds as a single burrow.

Figure 4. Plan view of Arctic Ground Squirrel burrow system. Scale: 1 inch = 1 meter. Small numbers indicate depth to floor of tunnel in centimeters. Grade arrows point down slope.

○ = Surface openings	● = Surface openings, plugged
⋯ = Fresh earth mounds	XXX = Plugged tunnels
N = Extant nest	(N) = Decayed nest

system. Observations of squirrels entering and leaving various holes of several of the mound systems which appeared single on the surface indicated that these also consisted of at least two non-connecting complexes.

Burrow systems on the study area averaged between 40 and 50 surface openings, though a maximum of just over 100 surface openings was observed. In average systems, 10 to 15 of these openings were accompanied by surface piles of reasonable freshness, the remaining openings appearing to be incaved holes through which dirt was never exhausted. The exact location of tunnels and surface openings seems to vary over the years at any given site--judging from the testimony of innumerable "fossil" openings, overgrown dirt piles, and caved in tunnels. The ever changing location of dirt piles causes the entire surface of the burrow system area to be raised above the prevailing contour of the terrain. It appears probable that the general perimeter of each successive pattern remains constant, however.

Openings with dirt piles tend to be funnel-shaped, flaring from a tunnel diameter of something less than 12 centimeters to a maximum of 25 centimeters. Incaved openings are nearly the same size as the tunnels that lead up to them, occasionally slightly smaller. Tunnels are more inverted "U"-shaped than the surface openings and average 20 to 25 centimeters across with some variability along the length of any particular burrow. Points of junction between the tunnels are expanded slightly, and nests are located in greatly expanded cavities. All observed nests in good repair were located at the end of blind tunnels. Remnants of nests were found in cavities communicating with two or more tunnels on opposite walls, but in these cases it appeared that the tunnel system had been altered after cessation of use of the nest.

The existence of the basic element of construction of duck holes seemed to be prevalent in burrow systems, but the great complexity of the structure obscures this element to a great degree.

Adventitious Burrows

Burrow systems existing on the study area were all of the type described above. A different and rather distinct type, however, was observed along the seasonally colonized beach bank between the study area and the mouth of Ogotoruk Creek, on the flood benches of the

Ogotoruk Creek itself, and along the Kissimilouk Creek about 5 miles southeast of the study area. All the areas are characterized by a seasonal establishment and subsequent destruction of the population. The burrow systems observed in these areas resemble the more complex of the duck holes in structure, and they are all relatively more simple than normal perennial burrow systems. They differ from true duck holes in that they contain nests and act as a base of operations for their residents. The two-complex pattern was not observed. The adventitious burrow was the only type of resident burrow system whose construction the author observed from inception to relative completion (actually, work continues to some extent throughout the life of any of the excavated structures). In all cases these burrows were produced by squirrels which moved into an area previously empty of squirrels and remote from established perennial burrow systems. Once a site was selected, work progressed steadily through the day from before 0800 hours to about 2000 hours with 5 to 10 minute pauses approximately every 1 to 1 1/2 hours for foraging and other behavior. By the end of the second day, a rather extensive system had been produced with surface openings (4 to 11) extending over a 2 meter radius. On the third day digging slackened off and nest material gathering began, continuing through the fourth day. After the fourth day, construction activities dropped into the normal pattern for established systems. Later in the summer a few duck holes were established in the vicinity of the main burrow.

The attrition rate among the adventitious burrow systems and their occupants was high as compared to that of the burrows on the study area. The vast majority of the systems observed along Ogotoruk and Kissimilouk creeks were destroyed by floods during the same year they were established. Less than half of those along the beach bank were so destroyed. No squirrels were observed to emerge from hibernation in the spring of 1961 from any of the three locations. Any burrows remaining by spring were filled with water and mud during the spring melt as their entrances were not cleared of snow.

Digging Behavior

Squirrels are expert diggers and proceed rapidly while working. Over-all accomplishment, however, is not great for, except in special circumstances as mentioned for adventitious burrow construction or in repairing bear-destroyed systems, the squirrels are not persistent in digging and usually become distracted or begin some other activity after less than 15 minutes of sustained work. When digging, the squirrel takes up a position very close to the site, with its back sharply flexed and fore and hind feet grouped closely together. The body weight is shifted to the hind feet and the front feet are raised off the ground. Usually there is a 2 or 3 second pause in this position as the squirrel investigates the ground ahead with its eyes and nose. Suddenly two to ten alternating strokes are made with the forefeet, and a small pile of dirt is loosened from the excavation site. At the same time as the dirt is loosened, the neck is extended distally and flexed sharply proximally, resulting in a caudad movement of the head; the forelimbs are fully extended. If roots or rocks are encountered, they are removed with the teeth. After one to five repetitions of this activity, the two forefeet are lowered simultaneously, cupped together, and used to push the accumulated dirt backward to the vicinity of the hind feet. This distance is short due to the high degree of back flexion. Much of the dirt pile is dumped on the hind feet. With the resumption of digging with the forefeet, the hind feet are moved slightly to maintain balance and come to stand on top of the pile. This sequence of events is repeated one to ten times, seemingly dependent upon the volume of dirt removed each time and upon the slope of the tunnel. In tunnels sloping sharply outwards, the loose dirt rolls down the tunnel and the squirrel will allow more to accumulate than otherwise. When about a single handful of dirt has accumulated under the squirrel's hind feet, the squirrel moves backward along the tunnel until its head is over the main mass of dirt. The hind feet continue to move backward until the back is fully extended. The forefeet are then cupped together and part of the pile is propelled by them backward with a sudden flexion of the back, the hind feet remaining fixed in position. The back is then extended again and more dirt is propelled outward down the tunnel. When most of the loose dirt has been

moved backward one squirrel's length, the whole operation is repeated. During the flexion stroke, the dirt is propelled so rapidly that much of it flies down the tunnel past the squirrel's hind legs, so that after the first movement down the tunnel, the dirt is spread out. If the mouth of the tunnel is inclined evenly with the surface, the above procedure is followed until the loose dirt is pushed onto the refuse pile. In many cases, however, the terminal 20 to 25 centimeters of the tunnel angles sharply upward at about 70 degrees. In this case the backward movement of dirt is impeded by the upward turn in the tunnel. Here the dirt is pushed as far as the upward turn and then is allowed to accumulate into a compact pile. The squirrel then moves forward, away from the compact pile of dirt, but soon returns with its head pointing in the direction of the dirt pile and the tunnel mouth.

(Most tunnels are too small to allow a squirrel to turn around; apparently they run down to the nearest junction or nest to turn around.) The squirrel now flexes its back, shifts its weight onto its hind feet and rotates its forefeet 180 degrees so that the palms point dorsally. The forefeet, cupped together, are then extended and inserted into the dirt pile. A quick flexion of the forelimbs and extension of the back propels dirt up and out through the tunnel mouth. Observations made of this operation, where the nearly vertical part of the tunnel was 20 centimeters in length, showed that dirt was propelled an estimated 40 centimeters above the mouth of the tunnel, the center of the resulting pile being 15 centimeters from the mouth. On windy days (which is most of the time in this location) very little dirt was observed to fall back into the tunnel; however, on calm days at least half re-enters the tunnel. Usually five or six handfuls are pitched out of the tunnel in rapid succession, followed by a 10 second pause, then five or six more handfuls. After the entire pile has been evacuated, the squirrel emerges from the tunnel and looks around the area. Then it either re-enters the tunnel and returns to the digging site, or it scrapes the dirt from where it landed to the refuse pile by the backward method. In all instances the dirt was eventually pushed onto the refuse pile, though this is sometimes done after several batches have accumulated.

The foregoing observations were made during the excavations of short tunnels or during operations at the mouth of long ones. It is

not known whether or not the underground procedures for moving dirt down long tunnels follow the pattern described above.

Squirrels will move dirt long distances along tunnels in order to dump it on an existing dirt pile, passing by many incaved openings (without dirt piles) along the way. This characteristic is indicated by the structure of the systems in relation to dirt piles and by one direct observation. A squirrel under observation was seen to break through the surface from below. It emerged from the newly created incaved surface opening, looked around for a few minutes, and re-entered the system by another (incaved) opening. Four minutes later, dirt was seen to fly from an opening with a dirt pile 4 meters (over the surface) away. The squirrel appeared at the latter opening for a minute, re-entered the burrow system by the same hole, and re-appeared at the newly created opening 30 seconds later. It re-entered the new hole and again 4 minutes later, another volley of dirt issued from the hole 4 meters away.

Most digging seems to be accomplished by the adult females. All sex and age classes were seen digging at times, but the adult females were the ones seen to conduct the massive "spring housecleaning" of the major burrow systems during May, removing large quantities of mud from existing tunnels and constructing new ones. As the female usually continues to occupy a given burrow system for the entire season, she is obliged to fight a perpetual battle against the collapse of the system. Adult males, although they are the first to emerge in the spring, apparently do not do any refurbishing of the systems, though upon first emergence and upon the advent of new snow they immediately clear snow from all the neighboring holes. When the females emerge about eight days later, they pretty well preempt the task. The males continue to live in the burrows from which they emerged (unless they are displaced during territory formation) until females on the territories have cleared most of the systems. Then the males are prone to change their home burrows frequently, but always using the systems already cleared by the females. The females do not seem to resist this "free-loading" by the males, although the female's presence at a particular site is sufficient to keep other females out (see Sexual Territories).

When entering new areas, males readily construct burrow systems, as described under Adventitious Burrows above. Satellite males use

existing burrow systems, which they maintain themselves. No such maintenance was observed, however, until late May in 1961.

Young squirrels were observed to engage in digging behavior shortly after their emergence from their natal burrows. They showed even less perseverance than did the adults at this activity, and much of the observed digging was pointless to the maintenance of the burrow system, occurring in the sides of refuse piles, etc. This activity is probably important as a practice exercise.

With the onset of fall territories, the division of labor largely disappears, as all sex and age classes set about refurbishing burrows for hibernation.

Genesis of Burrow Systems

Of the excavated structures made by squirrels on the study area, no burrow systems were destroyed by climatic factors during the course of the study and almost all were located in a special orientation to snowdrifts. The ground is frozen and unworkable to squirrels at all times when snow prevails, and rain does not fall in large enough quantities to cause flooding while the snowdrifts are still present. It seems unlikely that squirrels were able to inspect the terrain for likely burrow sites during two seasons and then build accordingly.

It was also observed that duck holes which sometimes flooded with water and mud, were not immediately rebuilt, and were not located in any observable orientation to snowdrifts. Boundary pits were almost all destroyed by the first flood of the season. Out of over a thousand boundary pits present during the formation of sexual territories, only about a dozen survived the season. Of the survivors, four had been converted into duck holes by resident females before the onset of ground frost in the fall.

On the basis of these observations, the following genesis of the burrow systems is suggested. The males dig boundary pits about their territorial areas in a semi-random fashion, primarily to aid in stabilizing their boundaries. A minimum amount of energy is expended in this task, and an immediate use is realized regardless of the life-span of the pit. If pits survive the annual floods, the females invest another increment of energy and convert them into duck holes, again

realizing an immediate benefit in terms of protection. The survival of duck holes formed from surviving boundary pits should be much higher than holes located at random. If the duck hole continues to survive, it is regularly cleaned of loose dirt by squirrels; and new tunnels are added over a period of years, resulting in an ever increasing volume of dirt upon the surface of the ground. As the duck hole survives year after year, its chances of continued survival become greater and the energy invested in the site by squirrels would be continually in proportion to the hole's chances of continued survival. Further, as the dirt pile increases, the chance of snow accumulation also increases, as snowdrifts always form in wind-shadows.

By the time the duck hole has reached sufficient complexity (about 8 to 10 surface openings) to present the required stimulus for hibernaculum construction, it has withstood the vagaries of several years' climatic impacts. It is thus virtually assured of continued existence, and it becomes a burrow system upon the construction of a nest there by the squirrel. Such a procedure for burrow evolution can be seen to be highly efficient and highly adaptive.

This sequence of burrow genesis would only become operative within, or on the outskirts of, an established squirrel colony. It would provide for an automatic replacement of burrow systems which can be expected to eventually become uninhabitable in the face of long range changes in drainage patterns, mud flows, solifluction slumps and frost heaves, all common to the environment of the squirrels. It would also allow the squirrels to hold more of their area in sub-climax vegetation.

The phenomenon of sudden burrow construction as seen in the location of adventitious burrow systems, seems to represent a different category of behavior, behavior connected with species dispersal. Although the chances are infinitesimally small for individual success, for the population as a whole it serves the purpose of limiting numbers in a predator dependent fashion such that a stable population is virtually assured in established colonies. At the same time, it allows for the occupation of areas previously undiscovered by the species or recently altered to meet their requirements.

Nests

Squirrels build large, but structurally simple, nests in their burrow systems. Judging from observations of squirrels gathering and transporting nesting material, construction proceeds throughout the active season. The greatest nest-building activity occurs in late May and late August when the females are constructing brood nests or when all members of the population are preparing for hibernation.

Nests are non-woven structures; they are roughly hemispherical in shape and usually have a diameter of 30 or 40 centimeters. A hemispheric depression in the center of the flat top has a diameter of about 10 centimeters and has no differential lining. The nest rests snugly in a spheric cavity where it fills the lower half. The major construction materials are several species of sedges, however traces of almost all the local vegetation can be found (See also Part B, June 1961 Botanical Progress Report). Dirt and small rocks are also found, the latter apparently having weathered off the roof of the chamber.

The upper parts of nests, the portions apparently in current use, are always dry in contrast to the dampness of the burrow. The nests become damper as the bottom of the chamber is approached, turning into a rotting, soggy mass, and finally into a rich humus that is difficult to distinguish from chamber floor. Thus, it would appear that the squirrels are continually adding to the top of the nest as the bottom decays. The top, dry part of the nests excavated by the investigator contained a few fleas and lice of the types common to the squirrels themselves, as well as a large population of plant mites. The lower, decaying parts contain a rich culture of Mustid fly larvae and also contain a few Carabid beetles. The beetles are also found in other parts of the burrow system.

Nest chambers excavated in early May, while the ground was still frozen to within an inch or two of the surface, were capped by an inverted cone of thawed ground about 15 centimeters in height, presumably melted by the heat of the nest's occupant and/or the heat of decay from the bottom of the nest. The decaying area of the nest was warm to the touch, but whether this can obtain during the winter when the squirrel is not adding heat to the system is not known.

Nest-building was not observed. Squirrels trapped on cold days were seen to scrape up lichens and mosses through the mesh floor of

the trap, heap them unceremoniously in one corner of the trap and sit on the pile. Such piles did not resemble the shape of a nest.

The author often observed squirrels gathering nest material. Squirrels typically worked along the edges of patches of sedges or grasses, cutting dry, standing blades off near the ground with their teeth. They picked these blades up with their mouths and manipulated them to a crosswise position between their incisors and molars. As more blades were collected, the growing bundle was continuously manipulated with the forefeet, though its original crosswise orientation was not changed. When the bundle reached about 1 centimeter in diameter, collection ceased. The squirrel then stood in an upright position and carefully doubled all trailing ends of the cut vegetation back into its mouth so that the bundle protruded only about 5 centimeters on each side of the head. The squirrel then returned to its burrow which it entered, re-emerging without the bundle in 15 seconds to 2 minutes. The whole operation was then repeated. The largest number of trips recorded without intervening periods of other types of behavior was 14. This number was uncommon; usually the squirrels collected only three to six bundles in one sustained effort.

Habitat Alteration

With the genesis of burrow systems over the years, fresh, loose dirt is thrown to the surface in considerable quantities, producing a generally raised area. This area is well drained and is kept in continual turmoil by the squirrels. A wind shadow is often produced, with resultant snow accumulation during the winter. Feces are worked into the soil. In this situation two communities of plants flourish: those that favor disturbed sites, and those that favor snow beds. The raised areas, or mounds, stand out as sharply delimited green circles when they exist in areas generally supporting stable site plant communities. In areas which already support disturbed site communities, such as ocean and creek banks, the squirrel mounds are much less conspicuous.

The organization of plant types on a fairly typical burrow system is shown in Figure 5. This burrow was located in an area of Dryas ~~Fellfield~~ and on a Dryas octopetala mat which extended 12 meters to

Figure 5. Distribution of vegetation on a squirrel mound.

- Squirrel burrow openings
 - /// Fresh dirt piles
 - Ericaceous snowbed plants
 - ≡ Tall Willows and Birch (9 to 15 cm.)
 - /// Grasses
 - ✱ Non-crustose lichens
 - /// Rocky soil with crustose lichens
 - Dryas mat
 - Boundary of general vegetation types
 - Boundary of mound vegetation types
- Scale: 1:39 1 inch = 1 meter
- Slope approx. 3.5% dropping southwest
- True North = up

Additional explanation in text

the northwest and 5 meters to the southeast. The mound was about 45 centimeters higher at its center than the surrounding terrain.

The most conspicuous plants of the squirrel mounds are the grasses and the willows, mostly because they are the taller plants, and on the tundra tall forms are not common. Following is a partial list of plants found on the burrow systems, including the species making up the largest bulk of the vegetation. For a more complete listing of squirrel mound plants, see Part B of the June 1961 Botanical Progress Report.

Equisetum arvense L.

Arctagrostis latifolia Griseb.

Bromus pumpellianus Scribn.

Deschampsia caespitosa Beauv.

Festuca rubra L.

Hierochloa alpina Roem. & Schult.

Koeleria asiatica Domin.

Poa glauca Vahl.

Trisetum spicatum Richt.

Kobresia hyperborea Pors.

Salix alaxensis Coville

S. glauca L.

S. pulchra Cham.

S. rotundifolia Trautt.

Betula nana L.

Draba hirta L.

Arctostaphylos alpina Spreng.

Cassiope tetragona Don.

Ledum decumbens Lodd.

Vaccinium uliginosum L.

The relationships between disturbed sites and the squirrels are difficult to delimit. Squirrels were observed to use the plants of the disturbed site community extensively for food and nesting material, although other plants were also used for both purposes. Since all established squirrel colonies are to some extent on disturbed ground (because of burrowing activities), comparison of population levels is difficult. Territories 1 and 2, however, located on large areas of disturbed ground,

supported higher squirrel populations per surface area than territories located in Dryas types where the mound itself was the only disturbed ground.

Of the squirrels observed moving into new areas and establishing adventitious burrow systems, all moved into disturbed ground situations, though none survived. The forces that maintained these areas in sub-climax, however, were catastrophic to squirrels. Evans and Holdenried (1943), Linsdale (1946), and Fitch (1948) show that the California Ground Squirrel, Citellus beecheyi, is tied to disturbed sites in the California locations they studied, and that the populations declined to the vanishing point once grazing by livestock was prevented and the plant communities developed a climax growth. Gunderson, et al (1955) report Citellus parryi associated with disturbed ground in the Northwest Territories, Canada.

DAILY ACTIVITY PATTERNS

Visual observations yielded considerable information on daily activity patterns in both 1960 and 1961. In order to supplement these data, activity recorders were installed on the study area in July 1961.

Sensitive switches, activated by the displacement of a fine steel wire, were installed at the eight most heavily used holes of a burrow system. These switches were wired in parallel with each other and in series with a 12 volt battery and a recording milliammeter. Four switch complexes (of 8 switches each) could be wired in parallel with each other to record on a single milliammeter; the records of each complex were separated by placing a distinctive line resistance in series with each switch of each complex. Resistors of 20,000 to 200,000 ohms were used.

Two Esterline-Angus recording milliammeters, equipped with spring-motor chart drives, proved very satisfactory in the face of rather severe cold and wind conditions. The electric and mechanical nature of the system proved particularly advantageous over an electronic circuit when field damage sustained from numerous assaults by grizzlies had to be repaired in an area remote from sources of regular repair parts.

The sensitive switches operated in any direction and made an identical mark on the chart whenever a squirrel passed either into or out of a burrow. Squirrels generally ignored the switch wire since it closely resembled the roots that normally dangle from the roof of the tunnels. Foxes, especially the young, were curious about the switches and lead wires, however, and caused malfunctions of the system from time to time. Grizzlies did not vandalize the switches and wiring directly, but destroyed the system when they dug out the burrow systems involved. The bears were attracted to the recording instruments, possibly because of the ticking noise they made, and on several occasions they severely damaged the instruments, including chewing up the paper charts and opening and emptying the inkwells.

The first instrument was placed in service at Burrow System 32 on 11 July 1961, operating with six switches. The second instrument was installed on Burrow System 81 on 23 July 1961. On 15 August 1961 the

circuit was expanded so that eight burrow systems were equipped with six switches each and tied into the two milliammeters. This set-up continued in operation until early October 1961 when sluggish ink flow and switch jamming, caused by low temperatures, rendered the system inoperative.

As a group the members of the genus Citellus are diurnal animals. C. parryi is no exception to this generalization. Even though daylight prevails for the entire 24-hour period from mid-June to early August, the squirrels do not take advantage of the situation, but follow their generic pattern. Within the confines of diurnalism, the activity pattern varies through the active season.

Post-Emergence Period

Squirrels emerging from hibernation in late April spent very little time above ground. Activity was concentrated into two periods of the day, one between 0800 and 1000 hours and another between 1330 and 1530 hours. More activity was evident during the later period, some individuals restricting activity to this period only. Any given individual remained active for a few minutes to 45 minutes per period. Eight individuals identified as active during the morning period were also seen during the afternoon period of the same day for three days, and all were active for lengths of time approaching 45 minutes during each period. Three squirrels known to be inactive during the morning period, but active during the afternoon period, had the shortest lengths of activity (10, 12, and 17 minutes) on each of the three days involved. During this season squirrels stay very near their hibernation burrows and do not come into contact with each other. Their major activity is feeding and related behavior and clearing their burrow entrances of snow.

Post-Breakup Period

With the onset of melting temperatures in early May, more squirrels enter the active population from hibernation, and each stays above ground for longer periods of time. Activities now include feeding, territorial defense, breeding, burrow construction, nest-building, and migration. Four rather distinct periods of activity emerge: 0400 to 0600, 0900 to 1030, 1330 to 1600 and 1830 to 2100 hours. Again, not all squirrels make an appearance at all periods, but above ground activity is much increased over the earlier season and virtually all individuals

are active during the two mid-day periods. The early and late periods are almost exclusively feeding periods in which squirrels do not move far from their burrows. They closely resemble the two mid-day periods of the post-emergence period. All the activities mentioned above occur during the mid-day periods, the 1330 to 1600 hour period showing the greatest intensity of territorial defense, sexual behavior, and longer-range movements. The 0900 to 1030 hour peak shows higher levels of burrow construction and nest-building.

Mid-Summer Period

During June and July, activities include feeding, birth and nest care of young, emergence of young, burrow construction, and remnants of territorial defense. The territories have become quite stable by this time, and their defense, although engaged in when intruders present themselves, does not occupy much of the territorial male's time due to the prevalence of quick and easy victories.

Figure 6 shows the per cent distribution by hour of the squirrels' activity during July. Squirrels stay active for long periods of time, as much as three hours in some instances, and the pattern becomes more diffuse than in the previous two seasons. The peak activities still fall at the same times, however. The emergence of the young near the first of July increases the population of the study area and the young seem to be more closely restricted to the peak activity times than do the adults.

This season is characterized by rainstorms which disrupt the pattern and add to the observed diffuse activity. Squirrels are active to some extent during rains but at a much reduced level in both numbers and in time spent above ground. Activities during rainstorms are virtually restricted to feeding. Overcast skies and fog have an effect similar to rain, but not to as great a degree. Following rains, there is a flurry of activity, focused around the clearing of mud from burrow entrances.

Late Summer Period

During August the fall territories are being established, and burrow construction reaches a yearly peak. Less time is expended on feeding; the main food source shifts over to berries and the squirrels do

not go far from their burrows. Local changes in the residence of individual squirrels, however, is evident.

Fall Period

During September and October, the surface activities of the squirrels show a steady decline in time and intensity. Figure 8 shows the recorded pattern for September. The number of squirrels contributing to the record has dropped from 13 in Figures 6 and 7 to 7, which may account for some of the loss in diffuseness of the pattern. Field observations, however, tend to indicate that the concentration of behavior into two periods is real. The steady decrease in day length and temperature seems to be responsible for the elimination of the early morning and late evening activity peaks found during the summer.

The trend noticed in September continues into October with squirrels spending less and less time above ground as the month progresses. No squirrels were observed afield when the temperature was below minus 15° C. When the temperature rose above this during the mid-morning and mid-afternoon periods, some activity was observed; activity was almost exclusively related to feeding--gathering frozen berries or digging Dryas roots.

Control of Activity

Field observations showed that the squirrels were diurnal in their activity, yet activity recordings (Figures 6 and 7) show low levels of activity during the "night" hours. In order to determine the cause of the "night" recordings, Burrow Systems 32 and 81 were observed closely during five nights in July. The two burrow systems had a total population of 13 squirrels.

Between 2130 and 2300 hours no activity was observed. Beginning at 2300 and continuing until 0230 hours, squirrels appeared at the burrow openings at the rate of one every 30 minutes at each burrow system observed. Most of these animals did not expose more than 3/4 of their body length above the burrow, but a few emerged fully; none moved more than 4 inches from the opening from which it emerged. Observatory positions were assumed and the average stay above ground was 4 minutes.

Between 0230 and 0430 hours these momentary emergences increased to an average of one every 15 minutes in each burrow system; the

Figure 6. Per cent distribution of squirrel activity by hours; July total. (Bering standard time)

Figure 7. Per cent distribution of squirrel activity by hours;
August total. (Bering standard time)

Figure 8. Per cent distribution of squirrel activity by hours; September total. (Bering standard time)

emergences followed the pattern given above, except that the average stay above ground increased to 5 minutes and about half of the emergents issued one relatively low volume "chick-chick" call (see Vocalizations) during their stay above ground, usually within one minute after emerging.

Between 0430 and 0445 hours the first squirrel that stayed above ground, emerged from a burrow. This first emergent, from the first minute above ground, began issuing loud "chick-chick" calls at the rate of 3 per minute. It did not move away from the burrow opening from which it had emerged for 6 to 9 minutes. Within 4 minutes after the first emergent began issuing "chick-chick" calls, more squirrels had appeared and also called. Within 15 minutes all the squirrels of the same mound as the first emergent were above ground and squirrels at near-by mounds were beginning to appear. Grooming, defecating, and observation postures were engaged in near the mouth of the burrow by each squirrel as it emerged and while it was still near the mouth of its burrow. The calls were issued from the observatory posture. After 5 to 12 minutes of this activity, the individual squirrel moved away from the burrow and began feeding; the "chick-chick" calls fell off in number until squirrels were generally silent after being above ground for 15 minutes.

By 0530 hours all the squirrels on the hillside had become quiet and were engaged in foraging (see Food Gathering).

These observations suggest that the squirrels sleep in a series of short naps and are, at intervals, sampling the environment in a conscious state. Their diurnalism appears to be controlled by visually detected stimuli, possibly light intensity or direction, and finely tuned by social facilitation. It would therefore seem that the high degree of synchrony of activity attained by this species can be explained by simple behavioral means without resort to complex and elusive groups of phenomena such as the "metabolic clock."

INDIVIDUAL BEHAVIOR

Food

The squirrels were observed to avoid bitter and salty foods and to favor sweet and sour foods. Within this framework, they are not markedly selective and consume a wide variety of stems, leaves, roots, seeds, fruits, mosses, lichens, fungi, and carrion. Almost all species of available plants were observed to be eaten at some time; however, mosses, lichens, sedges, and woody stems and roots were not taken regularly, even though they are common in the habitat of the squirrels.

Seasonal diet shifts were marked on the study area and seem to be controlled by availability of the various foods. During April and May roots of Dryas sp. and various berries, preserved frozen from the preceding fall, constituted the bulk of stomach content samples examined. Late in May unidentified mosses also occurred, as did seeds.

During June and July succulent stems and leaves made up the largest part of the stomach contents, identifiable items belonging to plants of the Dryas mat and Ericaceous Snowbed Communities. Although not identifiable in the stomachs, field observations showed the crowns of higher fungi to be heavily browsed. In August there was a heavy shift to fresh berries, those of Vaccinium uliginosum, the most common berry on the study area, forming the bulk of the diet. High berry intake continued through the first half of September.

In the last half of September, roots of Dryas appeared again as a major food item. By the first of October these roots made up about 50 per cent of the volume of the stomach contents, and by mid-October they comprised almost the entire diet.

At all seasons the squirrels eat carrion when available, mostly dead squirrel carcasses. Any squirrel carcass left on the study area was eventually eaten by other squirrels, if the foxes did not carry it away. On 1 May 1961 a squirrel carcass was observed melting out of a patch of ice in a vertical position, head up, near the burrow of an adult male squirrel. As the ice melted the male kept the carcass eaten level with the surface of the ice. The entire carcass had been consumed by 12 May, except for the tail, feet, fur, and large bones, which were picked clean and left lying about the site. In July of 1960 a

squirrel kept in captivity a few days tore a ham sandwich apart and ate the ham, rejecting the lettuce and bread. Geist (1933), Cade (1951), and Musacchia (1954) report carrion consumption in this species.

Squirrels living about the camp site on Ogotoruk Creek did considerable damage by breaking into camp stores. The greatest losses were sustained in cooked meat, fats, dried beans, flour, and rice. Apples were readily taken when available, but potatoes were consistently rejected unless cooked. Bread was taken on occasion, and several times a squirrel that had just rejected a piece of bread would take it after sugar had been sprinkled on it.

Food Gathering

Field observations indicate that most stems and leaves are eaten at the site of collection by the squirrel, whereas most fruits and seeds are placed in the cheek pouches and consumed in or near the burrow. In times of duress, such as when trapped, squirrels typically eject pouched food by manipulation of the jaw and cheek muscles.

In digging for Dryas roots, squirrels dig in under the mat in much the same way they dig at their burrows. The loosened dirt is never moved a second time, however, and if the accumulation of dirt obstructs digging operations, the site is abandoned. As dirt is scraped away, roots are exposed, and periodically the squirrel will halt digging and browse the roots back to the dirt level. Since most of the roots are hanging from the top of the excavation, the squirrel is often required to twist its body nearly 180° so that its hind feet are resting on the ground and its mouth is in contact with the roof of the excavation. While in this posture, the forefeet are used to brace the animal from the walls of the excavation. Digging is also done in a twisted posture at times, though the limit of twist seems to be about 90° . Once the roots have been clipped off, they are manipulated into the mouth. If they are under 2 centimeters in length manipulation is accomplished by the lips; if they are longer, a sitting posture is assumed and the forefeet are used in the manipulation. Roots that are attached by both ends are bitten free at one end and abandoned for the moment. They are eaten when the squirrel has worked around to the area where the other end is attached.

In heavily utilized sites an overhanging section of Dryas mat develops. When the overhang reaches about 3 or 4 inches, further digging is impeded, aggravated by the accumulation of loose dirt. The squirrel will then either abandon the site completely or begin digging at one of the side walls of the excavation, turning its body axis about 45° in the horizontal plane. In this manner, the excavation is extended to as much as 3 meters in width, 8 centimeters in depth and 6 centimeters in height. Since the squirrels always work these sites facing up slope, each excavation tends to be oriented parallel to the others, and sections of the Dryas mat in the study area where root gathering was heavy became shingled in appearance. In Dryas Step areas, the root gathering was always observed to proceed from the bottom of the step and in some places amounted to 50 per cent of the linear dimension of the steps. In these areas squirrel rooting activities appear to contribute substantially to the maintenance of the step conformation.

When feeding on grass seeds, squirrels approached the base of the plant, rose to a high upright posture, and grabbed the fruiting head of the grass with both forefeet. In the high prevailing winds, the heads wave rapidly, but the squirrels proved quite dextrous in grasping them. The fruiting head was then inserted into the mouth and the seeds stripped off by a combination of leg and neck extension. About half the seeds stayed in the squirrel's mouth, about $1/4$ fell to the ground, and about $1/4$ remained on the plant. The fruiting head was then released, and no further interest was accorded the seeds which remained on it. The seeds which stayed in the mouth were manipulated into the cheek pouches by working the jaws, cheek muscles, and probably the tongue. This manipulation required from 30 seconds to 2 minutes and was usually done from a sitting posture. The seeds that had fallen to the ground were then picked up with the mouth one by one, and at intervals these were also placed in the cheek pouches.

The various berries growing on the study area were all those of low plant species and were located less than 3 centimeters above the ground and singly on the plant. These berries were gathered without manipulation by the forefeet; the squirrel nosed through the bushes and picked the berries with its teeth. In a productive bush, the squirrel would forage for an average of 2 minutes; it then assumed an observatory

pose while both surveying the countryside and forcing the berries into the cheek pouches. Typically, berries were collected until the cheek pouches were distended so that, together, they equaled about 1/2 the volume of the head. The squirrel would then return to its burrow and disappear below ground, reappearing in a minute or two with empty cheek pouches to return to the berrying site. The largest number of berrying trips during one undistracted period observed was seven, though most squirrels would make five trips unless disturbed by some outside agent. Although these berries were obviously cached in the burrows at their time of collection, an absence of cached berries in the burrows excavated by the investigator tends to indicate that the caches represent very temporary stocks. Mayer (1953b) and Krog (1954) did locate food caches in excavated burrows. Possibly food caches are associated with the elimination, in September, of the activity peaks found in the early morning and late evening during which foraging was the major activity at earlier seasons.

Collection of stems and leaves was the major type of foraging observed, being nearly the exclusive mode of feeding during June, July, and August. During the year as a whole, stems and leaves probably make up 70 per cent of the squirrel's food intake by volume. Both stems and leaves are gathered in essentially the same manner and usually at the same time. The squirrel approaches the plant and smells it with neck extended and all four feet on the ground. It is probable that a visual inspection has already been concluded from a distance, though this is not apparent in recorded observations. The squirrel then moves its hind feet closer to the plant, flexing its back and lifting its forepaws clear of the ground at the same time. The leaf or stem is then clipped off with the incisors. A leaf is usually clipped off at the base of the petiole; a stem generally is clipped off within an inch of the ground. Just as the leaf or stem is separated from the plant, the forefeet are brought up simultaneously and grasp it. The squirrel then either raises to an upright position with the back extended and enters a period of about 5 seconds of observatory behavior, or it rises to an upright posture with the back flexed and proceeds with the foraging behavior. If the former option is used, it gives way to the latter and the item of food is raised by extension of the forefeet

to the vicinity of the mouth where a piece is bitten off with the incisors; the remainder staying in the forefeet is lowered to just below shoulder height. Mastication follows and is accomplished by a rotary motion of the lower jaw which moves either clockwise or counter-clockwise at different times in the same individual. Once chewing is started in one direction, it usually continues in that direction until interrupted by an outside agent or until another bite is taken. Successive biting and mastication continues alternately until the food item is either consumed or abandoned.

Having completed ingestion of one food item, the squirrels almost invariably move on to a new location from a few centimeters to many meters away. The few cases recorded where foraging continued on the same plant at the same time involved an isolated plant or a situation where the squirrel entered observatory and mild alarm behavior postures and then returned to foraging.

Progression

Squirrels were observed to move across the terrain in three distinct ways: walking, running, and crawling. Other motions, used only to move the squirrel short distances in special situations, were also observed and will be considered under the headings of the specific behavior complexes.

Walking was used to progress around the burrow mound, to move from plant to plant while feeding, to proceed when caution was required, and in sundry other situations where slow forward motion was necessary. It was the only method by which a squirrel was able to back up. Walking is accomplished by movement of the feet in diagonal pairs (i.e., a "trot" gait) with the abdomen held about 3 centimeters off the ground. Very little body sway was observed. The tail may be held in any position, and, although moved a great deal, it is not moved in any fixed pattern with the gait.

Running is the main method of rapid progression and is the most common form of squirrel locomotion. It can be accomplished at a great variety of speeds, but does not seem to grade into the walk in performance. The running motion is a mixed gait, probably a variation of a trot, in which the forefeet move alternately with an even beat, while the hind feet move alternately with a heavily syncopated beat such that

they approach unison motion. This gait causes the squirrel's rump to bob up and down markedly, and since the forequarters bob only a little, the whole animal gives the impression of having a rocking or "hobby horse" motion. The tail is usually held straight back or tilted slightly upward, and its tip is bobbed at the same rate, but inversely as the rump.

Crawling is essentially a modification of walking described above; the abdomen is held very near the ground by raising the elbows and lowering the knees. This position gives the squirrel an unusually wide, flat appearance and a speed comparable to the regular walk. This gait is used mostly when the squirrel is trying to avoid detection, and when using it the squirrel usually progresses along the natural depressions of the ground. The tail is trailed straight behind, flat on the ground. Mayer (1953b) observed this strange gait in the ground squirrels at Point Barrow and called it the "tundra glide."

Observatory Behavior

Ground squirrels are characterized by their alertness to movements and disturbances in the environment around them. Hardly any surface activity occurs for more than a few minutes without causing squirrels to pause momentarily to survey the terrain. These surveys are conducted from one of a continuum of standing postures. These postures are described below as four separate postures, even though all gradations between these four postures are common.

High sitting is effected by crouching with the hind quarters and extending the forelegs to raise the forequarters as high as possible. All four feet remain on the ground. The back is usually slightly flexed and the neck is extended as fully as possible. The head is held horizontally. The tail is held in almost any position and is not moved while the squirrel is looking; as soon as something is seen, however, the tip of the tail is waved or flicked slightly.

Low standing is a position similar to the above, but the body is now held at about 60 degrees to the horizontal and the forefeet are clear of the ground and held tightly against the chest; the wrists are together and sharply flexed so that the toes point toward the ground.

Standing is the most often used posture for observation and is accomplished by holding the back slightly extended and in a vertical

position with the rump resting firmly on the ground. The forefeet are held clear of the body with the wrists flexed and are constantly in motion to maintain dorsal-ventral balance, especially when the wind is blowing. The hind feet are firmly planted on the ground for their entire length and are used to maintain lateral balance. The neck is extended proximally, but is sharply flexed at the atlas-axis joint so that the head is held horizontally.

High standing is essentially the same as standing, except that the hind legs and feet are fully extended so that the squirrel is standing "tip toe." Balance becomes more difficult in this position, and when the wind is blowing the squirrels step backward, forward, and sideward to keep from falling over. If balance is lost, the squirrel usually goes back to a standing position for a moment. In the wind, squirrels may lean windward as much as 20 degrees forward or sideward, but not backward. The tail is used to help maintain balance, but is not braced upon the ground.

The amount of time spent in observatory behavior appears to be variable with the situation and the individual. In field notes covering a total of 18 hours of squirrel activity, where the squirrels appeared intent on another type of behavior and no cause for alarm was noticeable, the squirrels spent 14.8 per cent of their time in some type observation posture. This is generally spread out so that each observation is 3 to 5 seconds in length, followed by about a minute of some other activity. Observation time increases markedly when squirrels enter places where vision or motion is obstructed or when they see a strange or moving object. The reception of a warning call (see Vocalizations) from another squirrel causes the immediate assumption of an observatory posture which is usually held about 30 seconds in the absence of further stimuli; thereafter, for a period of 3 to 10 minutes, observation poses occur at a greater frequency than they did before the warning call was heard.

Comfort Behavior

Squirrels spend little time in comfort behavior when above ground. Perhaps the bulk of this type of activity occurs in the burrows. Dusting, scratching, stretching, grooming, and rubbing against foreign objects was observed.

Dusting was observed on only five occasions on the study area. Mayer (1953b) indicates that it was a common practice in Meade River squirrels. Mayer observed squirrels on sand dunes, and it may be that the conditions on the Ogotoruk Creek study area were not favorable for dusting sites. On the few occasions where dusting was seen, the squirrel flipped over in a rapid motion and flexed its back from side to side for about six or eight times; it then flipped back to its feet. The action extended over a period of not more than 8 seconds and took place in moist dirt freshly excavated from the burrow. The squirrel shook itself in the manner of a dog, clearing hair of dirt. Repeat dusting was not observed.

Scratching was observed commonly and was always done with the hind feet. The neck, ears, and head received most of the attention, though the sides, chest, abdomen, and back were also scratched. Most scratching was done from a sitting position with the body twisted into a sigmoid curve, the anterior convexity being produced at the intended scratching site. The appropriate hind foot was then extended and the claws brought in contact with the site with a series of rapid, short strokes. Scratching was often interspersed with grooming.

Stretching was most often observed on sunny days when the squirrels spend considerable time loafing around their burrow entrances. From a horizontal position the squirrel would extend its forefeet and rock backward, at the same time hyper-extending the forward part of its spine and flexing the posterior part. This motion caused the shoulders to be lowered and the rump to be raised. The zone of hyper-extension was then slowly moved posteriorly along the spine, ending with the body rocked forward over the forefeet (which were not moved throughout the stretching) and with the forward part of the spine flexed and the posterior part hyper-extended.

Single limbs were stretched; this action was performed by shifting the weight to the other three feet and extending the limb to the side.

Yawning occurs frequently and proceeds in the common tradition. It is often associated with other forms of stretching.

Grooming by squirrels was observed a great deal. One common type was "face washing" which was generally associated with feeding. In

face washing the squirrel entered one of the standing postures, freeing its forefeet. The forefeet were then raised simultaneously and brought into contact with the head between the ears and eyes. The forefeet were then raked over the face with a downward motion of the arms and an upward motion of the head. The forelimbs contacted the head from the wrist to the elbow; the soles of the forefeet were turned toward the ground. Three or four such raking motions were concluded in rapid succession, then the forelimbs were raised again and licked carefully, beginning at the elbow and working toward the wrists. Their medial surfaces received more attention than the lateral and posterior surfaces. The whole operation was sometimes repeated as many as five times. It is interesting to note that in this operation all the sensory vibrissae are cleaned, including those on the forelimbs; this may be the main function of the face washing type of grooming.

Unlike the above, other types of grooming seem to be directed toward the removal of a particular irritant. Usually the foreign body is first removed from the hair by biting and by combing the hair through the teeth or by pulling out the hair; the hair over the site is then smoothed by licking. When squirrels on the study area were marked with agents which caused the hair to stick together, the matted hair was quickly removed, leaving bald spots in place of their markings. Dyes which did not mat the hair were not disturbed in this way, so apparently it was not the discoloration which elicited the grooming reaction. When non-matting, alcohol solvent dyes were used, the squirrels licked the areas where the hair had been mussed by the application of the dye and were rather persistent in this endeavor, despite the necessity of stopping to attempt to clear their mouths of alcohol, which apparently burned their tongues. Once the hair had been smoothed, the dye marks were left alone.

Rubbing on foreign objects was observed only during May and early June. Shoulders and sides received all of the rubbing in instances observed. Squirrels came alongside a boulder, bank, or the edge of their burrow and leaned toward the object as they passed, making contact at the neck and always scraping in an anterior to posterior direction. Sometimes the forelimb on the side making contact was extended, causing the shoulder to rise on that side. Usually only one pass was

made, but as many as three were observed on occasion. This rubbing behavior pattern is discussed in this section on comfort behavior because of its form. It was suggested by Fitch (1948) that rubbing is connected with territorial defense and is actually a procedure to rub musk on the object. Fitch worked with Citellus beecheyi, in which shoulder scent glands have been described. The presence of such glands in C. parryi has not been investigated. Observed rubbing sites were near the boundaries of established territories and all identifiable animals seen rubbing were males. It is also true that rubbing occurred at a time of year when all males examined had scars and wounds from territorial defense fighting; few females showed such wounds. Perhaps the healing wounds itch and are therefore scratched by rubbing. Present data do not allow a choice between these possibilities.

Home Range

The activities of a squirrel center about the animal's burrow system. From the burrow the squirrel works out in all directions. For the purposes of this study, a polygon formed by connecting the farthest points that any squirrel was trapped or seen to wander was termed that animal's home range. Unlike a territory, the home range is not defended. Territorial males ignored other males met while on the outlying areas of their home range, but the same meeting on one of the male's territories quickly developed into a fight. Home ranges did overlap extensively with the territory on which the animal lived.

Home ranges on the study area were found to vary in area between 18,000 square feet and 640,000 square feet, with an average of 182,000 square feet. All the home ranges over 600,000 square feet belonged to satellite males. Territorial males had generally small home ranges, falling between 18,000 and 200,000 square feet. Home ranges were irregular in shape and seemed to consist of areas that were easily accessible from the home burrow. Although the females of one territory were not actively attacked when they entered a neighboring territory, they seemed to shy away from such neighboring territories, even though they met the inhabitants of other territories on the areas between territories with no show of belligerence.

The small size of the home ranges is interesting considering the mobility of the squirrels. The longest axis of any observed home

range was only about 875 feet, a distance that squirrels were often seen to cover in about 10 minutes, including stops along the way. In the extreme cases, squirrels were seen to spend their entire life on home ranges with a long axis of about 100 feet.

Changes in home range were common and accompanied changes in burrow sites. For example, Female 311, born in 1960, occupied a home range of 88,000 square feet with a long axis of 250 feet during 1960. In the spring of 1961, she moved, in one day, to a new burrow 1,050 feet away, and for the rest of the summer she was not seen to leave an area of 36,800 square feet around her new burrow system.

SOCIAL BEHAVIOR

Sexual Territories

Figures 9 and 10 show the boundaries of the sexual territories on the study area during 1960 and 1961, respectively. Each sexual territory is set up and defended by one adult male, and from it he excludes transgressions in so far as possible of all other males. The females are investigated when they first enter the territory, but are not molested; after they have taken up residence on the territory, they are generally ignored by the territorial male. Females do not contribute to the defense of the territory. The presence of a female at a particular burrow system causes other females to stay away from that system, but no overt defense of a female held burrow was observed.

Territory formation may be considered to begin with the emergence of the males from hibernation (20 April in 1961). The males immediately clear the snow from the openings of the burrow from which they emerged; any entrances not so cleared become plugged with ice as the melt progresses in early May. This plugging appears to result from the air temperature rising more quickly than the ground temperature, which in turn causes the melt water to be re-frozen as it enters burrow openings. The males stay very close to their original burrow system for the first few days; the distance that they will travel from the burrow slowly increases each day that they are out of hibernation. During 1961 males were ranging as far as 70 feet from their burrows by 25 April, and the first contacts between neighboring males were observed on that date. As soon as contacts are made, overt territorial defense becomes noticeable.

A complete behavior sequence during "boundary disputes" contains the following steps:

- (1) Two males sight each other and move toward one another rapidly and directly until the distance between them is less than 20 feet on smooth ground and as little as 10 feet on broken ground.
- (2) Their approach becomes somewhat circuitous and slow, motion being accomplished by a low, squatting crawl with the ventral surface of the body in contact with the ground most of the time. For about

Figure 9. Map of ground squirrel study area, Ogotoruk Creek, north-western Alaska, showing squirrel territories existing in June 1960.

Figure 10. Map of ground squirrel study area, Ogotoruk Creek, northwestern Alaska, showing territories which existed during June 1961.

1 second out of every 5 or 10, the squirrels (usually synchronously) stand in an erect "observation posture," high on their hind legs and face each other.

(3) At a distance of about 3 feet, the squirrels stop moving toward each other and begin moving parallel to each other, alternating between the crawl and a high, stiff-legged strut. After progressing parallel for 4 to 12 feet, the squirrels assume a normal sitting position and either remain motionless or begin nibbling at the vegetation or scratching at the ground. Step (3) behavior has been observed to occur as few as 4 or as many as 15 times for a maximum time span of 25 minutes.

(4) During the last of the strutting sequences described above, the squirrels change their direction of movement to about 20 degrees toward each other, instead of parallel as before. They maintain a parallel orientation of their body axis and accomplish a collision course by a slight side-stepping. During this activity both animals maintain a high, stiff-legged strut with the back sharply flexed. The animals make contact first with their hind quarters, then with the entire length of their trunks. Their heads are held apart and directed ahead.

(5) The squirrels lean against one another while still moving forward. Sometimes one of the squirrels will push harder than the other, and the pair will move on a diagonal course. Forward progress continues from 2 to 10 feet. Step (5) is exhibited only once.

(6) Suddenly a turbulent fight breaks out. The animals roll over and over each other, biting and clawing. This fight may last from 1 second to 1 minute.

(7) The combatants break apart and one animal runs away rapidly, usually in the direction from which it originally came. Occasionally an animal will run in a direction other than the one from which it originally came, but if so, it swings in a wide circle and picks up the original direction. If the pursuer catches up with the pursued, he will attempt to bite the latter on the rump. If this bite holds, another tumbling fight (6) ensues. A second, or even third fight has never been observed to reverse the roles of pursuer and pursued. If the bite does not hold, the pursuing squirrel usually pitches off

balance, tumbles and gives up the chase. If the pursued squirrel gains distance, the chase is usually abandoned after 30 to 200 feet. One chase, including two fights enroute, lasted over a total distance of 850 feet.

(8) Upon abandoning the chase for one reason or another, the former pursuer moves 10 to 50 feet in the direction of his burrow, stops, and digs a pit (boundary pit--see Burrowing Behavior) about 3 inches in diameter and 4 to 6 inches deep, usually to the frost line. He then begins a meandering course in the general direction of his burrow system, stopping to dig out roots here and there and often rising to a high standing observation pose.

The steps described above represent a complete sequence, and most boundary disputes do not continue through all the steps. At any stage, one of the contenders may retreat toward his burrow system, at which time the non-retreating male generally skips to step (8). If a boundary dispute ends in the same area as a former one, the victorious male may dig out an existing pit instead of starting a new one. Squirrels coming to the boundary of their territories will often dig at one of these existing pits even though they have not recently engaged in a boundary fight.

As the season progresses, a male who is victorious in a majority of his boundary disputes expands his territory at the expense of his neighbors' territories. Males who are displaced attempt to establish themselves elsewhere or drop into the category of "Satellite Males" and take up a semi-nomadic existence, defending no territory of their own and staying off defended areas. These males take up residence in burrow systems situated between defended territories; they often share these burrows with other satellite males, though each occupies a separate part of the system. In the event of the death of a neighboring territorial male, a satellite male will move onto the deceased's territory and defend it. A clear example of this was seen on the study area during 1960 when a territorial male holding territory number two was killed on 21 June. By 9 July one of the satellite males living in the area had established himself on this territory; his boundaries remained the same as his predecessor's. During 1961 this male was able to hold the territory from the first of the season.

In 1960 the study area was divided into 9 territories which persisted until about the first of August, though they were not actively defended in July. In 1961 the same area was divided into 13 territories which again endured until the first of August (see Figures 9 and 10). Approximately the same burrow systems were involved in the territories of the two years, they were just apportioned differently. The reapportionment of the burrow systems during the second year seemed to depend mostly on the vagaries of chance events in the history of their formation.

For example, Territory 3 was a disjunct territory during 1960, and between the two portions there existed a strip of ground widely used by passing squirrels and not defended by the owner of Territory 3, adult male number 4. Male 4 was killed on 21 July 1960 and was not replaced by a satellite male, as the territories in general soon began to disintegrate upon the formation of fall territories. In the spring of 1961, Male 10, who had been a satellite male during 1960 operating along the beach ridge between Territories 1 and 2, attempted to take over all of the old Territory 3. He was fairly successful in this venture and added the two mounds on the ridge of Ogotoruk Hill just to the north to the complex. The Territory was now divided by three obstacles: (1) the ridge of Ogotoruk Hill, (2) a large snowdrift, 200 feet in length, extending south from Ogotoruk Hill between the two sections of the old Territory 3, and (3) the creek.

On 3 May a new male (number 510) moved into the study area. Male 10, badly extended across the three obstacles, was unable to exclude Male 510 who took over the eastern end of the territory, and a new boundary developed along the creek. By 6 May, homeless males were numerous on the study area and the path along the snowdrift began to receive heavy use by wandering squirrels. These animals generally did not resist Male 10's attacks, but none the less they required a great deal of his attention. By 8 May adult Male 30, a satellite male living between Territories 3 and 9 during 1960, had established himself on part of old Territory 9 (Territory 11 in 1961) and, having a firm foothold on the ridge of Ogotoruk Hill to the west, began expanding eastward along the ridge, threatening Male 10's burrows there. An intense boundary struggle developed between Male 10 and Male 30 along

the ridge. Male 10 was able to hold the two burrow systems in question, but this required so much of his attention that he was unable to also fight the transients on the snowdrift and Male 510 to the east. The latter pushed across the creek and was able to set a new boundary along the snowdrift. At the same time Male 510 was being assailed from the west by Male 431 of Territory 5 and, with the acquisition of the entire eastern segment of the old Territory 3, Male 510 had inherited the problem of the transients passing along the snowdrift. He was unable to pursue the conquest of Male 10's territory further. These territories finally stabilized as shown in Figure 10. The difference between the territories in this area seems to result from the fact that in 1961, Male 10 was motivated to hold the Ogotoruk Hill ridge burrows at the expense of the eastern part of his territory; whereas during 1960, Male 4 was motivated to make the opposite choice. It seems that the motivation here involves in part the sequence in which the struggles took place, as well as the various participants' ability to handle the trouble. The reapportionments elsewhere followed this general pattern, but each hinged on its own specific problems.

By 15 May 1961, the final pattern of territories had emerged, and actual fighting began to subside rapidly. It seemed that squirrels had learned the boundaries and knew their neighbors by sight. An occasional threat could still be observed until 15 June, after which no overt territorial defense was seen in connection with sexual territories. The integrity of the territories persisted until about 1 August.

Sexual Territories and Females

As discussed above, the females did not engage in territorial defense. They were permitted free transgression on the territory on which they lived as well as on others; they were ignored by the territorial male after a brief investigation, which was believed to include their recognition as females. The females in turn mostly ignored the males, also.

When the females emerged from hibernation between 29 April and 4 May 1961, the formation of sexual territories was well under way. The females typically began to clear the entrances of their burrow systems and surrounding duck holes as soon as they emerged. Most stayed at their emergence site, but some moved into nearby burrow systems and

refurbished these. In all cases, the hibernation sites of the males were occupied by a female in early May. The male involved, if he was not displaced by territorial defense, continued to live at the site as well as at surrounding sites. He appeared to occupy a section of the burrow complex separate from the female. The females were finally distributed one to a burrow system after they had been active for about a week. No overt fighting could be observed between females. Some migration of females to new districts was observed and these probably represented animals displaced by the non-availability of burrows.

The males did not entice females to enter or stay on their territories in any overt way. Rather, the female seemed to choose a burrow system on its own merits, and the male was inherited along with the site. In cases where an occupied site changed territories, as discussed in the case of Territory 3, the females stayed with the burrows and thus came under the dominance of a new male. Mate selection would appear to result from two relatively independent phenomena: (1) female's selection of a burrow system, and (2) a male's dominance over the district in which that burrow system is located.

Fall Territories

The sexual territories cease to be defended in July and seem to continue to exist simply by reason of the inertia of memory or habit. The month is a peaceful one, and no clear evidence of fighting was observed in either 1960 or 1961. Early in August of both years, however, fighting was again observed and it increased in both intensity and frequency throughout the month. At this season, the fighting occurred between all members of the population and was relatively simple in form. When the owner of a burrow system saw another squirrel within 20 or 30 yards of its burrow, it would begin moving along a direct course in the direction of the intruder, but with innumerable pauses to feed, watch, stretch, and yawn (probably displacement behavior). The intruding squirrel would adopt the same attitude, and the two squirrels would thus approach one another. When the animals were somewhere between 20 and 5 feet apart, one would turn and bolt away for a few feet to 20 yards. The other would immediately bolt after it, stopping to maintain about the same distance as had existed before

the running occurred. The two squirrels generally stopped in such synchrony that it was impossible to see which had stopped first. An interval of observatory behavior (but sometimes feeding) would follow, only to be followed by another sprint. In most exhibitions observed, the direction of chase changed several times, but, in all cases seen, the animal which had first run away was the one which eventually departed from the area. Early in August either squirrel could win, but after 24 August 1961, the intruder always lost. In cases where the individuals could be identified, adult males always displaced females, and adults of both sexes always displaced young.

The object of these forays was the defense of a very small area, usually 30 feet in diameter, which centered around a burrow system. In many instances the squirrels, especially females, defended the burrows they had been occupying all summer. The males usually displaced one of the females from one complex of a burrow system on the territory which he had held earlier in the summer. In all 13 territories on the study area, the female so affected moved into the other complex of the same system. The young were driven out of their natal burrow system by a steadily increasing belligerence on the part of the female, though one would usually continue to occupy the second complex if it was not occupied by an adult male. Satellite males began to defend the burrow systems they had occupied during July, though if more than one was using a single system, all but one was displaced. No great emigration from the study area could be detected.

After 1 September all the squirrels seen chasing each other were young animals, and it appears that these are the last to find a fall territory. By mid-September no more overt territorial defense was observed, and the animals seemed to stay away from each other's burrows, even when two animals occupied burrows within 15 or 20 feet of one another.

Thus, by the end of September, the population of the study area had converted itself from a system of socially interacting groups living in a few centers of concentration to an evenly spread population of essentially solitary animals.

Sexual Behavior

The first females appeared above ground on 29 April in 1961 and were largely ignored by the males. The first overtures of sexual behavior were observed on 1 May and consisted of step (1) below. During early May, sexual activities became more common and more intense until the first copulation was observed on 10 May. Copulation was then observed almost daily until 20 May, after which no more activity clearly assignable to this type of behavior was noted.

A complete sexual sequence contains the following steps:

(1) A territorial male approaches from behind a female living on his territory. He approaches with a crawling gait, following the depressions in the ground.

(2) Male's nose contacts the female's rump about 2 centimeters above the base of her tail. Up to this point the female appears to ignore the male, despite the fact that he may step on her tail.

(3) Upon contact of the male's nose, the female spins abruptly around through 180 degrees with a short hop and faces the male. The male recoils at the same instant to a position about 30 centimeters away and faces the female. The pair remains in these respective positions for about 30 seconds. The female then turns around to her original position and moves ahead for 2 to 3 meters.

(4) Steps (1), (2), and (3) may be repeated from five to twenty times, the pair moving in a roughly circular path with a radius of about 15 meters. Occasionally, the female may enter a conveniently located burrow. The male then also enters the burrow. Within a few seconds the female reappears, followed by the male. About every fifth to tenth time that these steps are repeated the male may extend his head forward while the female still faces him, touch noses with the female, rotate his head 90 degrees from vertical and lock his incisors behind hers. Within a few seconds the female breaks from him, turns around, and moves ahead as before.

(5) The male approaches the female from behind as before, but just before his nose touches her rump, he alters his course slightly and rubs along her side, moving on past her by about 6 inches. At this point he turns 90 degrees directly in front of the female and moves toward her with a side-stepping gait. Before the male contacts

the female, she turns 90 degrees so as to face in the same direction as the male, then moves ahead about 2 meters. In the interval between the female's turning and moving, the male continues his side-stepping motion and at times may run into her, almost knocking her over. Step (5) may be repeated about eight times, the pair moving in a rough square about 2 meters on a side.

(6) As the female begins to move forward in the sequence described in step (5), the male gives a short leap forward at about a 45 degree angle, sliding up over the female's rump and onto her back. The female tries to scramble forward, but the male clasps her with his forefeet just behind her shoulders and by the nape of the neck with his teeth. The male vibrates his hind quarters for 3 to 4 seconds and releases the female, who scrambles forward about 2 meters. In two instances the male repeated steps (5) and (6).

(7) The male then raises to a low sitting position and begins licking his ventral and pelvic surfaces. The female begins doing the same to herself. After a few minutes of this grooming behavior, the pair begins to dig roots and slowly wanders apart.

The beginning steps of this sequence are often observed, but in most instances the participants fail to complete the behavior pattern and shift to other types of behavior.

Vocalizations

The squirrels of the study area are capable of rendering a wide variety of vocalizations. Fitch (1948) pointed out that noises made by Citellus beecheyi in his California study were not primarily information bearing "words" but were more a mirror of the squirrel's level of anxiety. Since levels of anxiety are similar from time to time, and from individual to individual when the same stimuli are perceived, the sounds do have some specificity for particular stimuli and therefore seem to function ecologically as announcements of the existence of specific events when the number of categories is small. The fact individuals issue the vocalizations in the absence of other squirrels shows a lack of communicative motive and therefore moves the vocalizations outside the classification of language (Hockett, 1960). It is possible for the human observer to learn the vocalizations and to identify the stimuli. To a limited extent, it is possible to elicit

predictable responses from squirrels by imitation of certain sounds. The main limiting factor in the latter seems to be the human's inability to produce the sounds faithfully.

Within the limits given, the sounds heard on the study area were divisible into three groups on an ecologic basis: alarm calls, fright calls, and belligerence calls. The spellings given below are, unfortunately, only gross approximations of the sounds, since the latter contain metallic clicks and chirps which cannot be indicated in the English language.

Alarm Calls

The noises most commonly heard on the study area are those issued by the squirrels when they see something unusual in their area, "think" they see something, or hear the vocalizations of another squirrel. The lowest intensity of these is the "Chick-chick" call. It would seem that the Eskimo language noun Sik-rik (= squirrel) derives from this call. The "Chick-chick" call appeared to be the only call rendered in the apparent absence of external stimuli. Squirrels observed using paths through tussock areas issued this call when they were more than 20 or 30 feet from their normal habitat type, even though no danger was evident. The call is commonly issued when a moving object is seen in the distance. It was used when a fox was seen moving at a distance of 900 to 2,000 feet. The human observer when moving elicited the call when at a similar distance, but when the observer was lying motionless on the ground, this call was used at distances as short as 200 feet. When a squirrel suddenly observed another squirrel at a range of about 200 feet, often the "Chick-chick" call was issued. In these cases the vocalizing squirrel apparently had not recognized the other as a squirrel, and in all instances, the calling was abandoned after the other squirrel moved.

The second intensity level of alarm is the "Cheek-cheek" call. This noise is longer, louder, and more metallic in quality than the "Chick-chick" call and is generally released by a moving object between 100 and 900 feet away. The observer lying still at ranges closer than 100 feet elicited this call.

The third intensity level of alarm is the "Cheek-chick-chick" or "Cheek-chick-chick-chick" call. No difference in stimulus could be detected between the two forms in the field, though some may exist. This call is elicited when a moving object approaches to within 20 to 50 feet of a squirrel after the squirrel has run to the burrow entrance, and just before it enters the burrow. Often it can be heard after the squirrel has entered its burrow, though usually in this situation one of the belligerence calls is given.

The alarm calls fit together into a series which serves, ecologically, as an alarm or warning system. The over-all functioning of the alarm system was observed on the study area whenever the fox moved about the area. It was also used in relation to the observer, but its functioning was more difficult to observe fully at such times, for the observer was necessarily in a single orientation to the progression of alarms. The reaction to the fox was similar on each occasion throughout the season that the fox was observed moving on the study area, in spite of the fox's continued presence in the area. The events of 11 July 1961 will serve as an example:

The adult female Red Fox was seen crossing a wet meadow and approaching the study area at a steady trot. When the fox was about 1,000 feet from the north boundary, a series of "Chick-chick" calls were issued by squirrels along that boundary. Four calling squirrels could be seen, but the calls came from a greater number. Squirrels in the vicinity of Territories 8, 13, and 6 ceased all former activity and assumed various standing postures. Squirrels in the vicinity of Territories 7, 8, 12, and 13 directed their attention in the direction of the fox, but those on Territory 6 directed their attention toward the squirrels on Territory 13. When the fox was 700 feet from the boundary of the study area, a quick series of "Cheek-cheek" calls was issued by the squirrels on Territories 7 and 12 and was quickly echoed by the squirrels on Territories 6, 8, and 13. The squirrels of these five territories began running for their burrows, where they station themselves on prominences near burrow entrances and continued issuing "Cheek-cheek" calls. A few scattered "Chick-chick" calls were heard from the vicinities of Territories 4, 5, and 11, and the squirrels of Territories 1, 2, 9, and 10 assumed alert postures. Territory 3

could not be seen by the observer, who was located on the ridge of Ogotoruk Hill between Territories 10 and 11. The attention of squirrels of Territories 1, 2, 9, 10, and 11 was directed toward the observer, whose position they knew from his movement through their area about 1 hour before. Their alarm calling from that disturbance had only died down about 20 minutes previously. As the fox arrived at the more northern burrow systems of the study area, the first few "Cheek-chick-chick" calls were heard, issued by squirrels as they entered their burrows as the fox passed them within 30 feet. As each "Cheek-chick-chick" call was issued, it initiated a synchronized wave of "Cheek-cheek" calls from squirrels over all the other territories. This performance was repeated again and again as the fox passed between Territories 7 and 12, across Territory 13, and stopped at her den between Territory 8 and the creek. Squirrels were seen to reappear above ground about 100 feet behind the fox and add their voices to the "Cheek-cheek" calls. When the fox stopped at her den and gave the dead squirrels she was carrying to her young, no more "Cheek-chick-chick" calls were heard and the "Cheek-cheek" calls lost their partial synchrony, which apparently had been imposed by the higher intensity call. The "Cheek-cheek" calls continued in a random pattern as long as the foxes were active near their den (15 minutes), but when the last fox finally lay down, there was a sudden change to the "Chick-chick" call. Within 4 minutes the squirrels on all territories except Territories 4, 6, 8, and 13 became silent and resumed other types of behavior. After the fox had not moved for 15 minutes, the squirrels of these latter four territories also became silent.

As can be seen from the above, a human observer can, without seeing the cause of the disturbance, determine its position, whether it is lying, standing, or traveling, and its rate of progress across the terrain. Probably the squirrels can also obtain at least this much information. Linsdale (1946) studied the alarm system of Citellus beecheyi and isolated separate calls issued in the presence of snakes, surface moving predators, and flying predators. The squirrels in the present study did not come in contact with snakes and were seen to ignore the many large birds flying over the study area. Birds on the ground elicited the same response as did the fox.

Fright Calls

Fright calls are high-pitched, nonmetallic, short squeals issued one, two, or rarely three in a series. No differential stimuli for the three forms could be determined; all are issued in the face of suddenly appearing danger, or supposed danger, or a sudden change in an already dangerous situation. The sound was most commonly observed when a squirrel was dumped out of a trap onto the ground or when it suddenly saw the observer lying less than 2 feet away in the shrubs of its burrow mound. On several occasions the squeal was heard when a squirrel was ambushed at its burrow by a fox and was given as the fox started its spring. It was impossible for the observer to surprise squirrels active above ground on the study area because of the aforementioned alarm system; but in other areas, where solitary squirrels existed, it was possible to approach unseen to distances of 10 feet or so when the squirrels were feeding in snow-bed depressions. In this situation a single squeal was issued as the squirrel bolted toward its burrow.

A squeal issued by a squirrel ambushed by a fox elicited the "Cheek-chick-chick" call from squirrels as far as 300 feet away, and, on one occasion, it set off a wave of "Cheek-cheek" calls beyond this. The squirrels issuing the "Cheek-chick-chick" call bolted for their burrows and entered them without hesitation, but they soon reappeared and joined the normal pattern of alarm which had developed toward the further movements of the fox. The squeal could be considered an element of the alarm system denoting ambush.

Belligerence Calls

Actually, it is not possible to separate attitudes of belligerence and fright in squirrels; however, for the present consideration, any sounds produced by squirrels fighting or held at bay by another species will be called belligerence calls. At such times the animals emit a strong musk odor, and their anal glands are excited. (In Citellus richardsoni the musk has been traced to these anal glands [Sleggs, 1926].) Most observations of such sounds were made on trapped animals approached by a human observer. These sounds are mostly low in volume and pitch and so are not amenable to observation at the great distances normally required to avoid disturbing the squirrels.

The lowest intensity level sound of this category observed was that produced by rattling of the molars. The incisors were generally exposed when the sound was made and they were not apparently involved. Molar rattling was usually sustained for 15 to 30 seconds at a time and sounded much like chattering in humans.

Growling was probably the next intensity level and resembled the low, humming growl of a dog, except that it was at times accompanied by a rattle produced deep in the throat, probably caused by saliva.

Growling often gave way to hissing as the trapped squirrel was more closely approached. This sound was produced with the mouth held widely open.

The familiar "scolding" call of other squirrels was heard often in the Arctic Ground Squirrel, but it was difficult to place in an intensity hierarchy with the other belligerence calls. It took a variety of forms, all composed of the base syllable "Cha" or "Ka" repeated in rapid sequence 5 to about 15 times. The repetition is usually too rapid to be counted. The sound was heard from burrows into which squirrels had been driven and from semi-tame squirrels living in the camp site at times when they were being teased by humans. It was almost always issued by trapped squirrels when the observer approached the trap. It seems that this call covers a wide range of anxieties and, the higher the level of disturbance, the more syllables are included.

HUMAN UTILIZATION OF SQUIRRELS

The Eskimo people of the northwestern Alaska coast commonly capture squirrels for use in the manufacture of clothing and, at times, for food for themselves and their dogs. At Point Hope, squirrel hunting is largely the work of women and children. The women use small steel-jaw traps which are checked at least daily; and the children use stones, sticks, hands, and rifles. Most of the squirrels are caught near the village or near seasonal camps.

The squirrels are skinned by cutting around the mouth and skinning caudally over the body, ending at the tail; the result is a bag-shaped skin which is dried without stretching until it is still just pliable. It is then kneaded with the hands until soft, soaked in water, and again dried until just pliable. This process is repeated several times until the skin is judged sufficiently soft. The skin is then slit into dorsoventral halves by cutting from the corners of the mouth, along the sides, to the tail. The top of the head is cut off. When 50 to 70 squirrels have been thus processed, all the backs are sewn together to make the back and sleeves of a parka. The ventral parts of the skins are used to make front and gussets, and the heads are used to make the hood. Squirrel parkas are commonly seen around the villages; they have a market value of something over \$200.00.

A family of Eskimos living near the mouth of Kissimilouk Creek trapped ground squirrels for pelts during the spring of 1961. They used the meat as food for themselves and their dogs during the period between the emigration of the caribou in April and the appearance of seal and whale in June. The dressed carcasses were placed in a vessel of water and boiled for several hours until the meat fell from the bones. Both meat and broth were consumed.

Although squirrel skins can be traded at the village stores at the rate of \$.45 per skin, few are so traded. Most are used to manufacture parkas by the extended family group which catches them, or are traded around the village privately.

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1962 ADDENDUM

Following the completion of the foregoing report, I returned to the study area at Ogotoruk Creek and made field observations on the ground squirrels from 19 April through 24 May 1962. Information from this period is covered in this addendum.

During the spring of 1962, sub-freezing temperatures and snow conditions prevailed about 20 days longer than during the spring of 1961. Mr. Kaye Everett of The Ohio State University and the Holmes and Narver Inc. winter caretakers had been watching for active squirrels prior to my arrival at the field site and reported seeing none until the day of my arrival, 19 April. Table A-1 shows the number of squirrels observed each day between 19 April and 24 May. From this it can be seen that, although the initial emergence of squirrels in 1962 corresponds well with their initial emergence in 1961, general surface activity was severely limited during 1962 until after 21 May, the date that general melting conditions commenced. During 1961 a substantial amount of surface activity was observed after 1 May, the date of commencement of general melting conditions for that year.

General Behavior

Between 19 April and 20 May the movements of squirrels was hampered by unseasonably deep, soft snow. The few animals observed above ground were not seen to wander far from their points of emergence and therefore social contacts were rare. After the appearance of females on 4 May, pre-copulatory sexual behavior was observed in situations where a male and female had emerged from the separate complexes of a single burrow system and therefore did not have to travel significant distances across snow to come into contact with each other. Most of the individuals were, when active, solitary, and food gathering in the near vicinity of their burrows was the only type of behavior observed. Harvesting of Dryas roots and willow buds was seen, and these two items constituted the entire identifiable portion of the stomach contents of animals collected.

TABLE A-1. Squirrels observed at Chariot Site, Spring 1962.

Date	Number of Squirrels Seen
<u>April</u>	
19	1
20	0
21	0
22	0
23	3
24	0
25	6
26	2
27	0
28	0
29	10
30	0
<u>May</u>	
1	4
2	7
3	0
4	6
5	6
6	0
7	0
8	0
9	4
10	4
11	0
12	9
13	3
14	8
15	0
16	0
17	0
18	0
19	0
20	7
21	57
22	35
23	60
24	23

On 20 May the air temperature rose abruptly and the snow began to melt. By mid-day on 21 May, an estimated 70 per cent of the surface area of the study area was clear of snow, and the squirrels' movements were virtually uninhibited. In place of the relatively orderly evolution of sexual territories which took place in 1961, followed by the breeding period, virtual chaos broke out on the study area. Male squirrels attempted to defend large territories, with which they were unfamiliar, and to simultaneously engage in copulation sequences. Boundary encounters in which the combatants alternately assumed the roles of the defender and the transgressor were observed commonly. No complete copulation sequences were observed; in each instance where this behavior was seen developing, the male was distracted by a transgressing male before actual copulation occurred.

Unfortunately, observations had to be discontinued before the impact of this late melt could be evaluated. On the basis of the relative order with which the squirrels reacted to the 1961 spring, however, it would seem that the conditions encountered during 1962 were the more unusual of the two.