POPULATION REGULATION
AND ANNUAL CYCLES OF ACTIVITY AND DISPERsal
IN THE ARCTIC GROUND SQUIRREL

by
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B.Sc., University of British Columbia, 1974

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in the Department
of
Zoology

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
JULY, 1977
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Abstract

Dispersal has been implicated as one of the potentially important factors of population regulation. Interactive behaviours, particularly aggression, have been suggested as the ultimate cause of dispersal. To determine if social behaviour is related to dispersal and to population regulation, I conducted a study of the population changes and behaviour of two populations of Arctic ground squirrels, *Spermophilus undulatus*, in Kluane National Park, Yukon Territory, Canada.

Within each study site, I established a control area and one experimental area in which resident animals were removed at regular intervals. On one site, I conducted two additional experiments. One involved the provision of an additional food supply and the other, a continuous removal of all adult males.

The annual activity pattern of Arctic ground squirrels in the Kluane region was characterized by a 7-8 month period of hibernation, emergence, establishment of territories, a short breeding period, development and emergence of young, restoration of fat deposits, establishment of fall territories and entry into hibernation. Two peaks of aggressive behaviour, as evidenced by interaction rates and wounding occurred, both coincident with the establishment of territories.

The number of resident breeding adults changed little during the two and a half years of this study. Some fluctuations in the total population occurred as a result of mature animal and juvenile dispersal and recruitment of young. Four possible sources of in situ loss were investigated; predation, disease,
starvation and dispersal. Loss due to disease or starvation was negligible. Interspecific predation accounted for an estimated 10-15% of the total annual loss. The three measures of dispersal: immigration to removal and control areas and emigration to control areas showed similar seasonal peaks. The correlation between the three measures indicates that dispersal is the major cause of in situ loss.

Mature females dispersed most in May and June. Dispersal of mature females was related to reproductive success. Juvenile male and female dispersal was highest in August. Juvenile male dispersal was related to body size. Larger juvenile males tended to disperse first. A hypothesis is proposed suggesting that body size is related to the initiation of adult : juvenile aggression and the subsequent dispersal of juveniles.

Behavioural comparisons of dispersing and resident animals indicated few differences. Overall, dispersing animals tended to initiate fewer and receive more agonistic behaviours than resident animals. Animals of one class received and initiated most agonistic behaviours with animals of the same age and/or sex. This suggests that aggression among animals of the same class may be an important cause of dispersal, particularly in juveniles. Further, related animals tended to show higher rates of amicable behaviour and lower levels of physical aggression than unrelated animals.

A graphical model of population regulation in Arctic ground squirrels based on behavioural and demographic relationships observed in this study, is proposed.
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I owe much to my supervisor, Dr. C.J. Krebs for his unfailing support, willingness to help, friendship and generous financial support. I am indebted to Drs. C.L. Gass and J.N.M. Smith for their guidance and comments throughout this study. Drs. R. Boonstra and R. Hilborn generously offered their time and expertise to teach me the basics of computer programming. Lastly, I would like to thank the faculty, staff and my fellow students at the Institute of Animal Resource Ecology for their very enjoyable and stimulating company.

During my field seasons in the Yukon, many people made this project possible. National Parks of Canada kindly permitted me to work within Kluane National Park. I owe special thanks to several of their personnel; L. Harbridge, J. MacIntyre and J. Masyck. I am indebted to the Arctic Institute of North America for their financial support and especially to Mr. and Mrs. A. Williams and their family as well as P. Upton for their hospitality and support. Mr. K. Olsen very kindly allowed me to use his cabin for the duration of the study. I cannot thank R. Carlson and B. Wolf enough for their thoughtfulness and friendship. C. Perrin, B. Muller, G. MacIsaac and I. Wingate, all willingly gave up time to help me when needed.

To my parents, Mr. and Mrs. G. Green, I offer a very special thanks for their endless patience, their willingness to help at all times and their continual support and encouragement.

The National Research Council of Canada generously provided me with a graduate scholarship in 1975 and 1976. The Computing
Centre of U.B.C. offered ample computer support. I would especially like to thank the keypunching staff for their service.

Without these people, this study would not have been possible, nor would it have been the very enjoyable and rewarding experience it was. To all I am very thankful.
INTRODUCTION

Dispersal has been implicated as one of the potentially important regulating factors of population numbers (see Krebs and Myers 1974 for a review). The determination of which animals are most likely to disperse and when such dispersal is likely to occur are perhaps two of the major problems of population ecology today. Of the factors which have been suggested as being important to the initiation of dispersal, the results of studies of the relationship between social behaviour and dispersal have been most encouraging (i.e. Barash 1974, Bekoff 1977a, 1977b, and Watson and Moss 1970).

Overall the main purpose of this study was to determine if social behaviour is related to dispersal and if dispersal is a significant factor in population regulation. I chose to study the Arctic ground squirrel, (Spermophilus undulatus plesius), which is commonly found throughout the southern region of the Yukon Territory, Canada. The Arctic ground squirrel displays a variety of social behaviours and is relatively easy to observe. In addition they occur in large numbers and are easily enough trapped to obtain sufficient demographic information.

Little quantitative information concerning the ecology of the Arctic ground squirrel is available at present. Carl (1971) presented a detailed but primarily qualitative description of the population ecology of Arctic ground squirrels in the region of Pt. Barrow, Alaska. Based on his observations over a two year period, he discussed the occurrence of behavioural changes in different age and sex classes during the active period of the
year and attributed increases in dispersal in certain age groups, particularly juveniles, to these behavioural changes. He concluded that both intrinsic and extrinsic factors were important to the regulation of population size in Arctic ground squirrels.

Based on proposals set forth in Carl's work, I planned a study of the changes in the demography and behaviour of two populations of Arctic ground squirrels. In particular I considered the following questions:

1. Do Arctic ground squirrel populations remain relatively constant from year to year? If so, how is this accomplished?
2. Do different groups of animals tend to disperse at different times of the year?
3. Which animals are most likely to disperse (i.e. morphological or behavioural attributes) during these peaks?
4. Do changes in amicable and agonistic behaviours occur and are these changes in social behaviour related to dispersal?
5. If social behaviour is important, which group of animals is most likely to influence the dispersal of animals of different ages?
6. Which types of behaviour between different age groups are most important to the initiation of dispersal?

During the term of this study, information concerning the annual cycles of activity, reproduction and growth of Arctic ground squirrels was also obtained. I will present some of this data and discuss it in relation to patterns of dispersal and social behaviour.
MATERIALS AND METHODS

Populations of Arctic ground squirrels were studied in the Slims River Valley, in Kluane National Park, southwestern Yukon Territory (Fig.1) over a two and a half year period from April 1975 to June 1977. Field research in 1975 began on April 25 and ended September 28. In 1976 work began April 9 and ended October 13. In 1977 the field season was short (April 15 – May 29) as the main interest was to collect information on over-winter survival and the spring breeding period.

Squirrels were studied in two main areas. The first, the Slims River Area (elevation 800m), was located on dry open hillsides largely dominated by *Artemesia frigida*, *Carex sp.*, *Agropyron yukonense* and *Penstemon gormani*. White spruce (*Picea glauca*) forests border the area on three sides while cliffs falling to a sedge marsh of the Slims River Delta form the boundary on the remaining side. The north-eastern portion of the area was designated as the control area (to be referred to as SRC) whereas the south-western area was used as the experimental removal area (SRR) (Fig.2). The SRC comprised an area of 18.3 ha, the SRR an area of 10.6 ha.

The second study site was situated on a sub-alpine plateau (elevation 1525m) referred to locally as Coin Creek tundra, approximately 9 km west-north-west of the first area (Fig.3). The main study area was made up of a mosaic of south-facing hillsides dominated by *Artemesia frigida* and distinct areas of
Figure 1: Location of the Slims River Valley, Kluane region, Yukon Territory.
Figure 2: Location of SRC and SRR within the Slums River area.
Figure 3: Location of CCC, CCR, CCF, and CCMR on Coin Creek plateau.
shrubs consisting mainly of \textit{Salix} sp., \textit{Betula} glandulosa and \textit{Potentilla} fruiticosa. The area was broken up into four study areas, separated from each other by at least 150m. The 4.5 ha control area (to be referred to as CCC) was situated in the north eastern corner of the area. The 3.7 ha removal area (CCR) was in the southwestern corner. A second experimental area (2.8 ha) in which feeding stations were maintained (CCF) was located mid-way between the control and the removal areas. Finally a small area (CCMR) (2.5 ha) located below the road, southwest of the feeding area, was used as an adult male removal area.

Detailed descriptions of the vegetation of the general area are given by Douglas (1974) and Hoefs (1976). The geology of the area has been summarized by Muller (1967). Bostock (1948) has described the physiography of the Kluane region.

The climate of the Kluane region is continental, the mean annual temperature being -4°C. The region lies in the rain shadow of the St. Elias Mountains and so is quite dry (the average annual precipitation rarely exceeds 25 cm) (Taylor-Barge 1969). During the three years of the study, melt-off usually occurred in late April to early May and all areas remained snow-free until mid- to late September although snowfalls did occur in most months except July. Weather information for the Slims River area and the Coin Creek area is available from Environment Canada (Whitehorse).
Trapping Techniques

At the beginning of a trapping season, I searched each area at least every other day for indirect signs of squirrel activity such as tracks, digging in the snow and digging on burrow mounds as well as actual sightings of squirrels. Once squirrels were seen, I observed and trapped the area for at least three days before beginning the regular biweekly schedule of trapping. In this way I obtained an accurate assessment of emergence in 1976 and 1977.

I trapped all study areas for two days every two weeks except the two removal areas which I trapped for three days every two weeks in 1975. National live traps (15cm x 15cm x 48cm - single door collapsible model) were set at sunrise each day of trapping and baited with a slice of apple and peanut butter. After three to four hours, all traps were checked then closed. On the last day, traps were removed and stored nearby. During peak population periods (for example at the time of the emergence of young) a second check was made on the first trapping day. Normally one check each trapping day was sufficient to catch most of the animals known (from behavioural observations) to be in the area. After the first month of trapping and behavioural observations in 1975, permanent trapping stations were established at sites at which capture of known animals was most successful. These were marked with a numbered wooden stake and were used throughout the study.

When first captured each squirrel was tagged in one ear with a monel metal tag (size 1, style 4-1005 National Band and
Tag Co., Newport, Kentucky). Each animal was also colour tagged so that it could be identified during behavioural observations. Two coloured pieces of plastic (Dymo Label Tape 1/4" size), one 2 cm long, the other 1 cm long, were attached to the other ear by means of the same type of metal tag (Fig. 4) such that the short piece overlapped the long piece. Thus both colours were visible. To further prevent mis-identification, each animal was given a black dye mark on part of the body (ie. paws, shoulder, side of the head, etc.) using Nyanzol A dye (Nyanza Dye and Chemical Co., Lawrence, Mass.) (see Melchior and Iwen 1965 for methods) such that no two animals had the same colour tag and dye combination. Lastly each animal was toe clipped to correspond to the last two digits of its tag number.

At each capture, I recorded the location of capture, sex, reproductive condition, weight (g), skull width (zygomatic breadth) (cm) and the number of wounds on the posterior body. If the dye mark had faded the animal was also redyed. The reproductive conditions noted were as follows: for males, testes scrotal or abdominal; for females, breeding (vaginal papillae swollen and pink) or non-breeding (vaginal papillae small and lightly coloured), lactation (small, medium, or large nipple size) and external signs of pregnancy. All animals were released immediately after processing except on the experimental areas during removal periods.
Figure 4: Construction of the coloured ear tag. Each piece of plastic tape was of double thickness and had a 0.3 cm hole punched in one end. A monel metal tag was inserted through the holes and the tag was attached to the ear. The short piece of plastic was positioned over the larger piece such that both were visible when attached to the squirrel's ear.
Behavioural Observation Techniques

I observed squirrels in three of the study areas every two weeks. Animals were initially identified using a spotting scope (Bushnell Spacemaster II (60mm) with 20-40x zoom eye piece). Subsequently the animals were usually observed through 7x35 binoculars.

A different method of recording behaviour was used in the first season than in the second. In the 1975 field season, I only observed animals on SRC and CCC. Each area was observed for 3 days every two weeks. A day's observation involved four 2-hour sessions from 0700-0900, 1000-1200, 1300-1500 and 1600-1800 hours. Each two hour session was divided into twelve 10 minute sampling periods. I observed single animals for 10 minutes as follows: during each 30 second interval I observed the animal for the first 20 seconds and coded the observed behaviour(s) on sheets during the last 10 seconds. If a animal went out of sight for more than two minutes and another animal was in sight, I began observation of the new animal. This is similar to the focal animal sampling scheme described by Altmann (1974). A total of 43 behaviours (based largely on those described by Sheppard and Yoshida 1971) were recognized and classified under 10 major groups of behaviours (Table 1). In the case of interactive behaviours, the tag number of the animal interacting with the animal under observation was also recorded.

The location of an animal during each behaviour was recorded in order to obtain estimates of daily movements. I marked out each observed area in a grid of 30 meter squares.
Table 1: Behavioural groups and individual behaviours recognized during behavioural observations. Interactive behaviours are based on the classifications of Sheppard and Yoshida (1971). Vocalizations were noted but were not included in the time budgets, as animals were always active in some other behaviour when vocalizing.
<table>
<thead>
<tr>
<th>Category</th>
<th>Behaviours</th>
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<tr>
<td>RECOGNITIVE BEHAVIOUR</td>
<td>nose-nose, nose-body, nose-anus, nose-genital, approach</td>
</tr>
<tr>
<td>COHESIVE BEHAVIOUR</td>
<td>social grooming, rubbing/crawling, crawling under, mounting</td>
</tr>
<tr>
<td>AGONISTIC BEHAVIOUR</td>
<td>threat, arching, warding, sparring, attack/pounce, fight, chase</td>
</tr>
<tr>
<td>AVOIDANCE BEHAVIOUR</td>
<td>avoidance, mutual avoidance, recoiling, submissive posture</td>
</tr>
<tr>
<td>INTERACTIVE</td>
<td></td>
</tr>
<tr>
<td>VOCALIZATIONS</td>
<td>single chatter, double chatter, triple chatter, squeal, growl</td>
</tr>
<tr>
<td>FEEDING BEHAVIOUR</td>
<td>mouth only, paw manipulation, nest gathering, feed search</td>
</tr>
<tr>
<td>POSTURING BEHAVIOUR</td>
<td>sitting, low crouch, high crouch, semi-erect, low erect, high erect, lie</td>
</tr>
<tr>
<td>MAINTENANCE</td>
<td></td>
</tr>
<tr>
<td>GROOMING BEHAVIOUR</td>
<td>licking, paw wash, scratch, dust roll</td>
</tr>
<tr>
<td>MOVEMENT</td>
<td>normal, fast run, hop</td>
</tr>
<tr>
<td>DIGGING</td>
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</table>
Coloured stakes marked the corners of each square. In addition the location of all burrows, runways, trees, shrubs and other readily identifiable objects was mapped on a scale of 1 cm:2.5 m. I recorded the coordinates of each new position of an animal under observation to the nearest meter, using either grid coordinates or specified map locations.

In the 1976 season, I observed animals on CCC and CCR for 2-3 days every two weeks, whereas those on SRC were observed for only one day every two weeks. I used the same four 2-hour periods but each period was divided into two 1-hour sampling intervals. For each hour, I selected a group of 10 animals in a specific order from the animals visible at that time. Choice was based on the extent of previous sightings (animals not yet observed during the biweekly sampling period were given priority to those already observed) and age (young animals were preferentially observed over adult animals). Using an electronic metronome (Wiens et al. 1970) set at a six second interval, I observed each successive animal in the group at each sounding of the metronome, such that each of the 10 animals in the field was observed once every minute. As each individual was observed, I recorded the type of behaviour seen (at the sounding of the metronome), the interactive partner (if applicable) and the location of the animal (if new) on a cassette tape using a portable tape recorder (Phillips 3/60 recorder) with a hand controlled on-off microphone switch. The latter allowed continuous scanning and location of animals while recording the data. The method of behavioural observation used in 1976 is comparable to Altmann's (1974) instantaneous sampling technique.
The focal animal sampling method used in 1975 and the instantaneous sampling method used in 1976 are both capable of collecting data suitable for the calculation of percentage behaviour budgets. The focal animal sampling method allowed me to obtain detailed information on only a small number of animals. Further, active animals tended to be observed more than less active animals. The instantaneous sampling method on the other hand allowed me to observe a wider range of animals at the same time and so sampling times for individual animals were more equal than in the focal animal sampling method. Unfortunately the instantaneous sampling method does not allow for the calculation of interaction rates. The advantage of increased sample sizes was thought to be more important.

**Experimental Areas**

**Removal Areas**

In 1975 a removal scheme similar to the continuous removal experiment of Myers and Krebs (1971) and Krebs et al. (1976) was used. By creating an area of very low animal density it was hoped that any dispersing animal encountering the area would become a resident. Thus it was assumed that new animals whose home ranges were primarily within the boundaries of the removal area were dispersing animals and would be characteristic of dispersing squirrels.

On both CCR and SRR, all animals were tagged, processed and
released when first caught. I removed an animal only when it had been captured in 3 consecutive trapping sessions. For example, an animal captured on all three days of one trapping period was removed on the last trapping day, as was an animal caught twice in one trapping week and on the first trapping day of the next week. This lessened the chances of my accidentally removing a resident animal from a nearby area which may have moved onto the removal area on a single day, while increasing the probability of removing animals resident on the removal area. Animals removed in 1975 were autopsied.

For each animal autopsied I recorded the same information as for a live-trapping capture as well as total length including the tail (fully extended), tail length, the amount of fat deposited in the abdominal mesentery (based on an index where 1=no fat to 5=heavy fat deposits) and internal reproductive condition. Internal reproductive condition was noted as follows: for males, testes weight; for females uterus size (thread-like, normal or enlarged), uterus weight, number of placental scars, number of embryos (if present) and previous breeding condition (nulliparous, primiparous or multiparous). Autopsy information was used mainly to verify external indicators of breeding condition.

In 1976 a pulsed removal scheme rather than a continuous removal scheme was used. This enabled observations of the squirrels coming onto and inhabiting the removal areas over a longer time period. Behavioural observations were completed on CCR only. Animals on both SRR and CCR when caught were tagged, processed and released. Then once every three trapping periods
(six calendar weeks), all animals caught at least once every trapping period were removed. In addition on CCR, any resident animal observed on the area, but not necessarily trapped in each period was also removed. Animals removed were transferred to a small island in the southwestern end of Kluane Lake.

The Feeding Area (CCF)

My trapping and behavioural results from 1975 suggested that juvenile growth and the time at which a juvenile reached adult size were important factors leading to dispersal. To test the predictions of this hypothesis, I attempted to increase juvenile growth by providing additional food. I constructed three feeding stations (Fig. 5) and installed these by three of the main burrow systems within the CCF area. Each was supplied with 9-10 kg of oats a week from May 1 to October 9, 1976 and from April 18 to May 18, 1977. CCF was trapped biweekly throughout the 1976 and 1977 season.

Adult Male Removal Area (CCM)

Several studies have shown that adult male aggression is important in the dispersal of juvenile animals (Armitage 1974, Barash 1975, Donaldson 1977). My results from the 1975 field season also suggested this in Arctic ground squirrels. To determine if the presence of adult males affected juvenile dispersal, I removed all adult males caught in two successive trapping periods on the area. If adult male aggression is
Figure 5: Construction of the feeding stations. Five gallon plastic pails with tops were used for the outer casing. Three openings, 8 cm in diameter, were cut about 16 cm from the bottom of the pails. The pails were then inserted into the ground up to the bottom of the openings. A funnel, constructed from the top of a metal 5-gallon drum, was inserted in the top of the pail. Oats were then placed in the funnel and allowed to feed out into the chamber below.
important to the initiation of juvenile dispersal, one would expect more juveniles to remain on the area than on the nearby control area. Success of this experiment was limited because of the very poor production of young in that area. Animals were trapped biweekly from May 3 to October 9, 1976.

Age Classification

Throughout the remainder of the Results and Discussion, I will use the terms adult, yearling and juvenile animals only for animals of known history. Adults are animals greater than 2 years of age. Yearlings are animals in their second spring and summer. The term mature animals will be used to refer to the combined adult and yearling age classes and will be used primarily where there is some doubt as to the actual age of some animals. Juveniles are animals born that year. On all trapping areas I recognized four major classes of animals; mature males, mature females, juvenile males and juvenile females.

Statistical Analyses

I tested the significance of comparisons of two data sets using a Student's t-test, which is suitable for samples sizes smaller than 50 (Elliot 1971). Comparisons found to be statistically significant are significant at the 0.05 level of significance. In all other cases when different statistical tests were employed, details are given in the text. The term $X \pm Y$ refers to the 95% confidence limits of $X$. 
RESULTS: PART I

I will present the results in two sections, the first describes important events in the annual cycle of activity and weight gain and the second, the demography and behaviour of the control and experimental populations. A discussion will directly follow both sections of the Results. To conclude the final discussion I will present a graphical model of population regulation in Arctic ground squirrels, incorporating information obtained during this study on activity patterns, demography and social behaviour.

Annual Patterns Of Activity And Weight Gain

The ecology of many of the southern species of ground squirrels has been extensively studied (ie. Fitch 1948, Michener and Michener 1977, Sherman 1976, Slade and Balph 1974). Little information is available on the more northern species, *S. undulatus* and *S. columbianus* however. To understand the demographic mechanisms of a population, one must know something of the basic reproductive, developmental and social biology. Social interactions for example would likely differ between the breeding period and the non-breeding period. Carl (1971) and Mayer (1953) have presented a qualitative review of some of the common events in the annual activity pattern of the Arctic ground squirrel while others (Mitchell 1959, Steiner 1972, Lincoln 1972) have discussed more detailed aspects of the biology of *S. undulatus*. Very limited quantitative information
is available however. I will first present some of the relevant data on activity patterns, reproduction, growth and behaviour obtained in this study and discuss these in terms of their significance to the demography as well as their similarity to other ground squirrel species. A generalized activity pattern and weight gain cycle over a year for mature and juvenile animals on SRC is shown in Fig. 6 (a similar pattern was also observed on CCC).

Emergence

Squirrels began to emerge from hibernation in the third to fourth week of April in the Kluane region. The dates of first emergence on SRC were April 24, April 19 and April 14 in 1975, 1976, and 1977 respectively. On CCC dates of first emergence were April 28 in 1976 and April 18 in 1977. Emergence data for animals on SRC in 1975 are limited due to problems associated with the establishment of trapping and observational areas. No data was obtained for animals on CCC in 1975 as the area was not trapped until June. Mean dates of first emergence for mature, adult, and juvenile, males and females for 1975-1977 are given in Table 2.

Males and females emerged at the same time. Only on CCC in 1977 was there a separation between the emergence dates of adults and yearlings of the same sex. Mature males tended to emerge first, followed by mature females, juvenile males and juvenile females in that order. Animals on the Slims River area began to emerge from hibernation before animals on the Coin
Figure 6: Annual pattern of activity and weight gain on SRC. Average body weights were calculated for each class. 95% confidence limits are indicated. Sample ranges for each class were as follows: mature males 2<N<17, mature females 1<N<22, juvenile males 2<N<9, juvenile females 2<N<10. Means are for 1975-1977 samples. There were no significant differences between years. Emergence, breeding and hibernation entry indicators are for the maximum ranges observed.

- Mature Males
- Mature Females
- Juvenile Males
- Juvenile Females
Table 2: Dates of emergence. The mean date of emergence, range of emergence dates and the number of animals in each sample are shown for mature males and females. Where possible, means, ranges and sample sizes are included for animals of known ages from the mature animal sample. Dates are shown for the spring of 1975, 1976 and 1977.
<table>
<thead>
<tr>
<th>AREA</th>
<th>CLASS</th>
<th>1975</th>
<th>1976</th>
<th>1977</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MEAN DATE</td>
<td>RANGE</td>
<td>MEAN DATE</td>
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<tr>
<td><strong>SLIMS RIVER CONTROL</strong></td>
<td>MATURE MALES</td>
<td>April 26</td>
<td>Apr.24-Apr.28</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>ADULT MALES</td>
<td>---</td>
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<td></td>
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<tr>
<td></td>
<td>YRLNG. MALES</td>
<td>---</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>MAT. FEMALES</td>
<td>April 28</td>
<td>Apr.27-Apr.28</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>AD. FEMALES</td>
<td>---</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>YRLNG. FEMALES</td>
<td>---</td>
<td></td>
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</tr>
<tr>
<td><strong>COIN CREEK CONTROL</strong></td>
<td>MATURE MALES</td>
<td>---</td>
<td></td>
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<tr>
<td></td>
<td>ADULT MALES</td>
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<tr>
<td></td>
<td>YRLNG. MALES</td>
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<tr>
<td></td>
<td>MAT. FEMALES</td>
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<td></td>
<td>AD. FEMALES</td>
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</tr>
<tr>
<td></td>
<td>YRLNG. FEMALES</td>
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</tr>
</tbody>
</table>
Creek area but animals on both areas had similar ranges of emergence dates.

**The Establishment Of Spring Territories**

The establishment of spring territories began shortly after emergence from hibernation and based on measures of wounding and interaction rates for animals on both SRC and CCC, involved relatively high levels of aggression.

Interaction rates (the mean number of interactions per day) for agonistic behaviours were calculated for each biweekly period of behavioural observations (Fig. 7). Behavioural information for the spring period was only available for 1976 on both areas. Similarly, the average number of wounds for each class was calculated for the animals caught in live traps during each biweekly trapping period.

Agonistic interactions reached a peak two to three weeks after first emergence. On SRC, mature male:mature male agonistic interactions were most common shortly after emergence (Fig. 8). On CCC a similar pattern was not evident in 1976 as only one mature male was present during the first two weeks. Mature female:mature female and mature male:mature female agonistic interactions became more common two to five weeks after emergence. Whereas mature male interactions largely involved chases and prolonged fights, mature female interactions were most often brief skirmishes or threats.

Mature males showed the highest number of wounds shortly after emergence (Fig. 9). Wounds varied from small puncture
Figure 7: Biweekly changes in the rate of agonistic interactions. The total number of agonistic interactions observed during each week of observations was divided by the number of animals observed on the area during the same period and was divided by the number of observational days (8 hours/day) for the period to obtain the number of interactions/animal/day.

△ SRC (1976)
● CCC (1976)
Figure 8: Proportion of interactions involving adults of each sex.

- Mature Males:Mature Males
- Mature Males:Mature Female
- Mature Female:Mature female
Figure 9: Seasonal changes in the number of wounds per animal. The mean number of wounds for each class during each trapping period was based on the number of wounds counted on the posterior half of the body. Counts of wounds were not begun until mid-August 1975.

- △ Mature Males
- ○ Mature Females
- ▲ Juvenile Males
- ■ Juvenile Females
wounds to large (1-2cm²) gashes on the rump and flanks. Occasionally wounding was found on the head and neck and in three instances bones were broken or exposed. No animals were known to die as a result of wounding. Mature females on the other hand showed a very low number of wounds during the same period. Mature female wounding was primarily small punctures on the posterior region of the body.

**Breeding**

All mature males caught within the first week after emergence had descended testes and were in breeding condition. By the third week after emergence however, the number of males still in breeding condition decreased and by the fifth week after emergence no scrotal males were captured (Fig. 10).

Most yearling males were scrotal when first captured and were assumed to be capable of breeding. All yearling males on SRC in 1976 and 1977 were scrotal at the time of first capture but none of the yearling males on CCC in 1976 were in breeding condition and in 1977 only 40% of the yearling males were scrotal. All breeding yearling males on CCC emerged at the same time as adult males whereas the non-breeding yearlings did not emerge until the third to fifth week after first emergence. It would appear then, that only the early emerging yearling males are scrotal at emergence.

All mature females showed external signs of breeding (enlarged vaginal papillae) in the spring (Fig. 11). Some females were not in breeding condition when first captured but
Figure 10: Reproductive condition of mature males. The mean percentage of the resident mature male population with scrotal testes in each trapping period during the spring and early summer of 1975-1977 are shown for both control areas. The time axis is based on the number of days after first emergence from hibernation.

△ Mature males SRC
● Mature males CCC
Weeks after first Emergence

% Res. Males
Figure 11: Reproductive condition of mature females. The mean percentage of resident mature females in breeding condition during each trapping period from April to September of 1975-1977 are shown for each area. The time axis is based on the number of weeks from the time of first emergence.

- ▲ mature females SRC
- ◆ mature females CCC
all were breeding at most three weeks later. Some males were still scrotal at this time and so all estrous females should at least have had the opportunity to breed. No copulations were seen during the spring period so I could not estimate the number of females that successfully bred. Four females were found to have vaginal plugs, 3 on April 29 and one on May 5 in 1977. Whitten (1956) used the presence of vaginal plugs in laboratory mice to determine when copulation occurred. All four females were captured the following day and none retained the vaginal plug. This suggests that successful copulations do occur up to at least three weeks after first emergence.

The external indices of female breeding condition used throughout this study appeared to be more closely related to pregnancy and lactation than to the period of estrous (assuming the period of estrous in S. undulatus is similar to the 4-6 hour estrous period of S. beldingi (Sherman 1976)). This was evidenced by the sharp decline in the number of breeding females in the tenth week after first emergence, coincident with the emergence of young on both areas. Similarly a decline in the percentage of females showing medium to large sized mammae also occurred within the same period (Fig. 12).

Although all mature females appeared to be capable of breeding, not all became pregnant or raised litters. Pregnancy was determined on the basis of external signs (visible swelling of the abdomen, deposition of fatty tissue around the base of and enlargement of the mammae, and/or a rapid drop in weight in the third or fourth week of May¹). The proportion of females pregnant was calculated by dividing the number of females
Figure 12: Mature female lactation. Nipple size was classified as small, medium or large. Sample sizes are shown for each weekly period. Time axis is based on the number of weeks from the time of first emergence.

- Small nipple size
- Medium nipple size
- Large nipple size
showing signs of pregnancy by the total number of females present on the area from May 1 to June 12. The number of females successfully raising litters to postweaning was determined by observing and trapping young as they emerged from the burrow and attributing the young to the female that had been actively using that burrow complex for the previous two weeks or more. In no case during the two years of the study did two females occupy a single burrow complex as their main centre of activity during the period of development and weaning of young. I am confident all mother-young associations were correct.

The proportion of females on SRC which became pregnant was .55 (N=24) whereas 0.73 (N=22) of the mature females on CCC became pregnant. An average of 0.40 and 0.55 of the mature females on SRC and CCC successfully raised litters to the post-weaning stage. Female reproductive success for each area and year is summarized in Table 3.

1. Mayer (1953) gave a figure of 25 days for the time of development of young, from birth to emergence from the natal burrow. The probable time of birth and obvious weight loss was calculated by subtracting 25 days from the dates of the emergence of young.

2. These dates were used to span the period from breeding to estimated birth of young. Females not remaining on the area during this period were not included as it was difficult to determine if the animal was pregnant or not, except near the end of pregnancy. Females entering the area and remaining past the time of birth were included.
Table 3: Reproductive success of mature females. Only females which remained on the area for at least four trapping periods in the period from May 1 - July 1 were included. Pregnancy was based on visual signs and/or a rapid change in weight in mid-May. Coin Creek was first trapped in July 1975 and as a result no pregnancy data was obtained that year. Similarly, trapping on both SRC and CCC ended in June 1977 and so data on the number of successful litters was not obtained.
<table>
<thead>
<tr>
<th>AREA</th>
<th>TOTAL #</th>
<th>%PREGNANT</th>
<th>N</th>
<th>% SUCCESSFUL LITTERS</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLIMS RIVER CONTROL</td>
<td></td>
<td></td>
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<tr>
<td>1975</td>
<td>7</td>
<td>85</td>
<td>6</td>
<td>43</td>
<td>3</td>
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<tr>
<td>1976</td>
<td>8</td>
<td>63</td>
<td>5</td>
<td>38</td>
<td>3</td>
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<tr>
<td>1977</td>
<td>9</td>
<td>100</td>
<td>9</td>
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<tr>
<td>COIN CREEK CONTROL</td>
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<tr>
<td>1975</td>
<td>7</td>
<td>-</td>
<td>-</td>
<td>86</td>
<td>6</td>
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<tr>
<td>1976</td>
<td>11</td>
<td>55</td>
<td>6</td>
<td>55</td>
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<tr>
<td>1977</td>
<td>11</td>
<td>91</td>
<td>10</td>
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</tr>
</tbody>
</table>
Litter Size

Placental scar counts and embryo counts were used to estimate the average litter size at birth. Only data from females removed during the initial trap-out of resident animals on the removal areas were included. The mean number of placental scars of females from SRR and CCR were 5.2 and 4.6 respectively. There were no significant differences between areas. Embryo counts were only possible on SRR as females had already given birth when CCR was established. The mean embryo count for SRR was 5.0. This was not significantly different from the placental scar counts for either removal area. The three counts were combined to give an average litter size at birth of \(4.9 \pm 1.6\). Mean litter size at emergence from the natal burrow on SRC and CCC were 3.5 and 3.6 respectively.

Seasonal Sex Ratios

Seasonal sex ratios were based on the minimum number alive for each time period. Spring and late summer sex ratios for mature animals as well as sex ratios for juveniles in the first two weeks after emergence, at one month and at two months after emergence from the natal burrow are given in Table 4.

In all years on SRC the sex ratio of mature animals was 1:1 in the spring (at breeding) and in late summer just prior to hibernation. On CCC the mature sex ratio was skewed towards females in the spring \( (x^2 = 4.00, 1\text{df}) \) and though not significant was also suggested in the fall \( (x^2 = 3.57, 1\text{df}, \text{in 1975 and } x^2 = \)
Table 4: Seasonal sex ratios. Sex ratios are expressed as the proportion of males. Ratios are based on the minimum number alive during the specified periods. Yearling ratios include only animals of known origin. Ratios significantly different from equality are marked with an * (0.05).
<table>
<thead>
<tr>
<th></th>
<th>1975</th>
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<th>1977</th>
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<tr>
<td><strong>SLIMS RIVER</strong></td>
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<tr>
<td><strong>CONTROL</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ADULTS</strong> (mid-May)</td>
<td>Prop. Males 0.56 N 18</td>
<td>Prop. Males 0.31 N 13</td>
<td>Prop. Males 0.47 N 17</td>
</tr>
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<tr>
<td><strong>ADULTS</strong> (mid-August)</td>
<td>Prop. Males 0.44 N 9</td>
<td>Prop. Males 0.33 N 9</td>
<td>-</td>
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<tr>
<td><strong>YEARLINGS</strong> (mid-May)</td>
<td>-</td>
<td>Prop. Males 0.38 N 8</td>
<td>Prop. Males 0.44 N 9</td>
</tr>
<tr>
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<td></td>
<td></td>
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<tr>
<td><strong>YEARLINGS</strong> (mid-August)</td>
<td>-</td>
<td>Prop. Males 0.25 N 4</td>
<td>-</td>
</tr>
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<tr>
<td><strong>JUVENILES</strong> (July)</td>
<td>Prop. Males 0.18* N 11</td>
<td>Prop. Males 0.70 N 10</td>
<td>-</td>
</tr>
<tr>
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<tr>
<td><strong>JUVENILES</strong> (August)</td>
<td>Prop. Males 0.13* N 8</td>
<td>Prop. Males 0.56 N 9</td>
<td>-</td>
</tr>
<tr>
<td></td>
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<tr>
<td><strong>JUVENILES</strong> (September)</td>
<td>Prop. Males 0.60 N 10</td>
<td>Prop. Males 0.57 N 7</td>
<td>-</td>
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<tr>
<td><strong>COIN CREEK</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><strong>CONTROL</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>ADULTS</strong> (mid-May)</td>
<td>-</td>
<td>Prop. Males 0.25* N 16</td>
<td>Prop. Males 0.38 N 21</td>
</tr>
<tr>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>ADULTS</strong> (mid-August)</td>
<td>Prop. Males 0.14* N 7</td>
<td>Prop. Males 0.22 N 9</td>
<td>-</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><strong>YEARLING</strong> (mid-May)</td>
<td>-</td>
<td>Prop. Males 0.38 N 8</td>
<td>Prop. Males 0.50 N 8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>YEARLINGS</strong> (mid-August)</td>
<td>-</td>
<td>Prop. Males 0.25 N 4</td>
<td>-</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>JUVENILES</strong> (July)</td>
<td>Prop. Males 0.46 N 24</td>
<td>Prop. Males 0.50 N 16</td>
<td>-</td>
</tr>
<tr>
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<td></td>
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</tr>
<tr>
<td><strong>JUVENILES</strong> (August)</td>
<td>Prop. Males 0.37 N 19</td>
<td>Prop. Males 0.50 N 12</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>JUVENILES</strong> (September)</td>
<td>Prop. Males 0.40 N 15</td>
<td>Prop. Males 0.50 N 10</td>
<td>-</td>
</tr>
</tbody>
</table>
Juvenile sex ratios were 1:1 at emergence, and at one and two months after emergence, except in 1975 on SRC. There, juvenile females were more abundant than juvenile males only at birth \( (x^2 = 4.46, 1\text{df}) \) and one month after natal emergence \( (x^2 = 4.5, 1\text{df}) \), but by two months after natal emergence the sex ratio was 1:1 \( (x^2 = 0.4, 1\text{df}) \).

The equal juvenile sex ratios but skewed mature sex ratios on CCC suggest that the change between juvenile and mature sex ratios may be due to loss in the late fall, during hibernation and early spring. If so, it should be reflected in the sex ratio of yearling animals the next spring. Unfortunately, the number of known yearling animals surviving to the next spring is low and does not allow statistical comparison. The data suggests that there is no significant change in sex ratio over-winter (Table 4). By late summer there was a trend towards a sex ratio favouring females. I do not feel this implies that the major loss of young males which results in skewed adult sex ratios occurs at this time. Rather young males are gradually lost over a long period (1-1/2 years) at a rate higher than that for young females. The change in sex ratio is not significant as a result, until the end of this period.

**Seasonal Changes In Body Weight**

Two distinct periods of weight change are apparent in Arctic ground squirrels. During the active period of the year, muscle tissue and fat stores depleted during hibernation are
restored. Conversely, in the hibernation period, fat stores are utilized as an energy source and some muscle tissue may also be metabolized (Morrison and Galster 1976). For convenience, weight changes will be discussed in terms of over-winter and active period weight changes.

**Over-winter Weight Loss**

Over-winter weight loss was calculated by subtracting the weight of an animal at first capture after emergence from hibernation, from its weight at last capture prior to hibernation, and was expressed as a percentage of the latter. As animals were trapped at biweekly periods throughout most of the season, animals may have been active up to two weeks after the last capture in the fall. Similarly, animals caught after the day of emergence may have gained weight by the time of first capture. Percentage weight losses presented here represent minimum estimates.

Mature males showed little weight loss over winter (2%-13%) (Table 5). Mature females showed the highest weight loss over winter of any class (22-37%). Juvenile males and females lost similar amounts of weight (7-29% for juvenile males versus 19-32% for juvenile females).

**Patterns of Weight Change During the Active Season**

Mature males (Fig. 6) steadily lost weight during the breeding season. In the third to fourth week after first
Table 5: Percentage over-winter weight loss. The mean percentage weight loss from the time of entry into hibernation until emergence for each class is shown. The number of animals in each class and the 95% confidence limits are also indicated.
<table>
<thead>
<tr>
<th>AREA</th>
<th>MATURE MALES</th>
<th>MATURE FEMALES</th>
<th>JUVENILE MALES</th>
<th>JUVENILE FEMALES</th>
</tr>
</thead>
<tbody>
<tr>
<td>SRC 1975-1976</td>
<td>13% 1</td>
<td>22 ± 19.0 3</td>
<td>7 ± 7 3</td>
<td>22 ± 27 5</td>
</tr>
<tr>
<td>SRC 1976-1977</td>
<td>3% ± 2% 2</td>
<td>32% ± 31 6</td>
<td>12.6 ± 1 3</td>
<td>19.0 ± 21 3</td>
</tr>
<tr>
<td>CCC 1975-1976</td>
<td>-</td>
<td>32 ± 8 6</td>
<td>25 ± 11 3</td>
<td>32 ± 10 4</td>
</tr>
<tr>
<td>CCC 1976-1977</td>
<td>2 ± 3 2</td>
<td>37 ± 8 7</td>
<td>29 ± 20 4</td>
<td>26 ± 3 2</td>
</tr>
</tbody>
</table>

% OVER-WINTER WEIGHT LOSS
emergence (mid-May) mature males began to gain weight and continued to do so throughout the season until the time of entry into hibernation.

Mature females gained weight from the time of emergence to the middle of May. A slight decline in the mean body weight of mature females accompanied the birth of the young and from then until mid-July mature females gained little weight. Limited weight gain during this period was probably due to the energetic costs of weaning the young. In July, just after weaning and the emergence of the young, mature females showed a steady increase in body weight to hibernation. Mature males and females showed similar body weights just prior to hibernation in both areas although the mean body weight of mature males was consistently greater.

Juvenile males were significantly heavier than juvenile females throughout most of the year on both areas. Both juvenile males and juvenile females grew rapidly throughout the active period until hibernation. On SRC, juvenile males entered hibernation at heavier body weights.

Skull breadth was also recorded at each capture as a second index of growth. Mature males and females showed little change in skull breadth over the active season (Fig. 13), indicating skull growth is complete in mature animals. In juvenile males and females, the change in skull breadth over the summer was similar to that for body weight. Body weight and skull breadth of juvenile animals were significantly correlated (Fig. 14).
Figure 13: Patterns of skull growth on SRC. Skull size (zygomatic breadth) was measured for all animals captured during each trapping period. There were no significant differences between years so all samples for each area were combined. Mean values shown are for 1975, 1976 and 1977 combined and 95% confidence limits are indicated. Range of sample sizes for each class are the same as in Figure 6. A similar pattern was also observed on CCC.

- △ Mature Males
- ○ Mature Females
- ▲ Juvenile Males
- ▼ Juvenile Females
Figure 14: Regression of juvenile skull size on juvenile body weight. All regressions were significant (P=0.05). $R^2$ values for each regression analysis were as follows:

- Juvenile males SRC $r^2=0.836$
- Juvenile males CCC $r^2=0.912$
- Juvenile females SRC $r^2=0.752$
- Juvenile females CCC $r^2=0.817$
SRC

Males

CCC

Females

Skull Breadth (cm)

Body Weight (g)
Weight Gain Over The Active Period

Weight gain over the active season was calculated only for animals which remained on the control areas from the time of emergence from hibernation (or in the case of juveniles, from the natal burrow) to the period of hibernation entry for the appropriate class. Maximum weight gain was estimated using the lowest and the highest weights for each animal during the active period. Sample sizes are low in all cases due to the small number of animals in each class remaining on the control areas throughout the active period.

No significant differences in the percentage weight gain over the active period were apparent between years for any age/sex class and samples for 1975 and 1976 were combined. Mature males on SRC gained an average of 43 ± 18% (N=7) of their emergence weight. One mature male remained on CCC the entire season in 1976 (no emergence data for 1975 on CCC) and showed a gain of 64%. Mature females on SRC and CCC respectively gained 46 ± 46% (N=11) and 73 ± 32% (N=7) (1976 only) of their emergence weight. Juvenile males showed an average weight gain of 166 ± 10% (N=2) on SRC and 134 ± 109% (N=10) on CCC, whereas juvenile females gained an average of 94 ± 19% (N=8) and 91 ± 71% (N=12) on SRC and CCC respectively.

Juvenile males gained the most weight during the active period, followed by juvenile females and mature females and males in that order.
Establishment Of Fall Territories

Prior to entry into hibernation, squirrels began to defend small areas around specific burrows, presumably their hibernaculum. Aggressive encounters increased in early August and remained relatively high (Fig. 7). Animals of all classes interacted; adult:adult, adult:juvenile, and juvenile:juvenile interactions were common.

All classes, most noticeably juvenile males, showed increased wounding in mid- to late August (Fig. 9). The majority of the wounds were small puncture wounds indicating that interactions were not as physically aggressive as in the spring.

Entry Into Hibernation

It is difficult to determine when an animal has actually begun hibernation. Animals may disappear through dispersal, death, or entry into hibernation. Indicators such as the restriction of movement to the vicinity of certain burrows (presumably hibernaculum), decreased weight gain, and very short daily periods of activity suggest that an animal is close to entering hibernation. Not all animals disappearing in late summer and early fall and reappearing the following spring displayed these signs, so I cannot use these indicators to define all hibernating animals.

The date of entry into hibernation for each age and sex class was estimated using the date of last capture or last observation of animals which survived the winter and emerged the
following spring. Any animal disappearing during the period of hibernation for its class was assumed to have entered hibernation. This method will include some loss due to mortality, predation or dispersal, as well as entry into hibernation. The number of squirrels immigrating onto the removal and control areas at this time (to be discussed in detail later) was small however, suggesting little dispersal occurred. Similarly, I found little evidence of predation of squirrels (ie. grizzly bear excavations) on the control areas or removal areas during this period. Most animals which disappeared during the calculated periods of hibernation entry were thought to have entered hibernation. As some error may be included due to loss by predation or dispersal, ranges for the dates of entry represent maximum estimates.

Mature females began to enter hibernation before mature males (Table 6). Differences in the range of entry dates were significant only in 1975 and 1976 on CCC. Similarly, juvenile females began to enter hibernation before juvenile males, but ranges of entry dates were overlapping in all areas and years. Adults showed a significant trend towards entering hibernation before juveniles of the same sex. In summary, classes entered hibernation in the order; mature females < (before) mature males < juvenile females < juvenile males, but there was overlap in the ranges of entry dates of all classes.
Table 6: Dates of entry into hibernation. The mean date of entry into hibernation as well as the range of entry dates are shown for each class. Procedures for the calculation of the dates are outlined in the text. Sample sizes are shown for each class.
<table>
<thead>
<tr>
<th>AREA</th>
<th>ADULT MALES</th>
<th>N</th>
<th>JUVENILE MALES</th>
<th>N</th>
<th>ADULT FEMALES</th>
<th>N</th>
<th>JUVENILE FEMALES</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>SRC 1976</td>
<td>Sept.8 ± 20 (Aug.26-Sept.20)</td>
<td>3</td>
<td>Sept.23 ± 18 (Sept.10-06)</td>
<td>6</td>
<td>Aug.14 ± 16 (Aug.12-Sept.9)</td>
<td>6</td>
<td>Sept.10 ± 0 (Sept.10)</td>
<td>2</td>
</tr>
<tr>
<td>CCC 1975</td>
<td>Sept.19 (Sept.19)</td>
<td>1</td>
<td>Sept.19 ± 1 (Sept.18-19)</td>
<td>7</td>
<td>Aug.32 ± 13 (Aug.21-Sept.5)</td>
<td>7</td>
<td>Sept.16 ± 11 (Sept.5-14)</td>
<td>10</td>
</tr>
<tr>
<td>CCC 1976</td>
<td>Sept.22 ± 0 (Sept.22)</td>
<td>2</td>
<td>Sept.16 ± 26 (Sept.7-22)</td>
<td>8</td>
<td>Aug.24 ± 19 (Aug.9-Sept.8)</td>
<td>9</td>
<td>Sept.6 ± 17 (Aug.27-Sept.22)</td>
<td>6</td>
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</tbody>
</table>
DISCUSSION: PART I

The activity pattern of Arctic ground squirrels in the Kluane region was characterized by a long period of hibernation, emergence, establishment of territories, a short breeding period, development and emergence of young, restoration of fat deposits, establishment of fall territories and entry into hibernation. As a result of the sharp contrast in the levels of activity between the summer and winter periods, the factors most affecting the demography of ground squirrel populations during these periods are likely very different.

Hibernation and Emergence

Arctic ground squirrels in the Kluane region hibernated for 7-8 months each year. Mature females tended to hibernate for the longest periods, followed by mature males, juvenile females and juvenile males. Hibernation is thus important in terms of the time period involved yet few field studies of hibernation have been conducted in any species of ground squirrels. Most work to date has involved laboratory studies of physiological cycles during hibernation (Morrison and Galster 1976, Drescher 1967). There is need for a better understanding of the causes and magnitudes of population losses during hibernation.

Emergence from hibernation began in the second or third week of April each year and animals rapidly came into breeding condition. Arctic ground squirrels in this study tended to emerge earliest in the warmest spring and appear earlier at
lower elevations than at higher elevations. Males tended to appear before females, in both adult and yearling classes, and mature animals tended to emerge before yearlings of the same sex. Similar sequences of emergence from hibernation have been noted in *S. undulatus* by Carl (1971) as well as in *S. richardsoni* (Michener 1977), *S. beldingi* (Morton 1975, Sherman 1976), *S. armatus* (Slade and Balph 1974), and *S. columbianus* (Adams 1961).

Despite differences in the time of first emergence, Arctic ground squirrels of different ages and at different elevations rapidly established breeding territories and showed very similar patterns of change in breeding condition. This suggests that the timing of reproduction in Arctic ground squirrels, especially in males may depend on internal rhythms rather than the actual time of emergence.

**Territoriality And Breeding**

The establishment of spring breeding territories involved some aggression in both mature males and females. In this study and Carl's (1971) study, mature males became highly aggressive towards other males. Whereas Carl concluded that mature females passively established breeding territories, females on both my study areas were aggressive and many suffered minor wounding. On the basis of the types of interactions and the degree of wounding however, mature females were not as physically aggressive as mature males. Animals failing to obtain territories are likely forced to disperse. During the breeding
period then, dispersal of mature animals appears to be closely related to social behaviour.

Mature males were most aggressive in the first and second week after emergence, suggesting that competition for territories is most intense then. Once territories were established, boundaries were respected and few territorial disputes occurred. Mature females were aggressive towards other mature males and females throughout the breeding period and in addition became increasingly intolerant of other squirrels towards the time of birth of the young. The increase in mature female aggression during this period may be a means of limiting intraspecific predation of juveniles (Sherman 1976) rather than strictly a continued defence of a breeding territory and burrow.

There appears to be considerable variation among species of ground squirrels in the abilities of yearling animals to breed. In some, both male and female yearlings are capable of breeding (S. undulatus (Carl 1971), S. armatus (Slade and Balph ), S. richardsoni (Dorrance and Keith 1974, Michener 1974, 1977, Sheppard 1972) and S. franklini (Murie 1973). In other species, yearling females are fertile whereas males are not (S. heldingi (Morton and Gallup 1975, Sherman 1976) and in some species no yearlings breed (S. columbianus (Michener 1977)). Most yearling males and all yearling females came into breeding condition. All yearling males on SRC become scrotal but on CCC less than half the yearling males became scrotal. Slade and Balph (1974) found that males that emerged late had small testes and that in some cases, late emerging males were non-scrotal and showed no sexual behaviour. Interestingly, during a 4 year period in which they
experimentally reduced the population on their area, they found that yearling males which had previously not bred (at high densities) became scrotal. This suggests that social pressure may be capable of causing delayed breeding in yearling animals. Male densities were higher on CCC in all years than on SRC and may explain some of the incidences of non-scrotal males. The late-emerging, non-scrotal males may, on the other hand, be a result of testes regression prior to their emergence.

**Female Reproductive Success**

Females on SRC and CCC showed similar reproductive success despite altitudinal and density differences. Estimates of litter size prior to emergence, based on placental scar counts and embryo counts were smaller in Arctic ground squirrels in the Kluane region than those reported by Carl (1971) (4.9 versus 5.9). Dorrance and Keith (1974) found that litter sizes increased in animals given additional food and suggested that differing food qualities and quantities could cause variation in litter size. Quite possibly, food resources could differ in quality and quantity between Carl's study area and mine. Further, the squirrels Carl studied were of a different subspecies than animals in the Kluane region (*S. undulatus parryii* versus *S. undulatus plesius*). Nadler and Hoffman (1977) found these subspecies to be genetically different on the basis of several polymorphic proteins and it is possible they may also differ in their reproductive potential.
Changes In Sex Ratio With Age

Mature sex ratios on CCC were skewed in favour of mature females despite the fact that the juvenile sex ratio was 1:1. Sex ratios were equal however on SRC in both mature and juvenile age classes. Similarly in a number of ground squirrel species, sex ratios are biased in favour of females among the breeding portion of the population (S. armatus (Slade and Balph 1974), S. beldingi (Sherman 1976), S. richardsoni (Dorrance and Keith 1974, Michener and Michener 1971 and Sheppard 1972), even though juvenile sex ratios at birth were equal. In S. franklini (Murie 1973) and M. flaviventris (Armitage 1974) sex ratios were equal in both juvenile and mature age classes. Sex ratios of Arctic ground squirrels in Carl's (1971) study (calculated from the population numbers in his Fig.6) were not significantly different from equality in adult animals. Juvenile numbers were grouped so juvenile sex ratios could not be calculated. Skewed adult sex ratios have been attributed to differential mortality (Dorrance and Keith 1974, Michener 1972, Yeaton 1972), differential dispersal (Quanstrom 1971, Yeaton 1972, Schmutz 1977) and differential over-winter mortality (Clark 1970, Michener 1972, Schmutz 1977). The effects of age and sex specific mortality and dispersal and their effects on the population structure of Arctic ground squirrels will be considered in a following section.
Patterns Of Weight Gain

Most studies of weight gain and loss in ground squirrels have indicated that both adults and juveniles steadily gain weight from the time of emergence to entry into hibernation (S. franklini) (Murie 1973), S. richardsoni (Clark 1970, Michener 1974), S. tridecemlineatus (Hohn and Marshall 1970) and M. flaviventris (Armitage 1976) although in some species a decline in the rate of growth occurred just prior to hibernation. S. Lateralis (Skyrja and Clark 1970) and S. beldingi (Morton 1975, Sherman 1976) as well as S. undulatus in this study were similar in most respects except that mature males tended to lose weight during the breeding season. Following breeding, males rapidly gained weight over the summer period until just prior to entry into hibernation.

Considering the short active season of ground squirrels and the large energetic demands of hibernation, it seems unusual that mature males lose weight during the spring. Morton (1975) found that the weight loss of male S. beldingi during the spring period was largely due to the loss of total body lipids. The simplest explanation then of the observed weight loss might be the lack of sufficient food. Adult females, however, showed no such weight loss in any of the studies during the same period, suggesting that although food may not have been abundant, sufficient food was available to allow some weight gain. Further, I found that despite the addition of 10-12 kg of whole oats per week to the feeding area in the spring of 1977, the two mature males present still lost weight rapidly up until the
fourth week after emergence.

Insufficient food does not appear to be a likely cause of male weight loss during the breeding period. Behavioural observations on both areas during late April and early May of 1976 indicated mature males do not spend as much time feeding as mature females. As male reproductive success in Arctic ground squirrels is largely dependent on the ability of the male to obtain and defend a breeding territory on a colony, perhaps the advantage of successfully maintaining a breeding territory may outweigh the disadvantages of losing weight. This is supported by the gradually increasing amounts of time mature males spent feeding as breeding territories were established. Body size has been found to be related to the ability of male Arctic ground squirrels to obtain and maintain territories (Watton and Keenleyside 1971). Perhaps one of the advantages of larger body size is the ability to endure longer periods of insufficient food intake and so the ability to spend more time defending a breeding territory. Body size may thus be an important factor in male dispersal, particularly during the breeding period.
Section Summary

In conclusion, intraspecific competition is intense during two periods of the year. The first is largely related to breeding success, in that both mature males and females compete for breeding territories. Male breeding success is largely dependent on the acquisition and maintenance of a breeding territory. Loss of weight in mature males during this period is indicative of the energetic costs of obtaining or defending a territory. The quality of mature male territories is most likely related to the number of breeding females within its boundaries. Female breeding success on the other hand may be more dependent on vegetational quality or quantity or the quality of the natal burrow. Much remains to be known of the determinants of mature male and mature female reproductive success.

All yearling females and some yearling males were capable of breeding. Density may affect the ability of juvenile males to breed. Differences in the juvenile and adult sex ratios indicate that male loss from the population is greater than female loss.

Of the factors considered, both body size and social behaviour appear to be important factors to dispersal during the spring and fall competition for burrows. Both these factors will be considered in the following sections.
RESULTS: DEMOGRAPHY

In this section of the Results, I will present information obtained during the schedule of biweekly trapping periods on all control and removal areas as well as the one feeding area. The main purpose of trapping was to obtain estimates of population size as well as to determine which animals were most likely to disperse and if seasonal peaks of dispersal were apparent. These factors as well as the relationship of body size and reproductive condition to dispersal will also be considered.

During the two and half years period of this study I tagged a total of 654 squirrels (171 on all Slims River areas, 391 on all Coin Creek areas and 92 in the peripheral trapping area on Coin Creek). Based on the number of animals of each age group caught during each trapping period, I calculated the minimum number alive for each class. In the following section the minimum number alive will be used in all calculations involving population size. Declines during the period of hibernation in each class are believed largely due to the loss of animals into hibernation. As a result, unless otherwise stated, I will restrict the discussion of results for each class to the period from the time of first emergence to the time of first entry into hibernation.
Population Changes

The number of mature males in each area was low and changed little throughout the season (Fig. 15). The only large decline in mature males was in the spring of 1975 on SRC (from 12 in early May to 4 in June). The number of mature females declined during May and June then remained relatively stable until hibernation. Conspicuous mature female declines occurred on SRC in 1975 and on CCC in 1976.

Juvenile males and females first appeared in late June and reached maximum numbers by mid-July to August. Juvenile males showed a steady decline in number throughout the period from late July to early September although in 1975 the number of juveniles on both SRC and CCC increased slightly in mid-September. On the other hand, the number of juvenile females changed little during July and August.

Survival

Changes in survival rates aid in determining when loss of animals in each class is most likely to occur. Biweekly survival rates were calculated for mature and juvenile males and females. From these, I calculated survival rates for the period from first emergence in the spring (for mature animals) or from first emergence from the natal burrow (for juveniles) until first entry into hibernation. Over-winter survival rates could not be calculated in the same manner because animals were in hibernation. Instead I used the ratio of animals emerging in the
Figure: 15 Seasonal changes in the minimum number alive. The minimum number alive in each class was calculated for each biweekly period. Trapping was not begun on CCC until early July in 1975.

△ Mature males
● Mature females
▲ Juvenile males
■ Juvenile females
Males

Females

Minimum # Alive

1975
1976
1977

1975
1976
1977
spring of those which were presumed to have entered hibernation the previous autumn. As a result I could not determine when during the period of hibernation the greatest loss occurred.

Both mature male and mature female survived well throughout the active period (averages of 0.87 and 0.88 on SRC and 0.85 and 0.83 on CCC for mature males and females respectively) (Fig. 16). Mature male and female biweekly survival showed few fluctuations during the active period except on CCC (Fig. 17). On CCC, mature male survival declined in both years. In 1975 this was largely due to the loss of one of the two resident males. In 1976, male immigration and turn-over was high.

The survival of juvenile males on SRC was lower in both years than on CCC (0.63 vs. 0.80). Juvenile females survived well on both areas (0.83 on SRC and 0.86 on CCC). On all areas, juvenile males consistently showed a decline in biweekly survival in the first two weeks of August. Juvenile females however showed few changes in biweekly survival throughout the summer period.

Mature males survived poorly overwinter (mean survivorship of 0.38 and 0.33 on SRC and CCC) (Fig. 16). Mature females on the other hand survived well (0.73 on SRC and 1.0 on CCC). Juvenile males suffered high mortality over-winter on both areas (survival rates of 0.48 and 0.33 on SRC and CCC) whereas juvenile females survived well on SRC (0.74) but showed poor survival on CCC (0.32).

In general mature males survived poorly over-winter whereas mature females survived well throughout the year. Juvenile males survived moderately well in their first summer but suffered high
Figure 16: Seasonal survival. Seasonal survival rates for each summer period and each hibernation period for male and female, juvenile and mature animals were calculated by methods described in the text. Survival rates for the active period are the means of biweekly survival rates for the season. 95% confidence limits are shown for the summer means only.
A) SRC

B) CCC

Summer '75  Winter '75  Summer '76  Winter '76
Figure 17: Biweekly survival rates. Biweekly survival rates were calculated for mature and juvenile males and females in 1975 and 1976. Trapping was not begun until July on CCC in 1975.

- Mature males
- Mature females
- Juvenile males
- Juvenile females
mortality over-winter. Juvenile female survival was good throughout the summer period and only moderate loss occurred over-winter. Overall, male loss from the colony was higher than female loss.

*Cohort Survival*

Decreases in biweekly survival rates and over-winter survival rates would be buffered by immigration. To determine what effects immigration may have on survival, I considered only the survival of juveniles born on the control area.

The proportion of the male and female cohorts surviving each spring and fall is shown in Fig. 18. Means for the 1975 and 1976 cohorts are given for the first fall and spring (there were no significant differences between years in the proportion of males or females surviving). Survival rates in the second spring and fall are for the 1975 cohort only.

In both areas, males did not survive as well as females. Male survival to the first spring was very low and by the second spring, no males born on the colony in 1975 remained in the population. All males present at that time (with the exception of several mature males of unknown origin that were present on the study areas in 1975) had immigrated onto the areas as juveniles or adults. There were no significant differences between areas in the proportion of males surviving in any one time period.

Female survival was also low throughout their first year of life but survival changed little in the second year. Females on
Figure 18: Cohort survival. The proportion of young born on the area, still resident in each spring and fall was calculated. Means for the two years are indicated for the first fall and the first spring. The range of values for each mean are shown for the two years. Data for the second spring and fall period were available for only the 1975 cohort. (FF = first fall, FS = first spring, SF = second fall, and SS = second spring)
SRC survived better in their first year than did females on CCC but the 1975 cohort suggest that this difference diminishes in the second and subsequent years.

Origins Of Resident Animals

The low rates of survival of juvenile cohorts compared to the overall survival rates for juveniles during the first year of life, indicate that some immigration must occur. This is supported by the composition of each class based on the origins of the resident animals (ie., born on the colony versus immigration). I determined this as follows. For each spring and fall period, I calculated the proportion of animals born on the area and the proportion of immigrants of the total number in each class. As the origin of mature animals caught on the control areas in 1975 was not known, they were included as animals of unknown origin. Only animals residing on the control areas for a minimum of two trapping periods and which were present in one of the last two trapping periods in August were included in the calculation of fall proportions. Similarly, only those animals present in the first three trapping periods after first emergence were included in the spring proportions. No juveniles are shown in the spring period, as surviving young (ie. yearlings) were included in the mature animal category.

On both SRC and CCC similar trends were apparent. The majority of mature males were from non-colony sources (Fig.19). No juvenile males born on SRC were present as mature males. On CCC only a few juvenile males remained as residents on the
Figure 19: Origin of control area residents
The proportion of the animals of unknown, colonial and non-colonial origin were calculated for each spring and fall period. Unknown animals are those animals present on the area when the study was begun. Colonial animals were those animals born on the colony. Non-colonial animals are immigrants.

- Unknown origin
- Colonial origin
- Non-colonial origin
control area. Mature females on the other hand were predominantly females that were born on the control area. Only a very small proportion of resident mature females had emigrated from other areas. Juvenile females were predominantly animals that were born on the area too. In all cases, a larger proportion of juvenile males than juvenile females were immigrants.

On the basis of cohort survival rates and the proportion of animals of the different age and sex classes born off the area, it would appear that males more often move between colonies than females. Larger numbers of males disappeared from the control areas as well as immigrated to the control areas. More females remained on the colony and in many cases survived to breed successfully as adults in the colony of their birth.

Loss From The Control Populations

The loss of animals from each class may be the result of many factors. I was only able to estimate the importance of four of these; predation (inter- and intraspecific), disease, starvation and dispersal. At best, only rough estimates can be made of the first three factors in this study. As the activity levels of ground squirrels differ greatly between the period of hibernation and the period of activity, one might expect mortality factors to also differ between seasons. For this reason, loss will be discussed in terms of the two activity levels each year.
Mortality During Hibernation

During the period of hibernation ground squirrels would be relatively inaccessible to most predators. All aerial predators and most ground predators would be inactive (i.e., grizzly bear), absent from the area (i.e., seasonal migrations of hawks and eagles) or unable to dig through the frozen ground to the hibernacula. Other ground squirrels (Mussacchia 1954) or small carnivores such as weasel may kill hibernating squirrels. In general though, predation would seem to be a minor factor in over-winter loss.

Starvation, as a result of an insufficient store of fat, is probably a major cause of over-winter mortality. Juvenile animals would be more likely unable to store sufficient fat as a result of the short growth period. Juvenile over-winter loss may often be due to starvation as a result. However, there was no indication that animals surviving the winter entered hibernation at larger body weights than animals not surviving. Large body size at hibernation does not ensure survival. Perhaps the quality of the hibernacula (i.e., poor drainage or snow cover or shallow depth) is also important.

Mature animal loss during the winter was higher than during the active period. Although the average life expectancy of Arctic ground squirrels is not known, Sherman (1976) found the average life expectancy of Belding ground squirrels to be 2.1 and 3.4 years for males and females respectively. Animals of at least three years of age were known on each control area. If life expectancies of Arctic and Belding ground squirrels are
similar, over-winter loss of mature animals may be the result of increased susceptibility with age to starvation (as a result of the inability to store sufficient fat), exposure (through a poorer choice of hibernaculum as a result of competition in the fall) or disease (Lechleitner et. al 1968).

During hibernation little loss through predation or dispersal is possible. Most over-winter loss is believed due to starvation or exposure.

Loss During The Active Period

Predation

In the two and a half years of the study, only 4 instances of interspecific predation were observed in the general locale of the study areas. Two kills were attributed to grizzly bear (Ursus arctos horribilis), one to fox (Vulpes vulpes) and one kill to marsh hawk (Circus cyanus). The two kills attributed to grizzly bear occurred on the Coin Creek area in June 1976. The adjoining burrow systems of an adult female and her yearling daughter had been excavated and the nest chambers exposed. The kill by the fox was seen about 0.5 km south of CCC in May 1977. The squirrel kill by a marsh hawk was seen in a white spruce forest on the road leading up to the Coin Creek plateau on September 1, 1976. No predation was noted on the Slims River area.

If I assume that the incidences of predation I observed, to
be typical of that which occurred when I was not present, I can use the ratio of the time I was actively trapping or observing an area, to the estimated maximum total time squirrels were active (12 hours/day), to obtain an estimate of predation. Using this method I obtained an estimate of 9 kills per season for all areas. This does not include predation by grizzly bear.

Grizzly bear hunt and kill ground squirrels by excavating the burrow system. Thus it is relatively easy to obtain some estimate of predation by grizzly by counting excavations. No excavations were ever seen on SRC. On CCC excavations were noted on each area during the study (Table 7). Most diggings occurred in late August to early September with the exception of one in June and one in July of 1976. Some excavations exposed only short segments of the burrow whereas others fully exposed the nest chamber. I assumed that only excavations which exposed the nest chamber were successful. If one attributes a kill of one squirrel to each excavation in which the nest chamber was exposed, a total of 5 and 6 squirrel kills in 1975 and 1976 on CCC were due to grizzly bear. This represents a success rate of about 65% (Carl (1971) estimated a success rate of 56%).

The number of tagged squirrels caught one or more times on all areas trapped on Coin Creek was 143 and 182 in 1975 and 1976. Grizzly predation would represent a loss of about 3% of the population per year. Other predation would account for 5% of the loss. Annual loss of animals on CCC (from one spring to the next) was 64% in 1975-1976 and 67% in 1976-1977. Assuming the annual loss of squirrels was similar on the Coin Creek area in general, predation would account for only 10-15% of the annual
Table 7: Predator sightings on SRC and CCC. The number of sightings of each type of predator during each month of the active period, are shown. Total numbers of sightings of all predators for each year are also indicated.
<table>
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<th>SPECIES</th>
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</tbody>
</table>
loss. This is further evidenced by the fact that the total number of predator sightings per month showed a gradual increase throughout the year (Table 8) yet highly seasonal peaks were observed in the loss of animals of particular age classes. Although predators probably kill some juveniles shortly after emergence, unless they are also highly age and sex specific in the spring and the fall, it seems unlikely that interspecific predation could account for the greater proportion of the seasonal losses observed on the control areas.

Predation on resident animals of established colonies is probably reduced by the system of warning vocalizations. Arctic ground squirrels have several distinct warning vocalizations specific to aerial predators and ground predators (Carl 1971, Melchior 1972). Sightings of various predators in the two areas in 1976 are listed in Table 8 and in all but 2 cases (both grizzly bear approaches), appropriate warning vocalizations were given.

Animals not responding to warning vocalizations or unable to find suitable refuge are presumably more susceptible to predation. Juvenile animals are not well coordinated when they first emerge and do not always respond to warning vocalizations or the presence of predators. On several occasions, when predators were approaching the colony, mothers were seen to chase their young into burrows when young failed to respond to warning vocalizations. In addition in early July, I was able to catch very young animals by simply waiting by the burrow mouth until they emerged. The approach of most predators is rapid and the failure to respond quickly should increase an animal's
Table 8: Number of burrows excavated by grizzly bear. The number of burrows which were excavated by grizzly bear on all areas of Coin Creek plateau are indicated. No excavations were ever found on SRC. The number of excavations in which the nest was exposed are also indicated. I assumed that only excavations exposing the nest resulted in the death of a squirrel. Totals are shown for 1975 and 1976.
<table>
<thead>
<tr>
<th>AREA</th>
<th>TOTAL NO. OF BURROWS EXCAVATED</th>
<th>TOTAL NO. WHERE NEST WAS EXPOSED</th>
</tr>
</thead>
<tbody>
<tr>
<td>CCC</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>CCR</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>CCF</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>CCM</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>TOTAL 1975</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>TOTAL 1976</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>
chances of being taken. Young would probably be more susceptible to predation than older juveniles or mature animals. As a result, I attributed much of the loss of juvenile animals during the first two weeks after natal emergence to predation rather than to dispersal.

Dispersing animals would presumably not be familiar with the terrain and in some cases may not be able to locate or use a burrow as a refuge. Thus they may often be more exposed than animals on the colony. Further, lone dispersing animals may be more susceptible to ambush due to the lack of warning vocalizations. Although anecdotal, the observation of the squirrel kill by the marsh hawk, which occurred at least 0.5 km from the nearest burrow system, is in agreement with this conclusion.

Interspecific predation accounts for only a small fraction of the total in situ loss. Much of this is likely due to the loss of very young animals. I believe however that predation is an important proximate cause of animal loss during dispersal.

Steiner (1974) reported some instances of intraspecific predation, particularly of juveniles near the time of emergence from the natal burrow, in a population of Arctic ground squirrels approximately 60 km east of my areas. Two instances of intraspecific predation may have occurred on my study in 1976. Both were very young animals (one on SRC and one on CCC) and were found in early July just after juveniles had emerged from the natal burrows. Both had large wounds (1.5–2 cm²) on their backs. The young on CCR was dead when found. The young on SRC was wounded when first captured and was infested with insect
larvae. The animal was found dead outside of one of the burrows several days later. When juveniles first emerged, no overt attacks on juvenile squirrels by mature animals were seen. Based on this and the fact that so few young were wounded or found dead, I feel that intraspecific predation is of minor importance in causing the observed decrease in juvenile numbers.

Disease And Predation

No animals caught showed any visible signs of disease, starvation or extreme parasitism. Examination of several intestinal tracts in 1975 revealed no large intestinal parasites. Most individuals carried the flea *Oropsylla idahoensis* but none appeared badly infested. Wounds sometimes became badly infected but all animals which remained on the colony with such wounds recovered, with the exception of the one juvenile already mentioned. The absence of diseased animals or animals showing signs of stress, the low degree of internal or external parasitism and the good recovery of known wounded animals suggest that neither disease, parasitism or starvation are important sources of loss during the active period.
Dispersal

Three methods were used to indicate the timing and extent of dispersal and the type of animals most likely to disperse: immigration to removal areas, immigration to control areas and emigration from control areas. If seasonal peaks of dispersal occur and if the above methods adequately measure dispersal, one should observe peaks in each of the above measures of dispersal during the same period. The magnitude of the peaks would not necessarily be the same however.

On the control areas, I assumed that all untagged animals as well as all tagged animals from other areas were dispersing animals. The only exceptions to this were young born on the area. After the establishment of each control area in 1975, few tagged animals which remained on the control area were not caught the next trapping period. A total of 9 animals missed one trapping period out of a total of 422 first captures in 1975-1977 on SRC and on CCC in 1975-1977, 11 animals missed one trapping period out of a total of 413 first captures. Further all untagged squirrels seen during behavioural observations and which took up residence were caught within one or two trapping periods. I am confident that I was able to trap almost all animals present on the control areas during each trapping period.

The removal areas were used to create an area of suitable habitat of low squirrel density. I assumed that squirrels immigrating to the removal area were representative of dispersing squirrels. On both SRR and CCR the first two trapping
periods in 1975 (during the establishment of the areas) were used to remove all resident animals and so will not be included in the analysis.

Emigration from control areas was perhaps the most difficult of the three measures of dispersal to assess. The disappearance of animals from the control areas could be attributed to predation, disease or dispersal. I believe little in situ loss, particularly the loss of juveniles, is due to predation or mortality. I will assume that animals disappearing from the control areas have dispersed with the understanding that some error is included due to a small number of deaths due to predation and old age.

**Dispersal Of Mature Males**

In both years on SRR few mature males immigrated onto the removal area (Fig. 20). In 1975 a low number of mature males were present despite continuous removal. A similar trend occurred in 1976 except that a slight increase in mature male dispersal was evident in late June. On CCR mature male immigration was low but in both years, increased immigration of mature males was seen in late July and early August. The increased movement of mature males at this time may be related to the establishment of hibernation territories which was occurring at this time on the control areas. Mature male immigration to control areas was low (Fig. 21) as was emigration (Fig. 22), but slight increases in emigration were evident in April and May.
Figure 20: Minimum number alive on the removal areas. The minimum number alive for each trapping period on SRR and CCR is shown for each age class. Animals meeting certain criteria (see Methods) were removed during each trapping period in 1975. Removal periods in 1976 are indicated by arrows. Animals removed during the initial two trapping periods on both areas were not included.

△ Mature males
● Mature females
▲ Juvenile males
■ Juvenile females
Figure 21: Number of immigrants. The number of immigrants to each control area are shown for 1975 and 1976. Juveniles born on the area are not included.

- Mature males
- Mature females
- Juvenile males
- Juvenile females
Figure 22: Number of emigrants. The number of animals disappearing from the control areas are shown for each trapping period. The majority of the animals which disappeared are assumed to have emigrated. Loss during the period of hibernation entry was not included.

- Mature males
- Mature females
- Juvenile males
- Juvenile females
Dispersal Of Mature Females

Adult females showed increased immigration in June on all removal areas. On SRR a prominent peak of mature female immigration was evident in late June, 1975. Similarly, female immigration to CCR remained high throughout June and July in 1976. During the remaining portion of the active period, mature female immigration to removal areas was low.

Few mature females immigrated to the control areas, except on SRC in early June, 1975. Four mature female immigrated onto the control area during the first week of June. This was just prior to the major influx of mature females to the removal area in mid June.

Like mature males, few mature females emigrated. In 1975 on SRC a total of 3 females emigrated in the last week of June, just prior to the large influx of mature females onto the removal areas. Few females emigrated from SRC in 1976 in agreement with the low estimate of dispersal from females immigrating to the removal area. In 1976 on CCC, emigration of mature females from the control area was highest during the peak period of immigration of mature females to CCR.

Dispersal Of Juvenile Males

There was an influx of juveniles males to all removal areas in August of each year. In 1975 on SRR a small increase also occurred in July and was attributed to the emergence of young on adjacent areas. Otherwise, juvenile male immigration to the
removal areas was marked by a single major peak of immigration in August, approximately 6-8 weeks after natal emergence. Similarly, peaks of juvenile male immigration to and emigration from the control areas were apparent in August.

*Dispersal Of Juvenile Females*

Juvenile female immigration onto removal areas in 1975 was higher on both SRR and CCR than juvenile male immigration. The sex ratio of juvenile animals on the control areas were biased in favour of females and so may account for the higher immigration of juvenile females. In 1976, no juvenile females appeared on SRR during the active period. On CCR, in 1976, a high of 6 juvenile females immigrated onto the area in late July versus a high of 12 juvenile males at the same time. Sex ratios were equal on both control areas in 1976.

Immigration and emigration of juvenile females was low on all areas in both years. Slight increases in juvenile female emigration were suggested on CCC in late August.

Overall, in mature females and all juveniles there was a correlation between the time of dispersal as indicated by increases in immigration to removal areas, immigration to control areas and emigration from control areas. It is unlikely that such a correlation would exist unless the changes were due to movement of animals over a wide area during the same period. This supports my hypothesis that loss during these periods is mainly due to dispersal. Seasonal changes in emigration and
immigration to all areas suggest:

i). Mature male dispersal was low throughout the year.
ii). Mature female dispersal increased in late May and June but was low the remainder of the active season.
iii). Juvenile males and females appeared to disperse most in August.

Qualitative Differences And Dispersal

Myers and Krebs (1971) and Krebs et. al (1976) found that dispersing animals tended to differ morphologically (body weights), behaviourally, genetically (on the basis of blood serum proteins) and in some cases reproductively from resident animals. To determine if dispersing Arctic ground squirrels differ from resident squirrels, I compared morphological and behavioural data. Behavioural differences will be considered in a following section.

Morphological Differences

Body weight has been shown to be an important factor in the success of Arctic ground squirrels in obtaining and defending a territory (Watton and Keenleyside 1971). The length of residency was also important. If dispersing animals are the losers of most aggressive interactions and are not successful in obtaining territories as suggested by Carl (1971), one might expect dispersing animals to be of a smaller body size than resident animals.

Two measurements of body weight were obtained for each animal trapped: body weight and skull breadth. To determine if
dispersing animals differ in terms of body size, the body weights and skull breadths of resident animals were compared with those of animals emigrating from the control areas or immigrating to the control or removal areas within the same trapping period.

Analysis of covariance (date of capture as the covariate) was used to compare the body weights and skull breadths of animals immigrating to the removal areas to those of animals of the same class on the control area, within the same trapping period. No significant differences between dispersing and resident animals occurred in any area or year.

Due to the small number of immigrants to each control area or emigrants from each control area, differences between these animals and resident control animals could not be compared using a similar statistical design. Instead, differences were compared using a Sign Test (Siegel 1956). Mean weights and mean skull breadths were calculated for each class within each biweekly trapping period. Dispersing animals were grouped according to whether their weight or skull breadth was larger or smaller than the control area mean for that period. Animals with the same body weight or having the same skull breadth as the control mean were treated as ties and so were not included in either group. Seasonal totals for each of the two classes were calculated and the probability of obtaining that distribution was determined.

Overall, the trend towards differences in the body size of colonial and dispersing animals was not clear in any class except juvenile males. In most cases no differences were
apparent. Further, in only two cases were the significant differences in the direction predicted; that is that dispersing animals were of a smaller body weight and skull breadth than resident animals on the control area in the same time period (mature males on CCR in 1975 and mature females on SRC in 1975). In the remaining cases, where differences in body size were significant, dispersing animals tended to be larger than resident animals (mature females on CCR in 1975 and 1976 and juvenile males in 1976 on SRC and CCC as well as on CCC in 1975).

**Juvenile Dispersal and Larger Body Size**

One of the important assumptions of the comparisons of the body sizes of dispersing and resident animals was that dispersing animals would be competing with animals of the same class. If however, juvenile:mature animal interactions are important in the initiation of juvenile dispersal, juveniles would be much smaller than adults within the same period.

When juveniles first emerged, very few agonistic interactions between juveniles and mature animals were observed. Juveniles at this time tended to interact mostly with other juveniles and their mothers. By mid-August however, juvenile:mature animal interactions became more common. This suggests that up to a certain period in the year, juvenile animals are treated differently from mature animals but at some point are recognized and treated as mature animals by territorial mature squirrels on the colony. Body weight seems a
possible factor in that juvenile animals below a certain size are treated as juveniles but once attaining or surpassing this size, are treated as mature animals. If this is the case, one might expect that juvenile animals that disperse first are those animals that grew fastest, attained a larger "mature body size" earlier and so came into competition with mature animals first.

To determine if increased growth and an earlier attainment of a large body size had any effect on dispersal tendencies, an additional food source was provided to a small group of squirrels on Coin Creek plateau. It was hoped that the addition of food would lead to increased juvenile growth and that changes in juvenile dispersal may result.

Growth curves for juvenile animals on CCF and CCC indicated a period of very rapid growth in July and August (Fig. 23). Juvenile animals on the control area in particular, showed a characteristic decrease in weight gain in the early fall. A Von Bertalanffy growth equation best approximates this type of curve (Ricklefs 1967). Maximum growth rates and regression equations were determined using the method suggested by Ricklefs (1967).

A regression analysis indicated that both juvenile males (P=0.006) and juvenile females (P=0.023) grew more rapidly on CCF than animals on CCC. The slope of the regression line which is proportional to the growth rate indicated that CCF animals grew faster than CCC animals (0.12 and 0.20 for juvenile males and 0.06 and 0.28 for juvenile females on CCC and CCF respectively).

On CCF the major increase in juvenile male emigration occurred in mid-July and by early August, no juvenile males
Figure 23: Juvenile male and female growth. Growth curves are based on biweekly body weights. Mean weights for each sex are indicated by closed circles. Means and 95% confidence limits are shown for juveniles on CCC and CCF.

- Juvenile males
- Juvenile females
remained on the feeding areas (Fig. 24). On CCC the peak was not reached until mid-August (Fig. 15). There appeared to be a clear two-week separation in the initiation of juvenile male emigration on CCF and CCC and a four week separation between the major peaks of emigration. Juvenile female emigration on both areas was minimal and so it is not possible to distinguish seasonal differences.

Weights of juvenile males just prior to emigration were 332 ± 92g (N=8) and 356 ± 195g (N=11) on CCF and CCC respectively. Skull breadths were 3.34 ± 0.24 cm and 3.46 ± 0.42 cm for the two areas. I found no significant differences in the weights or skull breadths of emigrating animals on the feeding area and control area.

In summary, juvenile animals on the feeding area grew faster than juveniles on the control area. Higher weights were attained earlier in the season and in juvenile males, dispersal occurred significantly earlier on the feeding area than on the control area.

Breeding Condition Of Dispersing Mature Animals

To determine if dispersing animals differed from resident control animals in terms of breeding condition, the proportion of scrotal males and breeding females on each removal area was compared to that on the control area. Mature males were only scrotal during the first five weeks after emergence so only this period will be considered. Similarly female reproductive conditions during the period from May 1 to July 1 will be
Figure 24: Number of emigrants from CCF. The number of animals of each class which disappeared and were assumed to have emigrated between trapping periods on CCF are shown. Loss during hibernation was not included.

- Mature males
- Mature females
- Juvenile males
- Juvenile females
considered. Breeding success (pregnancy and production of a litter) was also compared.

On SRC in 1975 and 1976, 100% of the mature males were scrotal whereas only 43% \((N=7)\) of the mature males on SRR in 1975-1976 were scrotal during the breeding period. On CCC in 1976 only 40% of the mature males were scrotal. On CCR, 50% \((N=6)\) of the mature males present were scrotal.

Fewer mature females on SRR were in breeding condition than on SRC (Table 9). Similarly, fewer females had medium or large sized mammae. Forty-seven percent of the mature females on SRR had medium to large sized mammae whereas all females on SRC did. Further, only 17% of the mature females on SRR showed signs of pregnancy whereas 83% of all mature females on SRC did. On Coin Creek plateau, all mature females on CCC and CCR were in breeding condition. More mature females on CCC had large mammae than on CCR but there was little difference between the number of females with medium sized mammae. More mature females on CCC showed external signs of pregnancy however than on CCR.

Dispersing and resident mature males and females showed few difference in the number which came into breeding condition. There were differences however in the breeding success of females. Fewer females on the removal areas showed signs of pregnancy or increased mammae size than on the control areas.

This conclusion was further supported by the data available from the autopsies of females removed from CCR and SRR in 1975. On SRR 7% of the mature females were nulliparous, 36% were primiparous and 57% were multiparous \((N=14)\). On CCR 14% were nulliparous, 57% were primiparous and 29% were multiparous.
Table 9: Reproductive condition of dispersing and resident mature females. The breeding condition and breeding success of mature females on each control and removal area during 1975–1977 are indicated. Percentage values are shown.
<table>
<thead>
<tr>
<th>AREA</th>
<th>% BREEDING</th>
<th>% LARGE LACTATION</th>
<th>% MEDIUM LACTATION</th>
<th>N</th>
<th>% PREGNANT</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLIMS RIVER REMOVAL</td>
<td>76</td>
<td>12</td>
<td>35</td>
<td>17</td>
<td>17</td>
<td>6</td>
</tr>
<tr>
<td>SLIMS RIVER CONTROL</td>
<td>100</td>
<td>39</td>
<td>61</td>
<td>24</td>
<td>83</td>
<td>20</td>
</tr>
<tr>
<td>COIN CREEK REMOVAL</td>
<td>100</td>
<td>12</td>
<td>54</td>
<td>24</td>
<td>24</td>
<td>21</td>
</tr>
<tr>
<td>COIN CREEK CONTROL</td>
<td>100</td>
<td>40</td>
<td>60</td>
<td>29</td>
<td>73</td>
<td>16</td>
</tr>
</tbody>
</table>
(N=7). The low number of nulliparous females in both areas indicates that most dispersing mature females breed. Further, assuming that most primiparous females are yearlings that had bred for the first time that year, the number of primiparous versus multiparous females on SRR suggests that more adult females immigrated to and took up residence on the removal area than did yearling females. On CCB, the opposite trend was apparent. More yearling females successfully immigrated to the removal area than adult females.
Interactive behaviours, particularly aggression, have been suggested as important factors in the initiation of dispersal and population regulation (King 1971, Chitty 1967). Armitage (1975) has also suggested that the lack of aggression and the degree of amicable social contact could be important to the initiation of dispersal of yearling marmots. Both amicable and agonistic interactions are likely related to dispersal. As a result I undertook a schedule of behavioural observations to obtain information on seasonal changes in behavioural budgets and the relative temporal importance of each type of behaviour, as well as to determine if dispersing animals differed behaviourally from non-dispersing animals.

I conducted observations only on the two control areas in 1975 and on the control areas and CCR in 1976. In all years the total number of animals observed per week was small despite a total of 111 hours and 104 hours of observations on SRC and CCC in 1975 and a total of 95, 209 and 98 hours of observations on SRC, CCC and CCR respectively in 1976. Variation due to the classification of behaviour should be minimal as all observations were done by myself during both years.

Behaviour observations were made by focal animal sampling in 1975 and instantaneous sampling in 1976. According to Altmann (1974), the two sampling schemes used give comparable results for percentage behaviour budgets and so can be compared between years. Interaction rates can only be calculated from data obtained with the focal animal sampling technique. The
instantaneous sampling technique is not suitable for the calculation of interaction rates on a true time scale as the interval period between behaviours is not known. Rates of behaviour calculated for 1976 will be used only to give comparable figures for animals within or between areas and are not comparable to rates in 1975.

Although 43 behaviours were recognized during observations on the study populations, the preponderance of some behavioural types and rarity of others made it necessary to combine related behaviours into groups as indicated in Table 1. The percentage of time spent in each type of behaviour was calculated for individual animals using the following formula:

\[
\text{%Time/behaviour} = \frac{\text{total time spent in the behaviours}}{\text{group total time for all behaviours}} \times 100
\]

In 1976 a similar formula was used:

\[
\text{%Time/behaviour} = \frac{\text{total # times a behaviour seen}}{\text{group total # of times for all behaviours}} \times 100
\]

Mean behaviour budgets for each age class were calculated as follows. First, only animals which were observed for 10 minutes or more per day (in 1975) or for 50 instantaneous sampling points per day (in 1976) were included. Animals seen for periods shorter than this tended to have a narrow range of behaviours and were not thought to represent behaviour budgets.

The percentage budgets for the four classes on CCC in 1976 are shown in Fig. 25. Budgets for SRC (1975 and 1976) and CCC (1975) showed similar trends. Generally sample sizes for the
Figure 25: Seasonal changes in behaviour budgets on CCC. For each observational period the mean percent time of the total time for all behaviours was calculated for each behaviour group in mature and juvenile males and females. Values plotted as an X on the x-axis indicate that no observational data for the age group was available in that time period. Similar patterns of change were observed in CCC in 1975 and on SRC in both years.

△ Mature males
● Mature females
▲ Juvenile males
■ Juvenile females
Recognatory

Agonistic

Movement

Burrowing

Percent Total Time

M  J  J  A  S

M  J  J  A  S

18.5
biweekly means of each class were below 5 animals. As a result the variance around the means for each behaviour group in each two week period is great and few differences between areas, years, or classes are significant. Similar trends are apparent on all areas and in some cases years. The consistency of these trends between areas suggests the phenomena are real.

Seasonal Changes In Behaviour Budgets

The most obvious feature of the average behaviour budgets for each age class was that feeding and posturing activity accounted for 80-90% of the total above ground time. In addition, feeding and posturing activity appear to be inversely correlated. Other maintenance behaviours (grooming, movement, and burrowing) accounted for 10-15% of the time whereas interactive behaviours rarely accounted for more than 5% of the total budget. The following trends were common to most control populations each year.

Mature animals fed a greater amount of the time each spring than at other times of the year. The proportion of the total time budget spent feeding decreased gradually until the middle of June when feeding again increased until the time of hibernation. Juvenile animals on all areas except SRC in 1976 spent roughly 40% of their total time engaged in feeding. Like adults, juveniles showed a slight increase in feeding activity towards the early fall period.

Posturing accounted for 45-55% of the active time of mature animals immediately after emergence from hibernation. Posturing
increased until late June and remained relatively unchanged until hibernation. Juveniles showed little change in the proportion of time spent in posturing behaviours except for a slight increase towards the late summer.

Grooming behaviours accounted for only a small percentage of the total time budget (0-7%). The highest grooming rates for mature animals were observed in the spring (May) and may be related to the increased levels of intraspecific wounding at this time. Juveniles showed little grooming activity.

Burrowing activity was rarely observed (maximum of 4% of the total time). Most burrowing activity occurred in the spring immediately following emergence and in late summer prior to hibernation.

Movement accounted for between 1 and 18% of the total active time. During the early spring mature males spent more time moving than at other periods of the year. Mature male movement declined in May but during the summer the time accounted for by movement increased. Mature females showed increased periods of movement in June and July, during the period when the young were just emerging. Similarly juveniles showed increased periods of movement just after emergence from the natal burrow, a low period of movement in July and August and increased movement in the late summer and early fall.

In mature males, amicable behaviours (recognatory and cohesive behaviours) were most common in early May. Mature females spent little time in amicable behaviours during the active season except shortly after the emergence of the young. The increase then was largely due to a high incidence of
mother:young greetings. Juvenile animals showed a similar pattern to that of mature females; low levels of amicable behaviour throughout the active period except shortly after emergence.

Mature males showed increased periods of agonistic behaviour in both the spring and the early fall. Agonistic behaviours accounted for only a small portion of the behaviour budget of mature females. A small increase was evident in late July however. Both juvenile males and females spent relatively high proportions of their time shortly after emergence engaged in agonistic interactions. Most interactions at this time involved play fights. In late August juvenile squirrels showed increased periods of agonistic behaviours which appeared to be associated with competition for hibernacula.

Behaviour Of Dispersing Animals

If behavioural factors are important to the intitiation of dispersal, several questions are of interest. First, do dispersing animals differ from resident animals in terms of their allotment of time to various behavioural types, either before or after dispersal? And secondly do dispersing animals differ from resident animals in terms of the social behaviours they initiate or receive? Differences in the behaviour of dispersing and resident animals can be determined by comparing the behaviour of removal animals to the behaviour of resident animals on the control area.
Behaviour Budgets Of Dispersing Animals

Animals immigrating to the removal areas showed similar seasonal trends of behaviour to control animals except in several instances (Fig. 26).

Juvenile animals on the removal areas showed increased percentages of time feeding in late summer (late August and early September) and less time posturing than animals on the control areas. Burrowing or grooming activities were rare. All classes except juvenile females showed very low levels of both amicable and agonistic behaviours compared to control animals. Juvenile females on the removal and control areas showed similar levels of amicable behaviours. Juvenile females on the removal area also showed a relatively large increase in agonistic interactions in the early fall.

Social Behaviours And Dispersal

Peaks of amicable and agonistic behaviour are evident during the periods of high mature female and juvenile dispersal. Interpretation of the different behavioural types is difficult. Amicable behaviours presumably indicate some strengthening of social ties within the colony perhaps through a clearer determination of social rank. On the other hand, the lack of amicable behaviour and/or increased agonistic attacks by resident animals may lead to a severing of social bonds. If these assumptions are correct and if social behaviours are important (as suggested by Bekoff 1977b) to the initiation of
Figure 26: Seasonal changes in behaviour budgets on CCR. Mean percentage times were calculated as in Fig. 25. Data is for the 1976 season only on CCR.

- △ Mature males
- ○ Mature females
- ▲ Juvenile males
- ■ Juvenile females
dispersal, one would expect dispersing animals to receive more agonistic behaviours and fewer amicable interactions than resident animals. They may also tend to initiate fewer agonistic interactions and tend to avoid other animals more than resident animals (Bekoff 1977).

**Amicable And Agonistic Interaction Rates**

To determine if dispersing animals initiated or received different amounts of amicable or agonistic behaviours, interaction rates for animals observed on SRC and CCC in 1975 and 1976 were calculated for the entire active period using the following equations. Admittedly it would have been preferable to compare dispersing and resident animals on a biweekly basis but due to the low number of interactive sequences seen each observational week, this was not possible.

In 1975 the number of interactions for each animal for the entire active period was determined. Average interaction rates (both for initiating and receiving behaviours) were calculated using the following equation:

\[
\text{# of interactions/hr} = \frac{\text{# interactions seen}}{\text{# minutes observed}} \times 60 \text{ min./hr.}
\]

In 1976 rates were calculated to provide comparable rates for all animals but are not directly comparable to true time rates. Rates in 1976 were calculated according to the following equation:

\[
\text{# inter./hr.} = \frac{\text{# interactions seen}}{\text{# hours observed}}
\]
No clear trends were evident in the rates at which dispersing and resident mature males initiated or received amicable or agonistic behaviours. On SRC dispersing males appeared to initiate and receive fewer amicable or agonistic behaviours whereas on CCC dispersing mature nature males tended to initiate and receive more amicable and agonistic behaviours (Table 10). However none of these trends were statistically significant.

Both mature females on SRC and CCC showed opposing trends in the interactive budgets of resident and dispersing animals. Dispersing females on SRC initiated fewer amicable behaviours than resident females whereas emigrating mature females on CCC initiated more amicable behaviours. Similarly, dispersing females on SRC received significantly less agonistic behaviour than resident females yet on CCC dispersing animals received significantly more agonistic behaviours than residents.

On both SRC and CCC, juvenile males tended to initiate more but receive fewer amicable behaviours than resident juvenile males. Significantly fewer agonistic interactions were initiated by emigrating juvenile males on SRC but on CCC, juvenile males initiated significantly more agonistic behaviours. Dispersing juvenile males on CCC also tended to receive more agonistic behaviours.

Unfortunately no emigrating juvenile females on SRC were observed for periods of sufficient duration for inclusion. On CCC emigrating juvenile females received more and initiated less amicable interactions and initiated fewer and received more agonistic interactions than resident juvenile females.
Table 10: Interactions rates of resident and dispersing animals. Interaction rates were calculated for the initiation (Init.) and receiving (Rec.) of amicable and agonistic behaviours in each class. Mean rates for each class are given and 95% confidence limits are indicated.
<table>
<thead>
<tr>
<th></th>
<th>RESIDENT ANIMALS</th>
<th></th>
<th>DISPERSGING ANIMALS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>AMICABLE INIT.</td>
<td>AMICABLE INIT.</td>
<td>AGONISTIC INIT.</td>
</tr>
<tr>
<td></td>
<td>RECR.</td>
<td>RECR.</td>
<td>RECR.</td>
</tr>
<tr>
<td>SRC 1975</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult Male</td>
<td>1.5</td>
<td>2.6</td>
<td>0.6±0.3</td>
</tr>
<tr>
<td>Adult Female</td>
<td>1.0±2.0</td>
<td>1.6±0.9</td>
<td>0.8</td>
</tr>
<tr>
<td>Juvenile Male</td>
<td>none</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>Juvenile Female</td>
<td>2.9±1.0</td>
<td>0.6±1.1</td>
<td>none</td>
</tr>
<tr>
<td>CCC 1975</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult Male</td>
<td>4.5</td>
<td>4.9</td>
<td>none</td>
</tr>
<tr>
<td>Adult Female</td>
<td>3.9±2.8</td>
<td>5.8±5.5</td>
<td>16.3</td>
</tr>
<tr>
<td>Juvenile Male</td>
<td>13.5±16.4</td>
<td>39.3±50.5</td>
<td>13.2±12.0</td>
</tr>
<tr>
<td>Juvenile Female</td>
<td>11.0±21.0</td>
<td>22.2±27.0</td>
<td>0.0</td>
</tr>
<tr>
<td>SRC 1976</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult Male</td>
<td>0.4±0.2</td>
<td>0.3±0.3</td>
<td>none</td>
</tr>
<tr>
<td>Adult Female</td>
<td>0.3±0.3</td>
<td>0.1±0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Juvenile Male</td>
<td>0.1</td>
<td>0.3</td>
<td>0.2±0.3</td>
</tr>
<tr>
<td>Juvenile Female</td>
<td>0.04</td>
<td>0.2</td>
<td>none</td>
</tr>
<tr>
<td>CCC 1976</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult Male</td>
<td>0.2±0.3</td>
<td>0.3±0.6</td>
<td>0.4±0.6</td>
</tr>
<tr>
<td>Adult Female</td>
<td>0.8±1.3</td>
<td>0.5±1.0</td>
<td>0.3±0.3</td>
</tr>
<tr>
<td>Juvenile Male</td>
<td>1.6±2.2</td>
<td>0.6±1.2</td>
<td>1.0±0.6</td>
</tr>
<tr>
<td>Juvenile Female</td>
<td>0.2±0.6</td>
<td>0.7±0.6</td>
<td>0.0</td>
</tr>
</tbody>
</table>
Few large differences between the rate at which dispersing and resident animals initiate and receive interactive behaviours are apparent. Trends based on the mean interactive rate for amicable and agonistic behaviours, indicated there were no consistent differences between emigrating animals and resident animals in terms of the number of times they initiated or received amicable behaviours. In most cases however, dispersing animals initiated fewer agonistic behaviours (with the exception of juvenile and mature males on CCC) while receiving more agonistic behaviours than resident animals (with the exception of mature males and females on SRC).

Initiators And Recipients Of Agonistic Behaviour

If dispersing animals do differ from resident animals in terms of the amount of agonistic behaviour they initiate and receive, some insight into the causes of dispersal may be gained by knowing which class most often received agonistic behaviours initiated by animals in each of the four classes. I determined this by summing the total number of interactions for resident and dispersing animals of each class. I then calculated the proportion of the total interactions involving recipients from each of the four classes.

Mature males and mature females on SRC were the most common recipients of mature male aggression. On CCC however, mature males interacted most with juvenile males, followed by juvenile and mature females. A comparison of resident males and dispersing males was not possible due to the low number of
interactions involving dispersing mature males (Table 11).

On SRC mature males received most agonistic behaviour initiated by either resident or dispersing mature females. In 1975 on CCC resident mature females more often initiated agonistic interactions involving either juvenile males or females, but in 1976, other mature females were more commonly involved. Dispersing females however interacted more with mature males in 1975 and mature females in 1976.

In both years the numbers of interactions involving juvenile males and females on SRC was too low to estimate recipient proportions. On CCC, both resident and dispersing juvenile males and females most often initiated agonistic interactions with other juvenile males and females. Dispersing juveniles also initiated slightly more agonistic behaviours with mature animals.

With the exception of mature males, resident and dispersing animals of one age class tended to interact most with other animals of the same age and sex class as themselves or with animals of the same age group as themselves (Fig. 27). There were no consistent differences between dispersing and resident animals in terms of interactive partners.

An alternate analysis of this data is from the point of view of the age classes as recipients of interactions initiated by other animals. That is that given that animals of a certain age class received a number of agonistic behaviours, what proportions of the total number of interactions were initiated by animals in each of the four age and sex classes. Results largely agreed with those just discussed. Mature males tended to
Table 11: Recipients of agonistic behaviour. For each class, the proportion of the total number of agonistic initiated by that class towards animals in each of the four classes was calculated. Proportions for each area in each year for all classes are shown. The number of interactions initiated by each class are indicated.
### Proportion of Agonistic Behaviours

<table>
<thead>
<tr>
<th></th>
<th>Resident Animals</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Dispersing Animals</th>
<th></th>
<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>AD.♂ AD.♀ JU.♂ JU.♀ N</td>
<td></td>
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<td></td>
<td></td>
<td>AD.♂ AD.♀ JU.♂ JU.♀ N</td>
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</tr>
<tr>
<td><strong>Adult Males</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRC 1975</td>
<td>0.0 0.7 0.1 0.2 18</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.0 1.0 0.0 0.0 4</td>
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<td></td>
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<tr>
<td>CCC 1975</td>
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<td></td>
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<td></td>
<td>- none -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRC 1976</td>
<td>0.5 0.4 0.1 0.0 19</td>
<td></td>
<td></td>
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<td></td>
<td>- none -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CCC 1976</td>
<td>0.0 0.3 0.0 0.7 3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.0 0.6 0.0 0.4 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Adult Females</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRC 1975</td>
<td>0.6 0.3 0.0 0.1 21</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.0 0.0 0.0 0.0 0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CCC 1975</td>
<td>0.1 0.2 0.4 0.3 87</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.9 0.0 0.0 0.1 7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRC 1976</td>
<td>0.9 0.1 0.0 0.0 16</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.0 0.0 0.0 0.0 1</td>
<td></td>
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</tr>
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<td>CCC 1976</td>
<td>0.1 0.7 0.1 0.1 37</td>
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<td></td>
<td></td>
<td></td>
<td>0.1 0.9 0.0 0.0 7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Juvenile Males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td>- none -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CCC 1975</td>
<td>0.1 0.1 0.7 0.1 317</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.0 0.0 0.7 0.3 186</td>
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<tr>
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<td>0.0 1.0 0.0 0.0 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.0 0.0 0.6 0.4 8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CCC 1976</td>
<td>0.1 0.1 0.5 0.3 17</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.14 0.14 0.14 0.57 7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Juvenile Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRC 1975</td>
<td>0.0 0.0 0.2 0.8 15</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>- none -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CCC 1975</td>
<td>0.02 0.01 0.79 0.19 121</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.28 0.32 0.0 0.4 25</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRC 1976</td>
<td>0.0 0.0 1.0 0.0 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>- none -</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CCC 1976</td>
<td>0.0 0.25 0.42 0.33 12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.0 0.0 0.5 0.5 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 27: Recipients of agonistic interactions. For each class, the proportion of the agonistic interactions initiated towards members of each of the four classes is shown. The length of the arrow directed towards each age class indicates the proportion of the total number of interactions initiated towards that class, except in the case of interactions with animals of the same class. The proportion enclosed in the smaller circle indicates the proportion of interactions with animals of the same class. Dispersing and resident animal proportions are indicated.

----- Dispersing animals

---------- Resident animals
most often be involved in interactions initiated by mature females (Table 12). Resident mature females were usually the recipients of interactions initiated by other mature females and mature males whereas dispersing mature females were most often involved in interactions initiated by mature and juvenile males. Juvenile males and females were commonly the recipients of juvenile male and female aggression whereas dispersing juveniles were most often involved in interactions initiated by juvenile males.

Overall differences between the tendency of dispersing and resident animals to be recipients of agonistic behaviour initiated by animals of a particular age class were not clear. No pattern of interactions was evident among mature animals but in juvenile age classes, agonistic interactions most often involved other juvenile animals (Fig. 28). This suggests that if patterns of agonistic behaviour are important to juvenile dispersal, that juvenile emigration from the colony may be most influenced by agonistic interactions with other juvenile animals, particularly juvenile males.
Table 12: Initiators of agonistic behaviour. For each class the proportion of the total agonistic interactions received from members of the four classes was calculated for the active period. The number of interactions received by each class is indicated.
## PROPORTION OF AGONISTIC BEHAVIOURS

### RESIDENT ANIMALS

<table>
<thead>
<tr>
<th>Age Group</th>
<th>SRC 1975</th>
<th>CCC 1975</th>
<th>SRC 1976</th>
<th>CCC 1976</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult Males</td>
<td>0.0</td>
<td>0.0</td>
<td>0.38</td>
<td>0.0</td>
</tr>
<tr>
<td>Adult Females</td>
<td>0.57</td>
<td>0.24</td>
<td>0.66</td>
<td>0.10</td>
</tr>
<tr>
<td>Juvenile Males</td>
<td>0.11</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Juvenile Females</td>
<td>0.22</td>
<td>0.12</td>
<td>0.0</td>
<td>0.14</td>
</tr>
</tbody>
</table>

### DISPERSING ANIMALS

<table>
<thead>
<tr>
<th>Age Group</th>
<th>SRC 1975</th>
<th>CCC 1975</th>
<th>SRC 1976</th>
<th>CCC 1976</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult Males</td>
<td>- none</td>
<td>- none</td>
<td>- none</td>
<td>- none</td>
</tr>
<tr>
<td>Adult Females</td>
<td>- none</td>
<td>1.0</td>
<td>- none</td>
<td>0.22</td>
</tr>
<tr>
<td>Juvenile Males</td>
<td>- none</td>
<td>0.25</td>
<td>- none</td>
<td>0.0</td>
</tr>
<tr>
<td>Juvenile Females</td>
<td>- none</td>
<td>0.0</td>
<td>- none</td>
<td>0.0</td>
</tr>
</tbody>
</table>
Figure 28: Initiators of agonistic interactions. For each class, the proportion of the agonistic interactions received from members of each of the four classes is shown. The length of the arrow directed towards each age class indicates the proportion of the total number of interactions received from that class, except in the case of interactions with animals of the same class. The proportion enclosed in the smaller circle indicates the proportion of interactions with animals of the same class. Dispersing and resident animal proportions are indicated.

----- Dispersing animals

----- Resident animals
Genetic Relatedness And Rates Of Interactions

During the analysis of amicable and agonistic behaviours it became apparent that in many cases, animals appeared to interact more with animals related to them than with unrelated animals. To determine if this was the case, I estimated the genetic relatedness of each pair of animals involved in an amicable or agonistic interaction. I then calculated separate amicable and agonistic interaction rates for related and unrelated animals during each biweekly observational period. As the genetic relationships of individuals present on the areas when the study was begun in 1975 were not well known, I will restrict the analysis to the 1976 season.

Genetic relatedness, as used in this analysis includes the relationships of brother : sister, mother : young, grandmother : daughter's young and sister : sister's young. The male lineage was not considered as no copulations were seen and hence the probable father of most young was not known. As all mature males on both controls were immigrants or were presumed to be immigrants, I assumed that all mature males were unrelated to the mature females on the colony. Also, several mature females present on each control area in the spring of 1975 still remained on the control areas in the spring of 1977. On the basis of social ties, the close proximity of their breeding burrows to other females and the fact that so few immigrating females became residents, I assumed that these females of unknown origin were in fact related to other females within the same grouping of burrows, even though the exact nature of the
relationship was not known. They were also included in this analysis.

On SRC, rates of amicable behaviours between related and unrelated animals were similar in the early spring (Fig. 29). On CCC however, related adults showed much higher rates of amicable interactions than unrelated adults. Amicable interactions in late April and early May were primarily between adult females or between adult females and mature males. On both areas, almost all amicable behaviours in June were between related adult females. In July, mature:juvenile interactions were largely between related animals as were most juvenile:juvenile interactions. In late August, amicable interactions involving both related and unrelated animals increased.

More agonistic interactions occurred between unrelated mature animals than related animals on both SRC and CCC in late April and early May. These involved mostly mature male: mature female interactions. Related animals (mostly mature female: mature female interactions) showed increased rates of agonistic behaviour in May and June. Increased levels of agonistic behaviours involving related juveniles and adults or related juveniles were common in July and involved mostly play fighting. By August however, levels of physical aggression increased. Agonistic behaviours involved both related and unrelated animals of all classes. These were presumed to be associated with competition for hibernacula. A similar increase in agonistic behaviours between unrelated animals was also evident.

Overall, related animals showed more amicable behaviour than unrelated animals. Agonistic behaviour however was common
Figure 29: Genetic relatedness and interaction rates. For each observational period, the interaction rates for amicable and agonistic behaviours involving related and unrelated animals were calculated. Rates for each period are shown. Shaded areas indicate the proportion of the interactions involving each of the following:

- Mature:mature animals
- Mature:juvenile animals
- Juvenile:juvenile animals
between unrelated and related animals. Unrelated animals were more agonistic in the early spring whereas related animals were more agonistic in May and June. As much of the agonistic behaviour between related animals in July and early August involved play fighting, related animals do not appear to be as physically aggressive as unrelated animals.
DISCUSSION: PART II

In the introduction I outlined a series of questions I felt were important in determining the relationship of dispersal to population regulation and the factors most likely to affect dispersal. I will discuss each of these in terms of information obtained in this and other studies.

Do Arctic Ground Squirrel Populations Remain Constant?

Arctic ground squirrel populations in the Kluane region showed relatively stable numbers of resident adults following the breeding period. Densities of mature males and mature females in early July on SRC were 0.27-0.33/ha and 0.38/ha and on CCC were 0.46-0.93/ha and 1.3-2.0/ha. Large fluctuations in total population size did occur however. These were primarily due to emigration of mature females and some mature males in May and June, the recruitment of juveniles in July and the subsequent dispersal of juveniles in August.

As in this study, the loss of animals, particularly juveniles is common to a number of Sciurids (S. armatus (Balph and Stokes 1963), S. beecheyi (Fitch 1948), S. richardsoni (Michener and Michener 1977, Schmutz 1977, Yeaton 1972), S. tridecemlineatus (McCarley 1966), S. undulatus (Carl 1971), in marmots (M. monax (devos and Gillespie 1960, Bronson 1964), M. flaviventris (Armitage 1974) and M. olympus (Barash 1972)) and in prairie dogs (Cynomys leucurus and Cynomys ludovicianus) (Tileston and Leichleitner 1966). Armitage(1974) and Carl (1971) too have found that the number of resident adults tended to
remain constant between years and that fluctuations in population size were largely due to changes in the recruitment and dispersal of juvenile animals.

In many of these species, juvenile males do not survive as well as juvenile females. It has not been possible to clearly separate loss from the colony due to dispersal from that due to various mortality factors. My data suggest that dispersal is more important than in situ mortality during the active period. During hibernation however, dispersal is highly improbable and most if not all loss in each class is due to mortality factors.

**Loss During Hibernation**

Over-winter survival of Arctic ground squirrels in Kluane was lower in males than in females. Generally adult males survived more poorly than juvenile males and adult females survived better than juvenile females (Fig.16).

Juvenile over-winter survival on SRC and CCC was usually lower or in some cases equal to that of mature animals. Poorer juvenile than adult survival has also been reported in *S. richardsoni* (Michener and Michener 1971, 1977, Sheppard and Swanson 1976) and in *M. flaviventris* (Armitage 1974). Two factors, both related to the energetic cost of hibernation contribute to these differences in survival. Juvenile animals have a shorter growth period than mature animals and so may not be able to develop sufficient fat stores to survive hibernation. Armitage (1974) found that the survival of young marmots and the duration of their first winter was inversely
correlated. This suggests that the "energetic costs" of hibernation in relation to the amount of stored fat may be one of the factors determining over-winter survival. Dorrance and Keith (1974) have in fact found that the body weight of S. richardsoni prior to hibernation was related to the probability of the animal surviving the winter. No such relationship was evident in this study, but admittedly samples for each class were small. Juveniles, particularly juvenile males are more likely to disperse and assuming dispersal is energetically stressful, this too would add to the likelihood of increased over-winter mortality.

The other factor which may influence over-winter survival is exposure. Carl (1971) suggested that juvenile animals are forced to use inferior hibernacula to those used by adults. As a result the energetic costs of hibernation may be increased in juveniles. Similarly Shaw (1926) found that the hibernacula of adult S. columbianus were usually deeper and more complex than those of juveniles.

Although I did not attempt to obtain measures of differences in hibernacula of juvenile and adult animals, the relationship between the density of animals on SRC and CCC and over-winter survival infer that the availability of hibernacula is important. Juveniles on SRC survived as well as adults in most cases. On CCC, juveniles tended to survive more poorly than mature animals. Densities of animals on SRC and CCC in early August (the period of competition for hibernacula) was 0.92 versus 5.8 squirrels/ha in 1975 and 1.03 versus 5.8 squirrels/ha in 1976. If the availability of hibernacula is related to the
total density of animals on an area, suitable hibernacula would be more readily available on SRC than on CCC and so may explain the differences in juvenile and mature animal survival observed.

Over winter survival appears to be largely influenced by factors affecting energetic demands during hibernation as well as those affecting the rate and extent of fat deposition. Studies of hibernation in ground squirrels (Davis 1976, Morrison and Galster 1976, Drescher 1968) have dealt largely with the physiological processes of hibernation. Little is known of the qualitative differences between hibernacula or of the differences in the hibernation physiology of individual animals and their relationship to over-winter survival. We need studies of this nature.

**Loss During The Active Period**

During the active period, predation and dispersal have been suggested as the major causes of loss from the population. Whichever factor is most important, it must be able to explain the seasonal and numerical differences in loss observed in each class.

**Loss Due To Predation**

Predation has been suggested as a major factor in the loss of animals. Luttich et. al (1970) thought that up to 33% of the loss of *S. richardsoni* from their study population could be accounted for by red-tailed hawk (*Buteo jamaicensis* ) predation. Similarly, Craighead and Craighead (1955) considered
S. richardsoni to be highly susceptible to raptor predation. I believe predation is largely an influence on only two groups of animals; very young and dispersing animals.

High susceptibility of juveniles to predation has been suggested as one of the factors contributing to high in situ juvenile mortality (Slade and Balph 1974, Schmutz 1977). Very young Arctic ground squirrels in the Kluane region were thought to be more susceptible to predation than older juveniles as a result of their lack of physical coordination and in some cases, their failure to respond to alarm calls. Armitage (1974) similarly found that young M. flaviventris were more commonly taken by eagles than other age classes. Schmutz (1977) found that juvenile S. richardsoni were killed by hawks more often than adults and that juvenile males were more often killed than juvenile females. Luttich et. al (1970) and Sheppard and Swanson (1976) however, found that the proportion of young killed by predators did not differ from the proportion of young in the population. The role of predation as a factor in early juvenile loss is unclear and continued study is required.

Dispersing animals are also likely more susceptible to predation (Armitage 1974, Carl 1971, Slade and Balph 1974, and Michener 1972). Presumably dispersing animals would be exposed for longer periods and being unfamiliar with the terrain would be unable to reach refuge easily. Further, they would be much less likely to be warned of the approach of a predator than colonial squirrels. Studies on the relationships between dispersal and predation to date have been restricted to laboratory situations. Metzgar (1967) found that mice
(Peromyscus leucopus) which had been allowed to become familiar with an experimental arena, were less likely to be taken by a Screech Owl (Otus asio) than mice that had just been exposed to the experimental arena. Metzgar attributed this to the increased exploratory behaviour of newly exposed mice compared to that of the "resident" mice. Similarly, Snyder (1975) found that active mice were taken more often by red-tailed hawk than inactive (drugged) mice. Both studies suggested that an animal's level of activity influences its chances of being taken by aerial predators.

Assuming the results of these studies are applicable to the field situation, juvenile male ground squirrels, as a result of their greater likelihood of dispersal and so increased exposure, should be more susceptible to aerial predation. Schmutz (1977) in fact found that juvenile male S. richardsoni, which showed larger ranges of movement and a longer active period than juvenile females, were taken more often by hawks near her study areas than were juvenile females.

Little is known of the susceptibility of dispersing animals to ground predators. With the exception of grizzly bears, predation on resident colonial animals was limited by warning vocalizations. My estimates of predation accounted for only 10-15% of the total annual loss. Although my results are only inferential, it seems unlikely that predation is the ultimate cause of the disappearance of animals from the colony. Rather it would seem that predation is a very important proximate cause of mortality during dispersal.
Seasonal Trends Of Dispersal

Dispersal appeared to be the major cause of in-situ loss from both SRC and CCC. The correlation between seasonal peaks of immigration to the control and removal areas, with loss from the control areas, suggest that much of the loss is due to dispersal. Further the similarity of seasonal dispersal peaks on SRC and CCC suggest that seasonal dispersal is a regular and innate component of the yearly patterns of population change in Arctic ground squirrels. Two main peaks of dispersal were apparent in Arctic ground squirrels in the Kluane region. Mature females showed increased dispersal in May and early June and juveniles, particularly juvenile males showed increased dispersal in August. Carl (1971) (in his Fig. 6) indicated that in Arctic ground squirrels in the vicinity of Pt. Barrow, Alaska, mature males and females similarly showed the greatest loss of animals (not attributable to hibernation entry) in May whereas the largest loss of juveniles from the the colony was in July and August. Mature and juvenile S. arnatus also showed similar patterns of seasonal dispersal (Slade and Balph 1974).
Which Animals Disperse?

Morphological Differences

Dispersing Arctic ground squirrels showed some morphological differences from resident animals. Dispersing juvenile males tended to be heavier and have larger skull sizes than non-dispersing animals. Dispersing mature females on the other hand often failed to reproduce. Few other studies of dispersing animals have been conducted. Slade and Balph (1974) found no significant differences in the body weight of dispersing and resident *S. armatus*. Dispersing *Microtus pennsylvanicus* however were smaller than resident animals (Myers and Krebs 1971). This was attributed to the emigration of sub-adult animals just at the time they became reproductively active. Few adults emigrated.

Among juvenile male Arctic ground squirrels, the heavier individuals tended to disperse first, suggesting that the attainment of an adult body size and possibly increased competition with adult animals may be important causes of dispersal in juvenile animals. Barash (1974) suggested that in marmots the social systems have evolved to allow juvenile animals to obtain optimal size (for successful dispersal and reproduction) before dispersal. The two hypotheses are basically in agreement that animals reach certain threshold sizes or size ranges at which animals are treated as adults and so must compete for territories within the colony. This optimal size
should coincide with the stage of development at which juvenile animals are able to become totally independent from the family group. Dispersal then should occur just prior to the time at which juvenile or young animals became reproductively active.

In most ground squirrels, juveniles are capable of breeding the spring following their birth. *S. columbianus* is the one exception; most animals are not capable of breeding until their second spring. In agreement with the theory, most juvenile ground squirrels disperse before their first spring, whereas *S. columbianus* do not appear to disperse until their second summer.

Barash (1974) found that marmots that dispersed as juveniles (*Marmota monax*), bred as yearlings, were solitary (except for mother : young groups) and showed little social behaviour. In species that dispersed as yearlings or two-year olds, animals were more social and tended to show much more amicable behaviour. Barash suggested that there was a correlation between the sociality (amount of agonistic versus amicable behaviour towards conspecifics) of a species, the length of growing season and the age at which animals were likely to disperse.

Perhaps a similar relationship exists in Spermophiles. *S. columbianus* and *S. undulatus* appear to have a very similar social organisation (Steiner 1970, Michener 1973, Carl 1971, this study) and compared to most other ground squirrels are quite social species. The dispersal patterns of *S. columbianus* support Barash's hypothesis whereas, Arctic ground squirrels might be expected to disperse as yearlings rather than as
juveniles. *S. columbianus* predominantly inhabits alpine meadows and has a short active season (Michener 1977) in comparison to Arctic ground squirrels. Young Arctic ground squirrels may thus be able to reach a sufficiently large size in their first summer to disperse whereas juvenile *S. columbianus* cannot.

**Reproductive Condition And Dispersal**

In mature female Arctic ground squirrels, breeding success was related to dispersal. During the breeding period, most immigrants to the removal areas were in breeding condition as were all mature females emigrating from the control area in May and early June. However few mature females on the removal period in May and June showed signs of becoming pregnant and fewer still were known to successfully give birth. Dispersing mature females appear to be those females who for some reason failed to complete pregnancy.

Reproductive failure in dispersing mature females has similarly been reported in several species of ground squirrels. Carl (1971) found that all non-breeding female Arctic ground squirrels in the main colony emigrated before the emergence of the young and on an area of temporary beach ridges, no immigrating females successfully reproduced. Similarly, mature female *S. armatus* which failed to have young, disappeared from the colony in the spring before young were born (Slade and Balph 1974). Sherman (1976) observed that mature female *S. beldingi* which lost litters to predation or which presumably aborted, always emigrated to another area of the large meadow and, in
some cases, attacked and killed young of neighbouring females at the new site.

Few explanations have been offered for the emigration of non-breeding females in the spring. Sherman (1977) suggested that females left the area in search of a safer, more predator-free site and once reaching such an area, killed off neighbouring young to limit competition in the area in which they might reproduce the following year. In the Kluane region, mature female: mature female agonistic interactions increased during the period of mature female emigration (Fig. 22) suggesting that female aggression may be important in the initiation of mature female dispersal. There did not appear to be any relationship however, between the number of agonistic or amicable interactions a female initiated or received and her eventual fate that spring (ie. dispersal versus residency). Little is known of the factors influencing the initiation of dispersal of mature females in any ground squirrel species, except that reproductive failure is related to a tendency to disperse.
Are Dispersing Animals Behaviourally Different?

Social interactions have been suggested as one of the important causes of dispersal (Chitty 1967, Krebs and Myers 1974, Watson and Moss 1969, Wynne-Edwards 1962, Wilson 1975). More specifically, Carl (1971) suggested that young Arctic ground squirrels are driven out by the increasing belligerence of mothers towards their young. If social behaviours are a regulating factor, a relationship between population change and the rate and intensity of social interactions must exist (Watson and Moss 1969, Armitage 1975).

The relationship between social behaviour and population density is difficult to assess. Seasonal changes in social behaviour may be due to a variety of responses to different stimuli (i.e. the breeding period versus the non-breeding period, the establishment of breeding territories versus the establishment of fall territories etc.). Armitage (1975) solved this problem to some extent by using the mean interaction rate and the mean population density for the active period. He found no correlation however, between the rates of amicable or agonistic behaviour and the mean population density over a ten year study of several M. flaviventris colonies.

I was not able to determine if social behaviour and population density were correlated in Arctic ground squirrels as I have only two values for each area and rates between years are not comparable. Interaction rates (see Table 12) were higher on CCC than on SRC. Maximum densities for each year on CCC were close to six times that on SRC (mean maximum density of 6.23
animals/ha on CCC and 1.04 animals/ha on SRC). This suggests that social behaviour and population density may be positively correlated. This could simply be due to the close proximity of animals on CCC compared to SRC and so a higher interaction rate due to the increased probability that animals will encounter another animal, but alternatively could be due to increased social stress with increased densities. Continued study of social behaviour and population density of these populations is needed. Slade and Balph (1974) and Carl (1971) suggested that S. armatus and S. undulatus populations respectively are at least in part, intrinsically regulated by socially mitigated dispersal. Similarly, Barash (1974) suggested that M. olympus populations were able to regulate the population densities of colonies by adjusting the dispersal rates of two year olds through changes in social behaviours.

Behavioral Differences

Behavioral observations of animals immigrating to the removal areas indicated there were few differences between the behaviour budgets of resident animals and dispersing animals. Dispersing juvenile animals fed more in the late summer, suggesting that increased feeding is necessary to make up for the energetic costs of dispersal. The most obvious differences however were the lack of amicable and agonistic behaviours. As a result, differences in the social behaviours of dispersing and resident animals on the control areas were more closely investigated.
Dispersing animals initiated fewer and received more agonistic interactions than resident animals. No trends in amicable behaviour were apparent. This suggests that agonistic behaviour may be an important cause of dispersal. Further evidence is required. Experiments manipulating the level of aggression within a colony may provide some insight. One could increase the level of aggression as did Watson (1970). They were able to increase the aggressive behaviour of male red grouse (*Lagopus lagopus*) by injecting the birds with androgen. Alternatively, levels of aggression could be decreased by the removal of adult females (Schmutz 1977) or males (Donaldson 1977). Subsequent changes in dispersal, particularly juvenile dispersal, would strongly implicate aggression as one of the ultimate factors of dispersal.

**Which Animals Most Influence Dispersal?**

Agonistic behaviours appear to be an important cause of dispersal in Arctic ground squirrels. To determine which animals are most likely to influence dispersal, for each class I determined both the most common initiator of agonistic interactions towards the class as well as the most common recipients of the agonistic interactions initiated by the class. Both provide some indication of social hierarchies within the colony.

The most common recipients of agonistic behaviour of both resident and dispersing animals were animals of the same age or sex (Table 11). There was a suggestion that dispersing juvenile
animals tended to also interact more with mature animals than resident animals. Perhaps, resident juvenile squirrels are better at avoiding adults than dispersing animals. Alternatively, dispersing juvenile may simply be more intolerant of other animals (Slade and Balph 1974). Similarly, Armitage (1974) has suggested that male yearling *M. flaviventris* disperse to avoid territorial adults, particularly adult males.

Dispersing and resident squirrels also tended to receive most agonistic behaviour from animals of the same class (Table 12). Sample sizes for dispersing adult animals were small so little can be said of the relative importance of interactions initiated by either adult males or females towards other adults. Resident juveniles however, received more agonistic interactions initiated by mature animals than did dispersing juveniles. Dispersing juveniles instead were approached largely by male juveniles. If all agonistic interactions are equally important, this suggests that adult:juvenile interactions are not as important to juvenile dispersal as juvenile:juvenile interactions.

Within one class, the subordinate individuals may thus be the most likely animals to immigrate, being less likely to be able to successfully compete with dominant individuals. Carl (1971) suggested that hibernacula may be a limiting resource. The chances of a juvenile animal competing with a resident adult animal for a fall territory or hibernacula and successfully obtaining a territory should be small. Thus juvenile competition for the remaining vacant hibernacula would be intense and so may lead to the dispersal of some juveniles. Adult:juvenile
interactions then, may lead to the movement of juvenile animals to peripheral areas. There juvenile:juvenile interactions are likely important in the establishment of juvenile fall territories and the eventual dispersal of defeated animals.

Fewer juvenile females dispersed than juvenile males. This may be a result of the formation of related female social complexes (i.e., mother:daughter groupings) which were common on both SRC and CCC. Similar groupings have been reported in S. beldingi (Sherman 1976), S. richardsoni (Yeaton 1972, Quanstrom 1968) and S. tridecemlineatus (Rongstad 1965, McCarley 1966). As a result, juvenile females may not be subjected to the same level of competition for hibernacula or breeding sites as males.

**Genetic Relatedness And Social Behaviour**

Genetic relatedness as well as age and sex appear to be important in determining which animals a squirrel is most likely to initiate interactions towards or receive interactions from.

Related animals on both my study areas showed higher levels of amicable behaviour than unrelated animals. Amicable behaviours largely occurred during the spring and early summer. Adult:adult interactions were primarily between related females and involved mostly recognatory behaviours. Similarly, adult:juvenile interactions occurred between mothers and their young and most often involved nuzzling or nose-nose greetings. Amicable interactions are likely important in the establishment of social contacts and the maintenance of the family unit.
following the emergence of the young from the natal burrow.

Agonistic interactions were common between both related and unrelated animals in the early spring. Male:female contacts were more frequent then and were probably associated with breeding whereas male:male and female:female contacts were more likely associated with competition for breeding territories. Similarly in the fall, both related and unrelated animals interacted. Juvenile: mature animal contacts predominated however, supporting the contention that during the period of competition for fall territories, mature animals primarily reassert their territorial "rights" over juveniles rather than other territorial animals. Agonistic interactions between related animals were common in May, June, and July and involved mostly mature females. Like *S. beldingi* (Sherman 1977), mature female Arctic ground squirrels became increasingly agonistic during pregnancy and the weaning of young, and appeared to defend the area around the natal burrow from all mature animals regardless of their relationship. Sherman (1977) suggested that this may be an adaptation to minimize intraspecific predation.

Overall, related animals showed higher levels of amicable behaviour and similar levels of agonistic behaviour to unrelated animals. Much of the agonistic behaviour of related animals involved play fighting and so related animals tend to be less physically aggressive than related animals. Similarly, Sheppard and Yoshida (1971) found that in *S. richardsoni*, amicable behaviour was more common between related animals whereas agonistic behaviour was more common between unrelated animals. Michener and Sheppard (1972) and Michener (1973) extended this
approach to the interaction regime between a mother and her own or alien young. Little agonistic behaviour occurred between related animals but was common between unrelated animals. Further, within a litter, males tended to receive less amicable behaviour from their mothers. The influence of the mother appeared to have effects on the eventual dispersal of juveniles (Michener and Michener 1973). Juvenile females always occupied burrows closer to their mothers than juvenile males. Further, juvenile males whose mother died, did not move long distances away from the natal burrow, whereas juvenile males whose mothers were still alive, did. Similarly, Carl (1971) has suggested that agonistic interactions by a mother towards her young, result in the dispersal of young away from her fall territory and hibernaculum.

In summary, social interactions appear to be an important ultimate cause of dispersal in Arctic ground squirrels. Interaction rates and maximum population densities for both control areas suggest that social behaviour and population changes in Arctic ground squirrels may be related. Similar relationships have been reported in S. armatus (Slade and Balph 1974) and M. flaviventris (Armitage 1974).

Age, sex, and genetic relatedness are important factors in the initiation and receiving of social interactions. Resident and dispersing animals tended to interact largely with and receive agonistic interactions from, animals of a similar age and sex. Amicable interactions were more common between related animals than unrelated animals, whereas agonistic interactions were common between related and unrelated animals. Agonistic
interactions between unrelated animals were more physically aggressive however.

Dispersing adult males are most likely animals which were not able to obtain spring breeding territories or hibernacula. Dispersing mature females on the other hand were often females that failed to successfully reproduce. The exact cause of mature female dispersal is not known. Mature animal:juvenile interactions likely force juveniles away from the natal burrow. Often juvenile females remain in the vicinity of their natal burrow and so related female social complexes are common. Dispersing juvenile males are often larger than resident juvenile males suggesting that larger juveniles are more likely to elicit mature animal aggression. Smaller animals may avoid mature animal aggression as a result of mature animals entering hibernation. Most juvenile males and some juvenile females are forced to move to peripheral areas of the colony. There juvenile:juvenile competition for vacant hibernaculum may be intense and so be an important cause of juvenile dispersal in August.
Population Regulation and Dispersal

Carl (1971) concluded that "based on a complex pattern of social behaviour, colonial populations of (Arctic ground) squirrels recruit members by reproduction and lose by emigration while buffering themselves from immigration and loss by mortality". Further, he proposed that the maximum population size was determined by the number of suitable breeding burrows and so the the number of breeding females.

Arctic ground squirrels in the Kluane region showed many similarities to those studied by Carl (1971) at Pt. Barrow, Alaska. Recruitment of young followed similar seasonal patterns as did peaks of emigration and immigration. Relative magnitudes of dispersal within each age and sex class were also similar. Loss due to mortality was greatest over-winter. Predation was an important source of loss of very young animals as well as of dispersing animals and animals in temporary habitats. In the Kluane region, however, the number of breeding burrows did not appear to be the only limiting factor.

Large differences in density were noted between the Slims River and the Coin Creek areas, the density of animals on the latter being approximately six times that on the former area. On SRC, several of the major burrow systems were vacant and were used little throughout the two and a half year period of this study. On CCC, few burrows were vacant. Breeding burrows as well as suitable hibernacula may be limiting factors on CCC. If competition for burrows does lead to dispersal, one would expect few animals on SRC to disperse. The low density of animals and
the failure of animals to occupy vacant burrows on SRC suggest that other factors may be important.

Dorrance and Keith (1974) suggested food as a limiting factor in *S. richardsoni*. Food may also be limiting on SRC. On SRC, a number of herbivores are possible competitors of Arctic ground squirrels. Dall Sheep (*Ovis dalli*) frequent the vicinity of my study areas; this area being an important over-wintering range for the rams. As the diet of Dall Sheep (M. Hoefs 1976) includes many of the important food species of Arctic ground squirrels observed in this study (ie. *Carex* sp., *Artemesia frigida*), the potential for competition exists. *Eutamias minimus* and *Peromyscus maniculatus* are relatively abundant throughout the same area and are also potential competitors for many of the major food species of Arctic ground squirrels. M. Hoefs (*pers. comm.*) has suggested that in recent years, the Slims River area has become overgrazed. This, in itself, would intensify any competition between these herbivores. I suggest then that on SRC, food resources have set an upper limit to the population size.

On CCC, however, sheep grazing was minimal compared to that observed on SRC and in general, the vegetation is much more dense on CCC than on SRC. Some food types are similar (ie. *Artemesia frigida*, *Carex* sp., and *Penstemon gormanii*) but several species, highly utilized by squirrels were only available on CCC (ie. *Dryas* sp., *Salix* sp. and *Arctostaphylos rubra*). Food resources on CCC appear to be much more abundant than on SRC and I believe the availability of burrows is a more important, proximate limiting factor.
The relationship between the availability of burrows and sufficient food resources may be important in the determination of maximum population size. When food is abundant the number of existing and potential burrow sites would limit the population size. I believe this is the case on CCC. As a result, the recruitment of juveniles would depend on the number of vacant burrows created by the loss of mature animals. Excess young would be forced to disperse. When the quality or quantity of food decreases however, social mechanisms, such as increased territory size, would lead to a decrease in population size thus leaving some sites vacant. I believe this has occurred on SBC. Despite the excess burrows, young are forced to disperse and only when occupied sites become vacant, do young recruit to the breeding population. There is the possibility however that young which are able to successfully challenge territorial animals, do recruit to the breeding population. In both cases, dispersal as a result of social stress is the likely ultimate regulating mechanism.

Dispersal is common in many species of ground squirrels, marmots, and other small mammals, suggesting that dispersal may indeed be of some adaptive significance. Howard (1960) suggested that genetic polymorphisms for dispersal tendencies may exist within small mammal populations. He termed animals likely to emigrate from a population due to genotypic effects, innate dispersers. Animals emigrating in response to increased densities (i.e. competition for mates, territoriality, lack of homesites, social interactions etc.) were termed environmental dispersers. Innate dispersal is independent of density whereas
environmental dispersal is density dependent. Murray (1967) felt that the observed non-random distribution of dispersal distances was determined by the distribution of breeding sites unoccupied by dominant animals. Dominant animals were able to reproduce on or near the colony whereas subordinate animals could maximize their chances of reproducing by moving away from their birthsite. Dispersal polymorphisms were the result then, of behavioural differences. It is not known, however, if behavioural differences are genetically controlled. Bekoff (1977) agreed that dispersing animals may maximize their chances of reproductive success through dispersal but thought that dispersing animals were not always subordinate. Instead, he suggested that animals failing to develop social ties were more likely to disperse.

Group selection has been suggested as a means of explaining individual dispersal tendencies (Wynne-Edwards 1962, Howard 1960). Lidicker (1962) however, suggested that there were several advantages to the individual that dispersed. Dispersing animals might come into contact with more conspecifics and so breed more often. Further, dispersal would lead to the transfer of genetic material and so increase the chances of producing new, advantageous recombinations (offspring may be more heterozygous and so may be more fit). Dispersing animals too may be able to avoid population declines or local extinctions.

The widespread dispersal of juvenile males and the limited dispersal of juvenile females in Arctic ground squirrels offer some support to several of these theories. Throughout most of its range, Arctic ground squirrels face a relatively short
active season in which they must reproduce but still acquire sufficient fat stores to survive through the winter. Male reproductive costs are lower than that of the female yet males have a longer period to replenish their fat stores. Dispersal is presumed to be energetically expensive. Males would be more able to "afford" to disperse and still be able to reproduce the following spring. Further, in a polygamous mating system, daughters would more likely be able to successfully reproduce. Sons would have to compete with their father or other males and so would maximize their chances of reproduction by dispersal. The chances of successful dispersal may be low but successful male dispersers (ie. those obtaining a territory elsewhere) would have a high probability of fathering many young and so would be genetically more fit (Carl 1971).

Little is known of the importance of dispersal in the transfer of genetic material between populations of small mammals. Myers (1974) studied populations of feral Mus_ musculus_ and concluded that on the basis of several polymorphic blood proteins, that dispersal did lead to the transfer of genetic material between subpopulations. Michener and Michener (1977) compared the frequency of three transferrin alleles in juvenile and adult squirrels, males and females and in resident versus immigrating (unmarked) individuals. No significant differences were found.

Both extrinsic and intrinsic factors appear to be important to the population regulation of Arctic ground squirrels (Carl 1971, this study). I would like to propose a graphical model of population regulation based on the relationship between
demographic changes and social behaviour observed in this and other ground squirrel studies.

A Model Of Population Regulation In Arctic Ground Squirrels

In the early spring, just after emergence, the mature animal population size is determined by the number of mature and juvenile animals surviving over-winter (Fig. 30). The number of juveniles successfully recruiting to the mature resident animal population is similarly determined by the number of vacant territories as a result of over-winter mature animal mortality.

Males compete for breeding territories in the early spring with the larger and longer-residency animals more likely to win territorial encounters (Watton and Keenleyside 1974). Yearling males thus have a lower probability of recruiting to the resident breeding population. The establishment of female territories involves less physical aggression than males and daughters are often allowed to remain in the vicinity of the mother's burrow. The number allowed to remain on the colony would depend on the number of available breeding sites. As Arctic ground squirrels are polygamous, all females obtaining breeding territories are bred.

Male and female territory size may be determined by the food resources and burrow availability. Whereas the quality of male territories is likely based on the number of breeding females, the quality of a female breeding site is likely based on the quality of the burrow and food resources.

During the development and weaning of the young, breeding
Figure 30: Graphical model of population regulation in Arctic ground squirrels. The model is described in the text. Recruitment to the population due to birth or immigration is indicated with dotted lines. Loss from the population due to emigration or other mortality factors is indicated with a dashed line. Waved lines indicate the periods where extrinsic factors may be important to population limitation. The following extrinsic factors are likely important at:

1. The number of vacant breeding territories.
2. The number of hibernacula.
3. Hibernaculum quality, fat stores and exposure.
Mature Animals at Emergence

Spring

- Maturity of resident animals
- Immigration

Summer Population

- Breeding resident animals
- Emigration of mature females
- Birth of young

Fall

- In late summer
- Immigrant maturity
- Immigration of juveniles
- Dispersal of juveniles

Winter

- Mortality due to exposure and starvation
- In fall with hibernacula

Loss of young to predation

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females become increasingly more aggressive, presumably to minimize disturbance of the young. Females which for some reason fail to reproduce, disperse. When the young emerge, amicable social contact between mother and young and between sibling young is high and family units are maintained. Some loss of young due to predation occurs shortly after emergence when young are most susceptible to predation.

In August, fall territories and hibernaculum "rights" are established. Resident adult animals appear to recognize territories whereas juveniles do not. As a result, most interactions during this period involve juveniles and adults. Larger juveniles, particularly juvenile males approach adult "size" sooner and so receive more agonistic behaviour initiated by adults. As a result they are more likely to disperse. Whereas juvenile males compete with territorial males, juvenile females benefit a male by increasing his degree of polygamy (Downhower and Armitage 1971) and so receive less agonistic behaviour from the territorial male than juvenile males. Juvenile females may similarly compete with resident mature females but if allowed to remain on the colony, ensure moderate reproductive success for her mother. Some juvenile females are as a result, allowed to remain near their birth site, whereas almost all juvenile males are forced to move. Juvenile animals forced away from the natal burrow and not able to obtain and hold another hibernacula on the colony may move into peripheral areas or inter-territorial sites. Hibernacula may be limiting and hence juvenile: juvenile interactions increase. Juveniles failing to obtain a hibernaculum disperse. Over-winter survival is then determined
by environmental conditions, hibernacula suitability and amount of fat stores.

Adjustments to increased density or decreased density are possible through social behaviours as suggested by Barash (1974). If over-winter survival is high, few vacant territories on the colony are available and dispersal during the spring period is high. Conversely, if over-winter survival is low, many vacant positions are available and dispersal will be low. The adult resident population is thus kept at relatively constant numbers. In cases where over-winter survival is low and yearling recruitment is insufficient to occupy all territories, immigration from other colonies may moderate the loss.

Although I have shown that definite seasonal peaks of dispersal occur in each age and sex class of Arctic ground squirrels in the Kluane region, I could only estimate the relative magnitudes of losses due to dispersal, predation and other forms of mortality. We need to know more of the magnitude and importance of losses due to predation and over-winter mortality to population change. Similarly, I was not able to show that definite morphological or behavioural differences occurred between resident and dispersing animals. Some interesting and suggestive trends were apparent but further evidence is needed to determine if these trends are real. Particularly, the relationships between body size, breeding condition, social behaviours, and dispersal tendencies must be clarified. The collection of adequate demographic information is relatively easy whereas the collection of adequate behavioural
information is not. The collection of information pertaining to the social interactions of even a small group of animals is time-consuming. New methods of behavioural data collection are now becoming available (ie. behavioural coding digitizers (Gass 1976)) permitting almost continuous observations. With such aids as these and/or ample manpower, sufficient behavioral information on populations, particularly the social interactions budgets, could be obtained. We need to clarify the relationship of amicable and agonistic behaviour as well as the intensity of these behaviours, to dispersal. Age, sex, and perhaps most important, genetic relatedness must be considered in any study of the relationships between social behaviour and population regulation. Ground squirrels, particularly Arctic ground squirrels are easy to trap, are readily observable, and are sufficiently abundant to obtain adequate information of this sort. Continued study will hopefully provide the information needed to determine if indeed social behaviour is a critical factor to the initiation of dispersal and the regulation of population size in small mammals.
CONCLUSIONS

Social behaviours, particularly aggressive behaviours, are potentially the major cause of dispersal in Arctic ground squirrels. Adult: juvenile agonistic interactions force young to move to peripheral areas or inter-territorial areas of the colony. There, juvenile: juvenile agonistic interactions are likely an important cause of more widespread juvenile dispersal.

Body size and reproductive success were related to dispersal of juvenile males and mature females respectively. No conclusive trends were apparent in mature males or juvenile females. It is suggested that the attainment of an "adult" body size leads to a sharp increase in adult: juvenile aggression. The "adult" body size may, as Barash (1974) has suggested, be related to an optimal size for successful dispersal and reproduction. The relationship between mature female dispersal and reproductive success is unclear and further study is needed. Behavioural parameters indicated that dispersing animals receive more and initiate less aggressive behaviour than resident animals. This suggests that dispersing animals are subordinate to resident animals. Social interaction budgets for each class indicate that age, sex and genetic-relatedness are important factors in social interactions and hence dispersal. They must be considered then in any study of the mechanisms of population regulation in Arctic ground squirrels.

Cohort survival and the origins of resident adult animals indicated that in Arctic ground squirrels, males are more likely to move between colonies whereas mature females are more
likely to remain near their site of birth. As a result, resident adult males are often not related to resident adult females, whereas resident females are often closely related to other females inhabiting burrows nearby. Related female social complexes were common in both of the populations I studied. The overall suggestion is that a greater proportion of the inter-colony movement of genetic material is due to male dispersal but further study is required.

Social behaviours are strongly implicated as the cause of dispersal and the subsequent regulation of population changes. We need more information however, concerning:

1. The relationship of rates and intensities of agonistic and amicable behaviour to dispersal and population regulation.

2. The relationship between genetic relatedness and dispersal.

3. The relationship of adult female reproductive success to dispersal of mature females.

4. The relationship between food resources and burrow (hibernacula) availability and its importance to population limitation.

5. The importance of over-winter survival to population change.

6. The importance of interspecific predation to population changes, particularly the effect on dispersing animals. Include
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