SPACE USE IN A POPULATION OF LEAST CHIPMUNKS
IN THE SOUTHWEST YUKON

by

Linda Cuffableness Glennie
B.Sc., McGill University, 1984

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
(Department of Zoology)

we accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA
September 1988
© Linda Glennie, 1988
In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia
Vancouver, Canada

Date 9/9/88
This thesis describes an investigation of space use in least chipmunks at Kluane Lake, in the southwest Yukon. I examined demography, home range and habitat use patterns in the population. Based on live-trapping data from two grids over two summers, mean number of animals on the study area was \( \frac{22.6}{\text{grid}} \), similar to chipmunk numbers measured there over the previous four years. The population was lower than is generally found in the same species further south, although year-to-year stability was typical. Chipmunks preferred open forest and shrub-land to closed-canopy forest, which is also typical of the genus. Home range sizes measured using telemetry averaged \( 4.86 \text{ ha} \), higher than in any previously published study of the genus.

I examined the relationship between social spacing and space use. Home range overlap averaged 93.4%; chipmunks do not appear to defend exclusive core areas. Provoked interactions among neighbours suggested that social dominance was based on age, weight, and breeding condition, rather than ownership of space. Although provoked interactions were generally aggressive, the telemetry data suggest that such behaviour was artifactual. Comparing the encounter frequency of radio-collared animals to that generated by a random model showed that chipmunks avoided encounters, except when harvesting seasonally abundant food.

Grid-trapping did not increase food or cover availability enough to affect home range size. There was evidence that the
presence of traps affected use distribution, but not enough to invalidate trap-based home range estimates. Comparison of trap and telemetry based estimates of home range size yielded no significant differences.
# Table of Contents

**ABSTRACT** ......................................................... 11

**Table of Contents** ...................................................... iv

**List of Tables** .......................................................... vii

**List of Figures** ........................................................ viii

**ACKNOWLEDGEMENTS** .................................................... ix

**CHAPTER 1: GENERAL INTRODUCTION** .................................. 1

**CHAPTER 2: DEMOGRAPHY, HABITAT USE, AND HOME RANGE OF THE LEAST CHIPMUNK IN THE SOUTHWEST YUKON** ................. 3

**INTRODUCTION** ......................................................... 3

**METHODS** ............................................................... 4

  - Study area ......................................................... 4
  - Live-trapping ....................................................... 4
  - Radio-telemetry ...................................................... 8
  - Habitat classification ............................................. 9

**RESULTS** ............................................................... 12

  - Demography ......................................................... 12
  - Home Range .......................................................... 19
  - Habitat preference ................................................. 20

**DISCUSSION** ........................................................... 28

  - Demography ......................................................... 28
  - Habitat use .......................................................... 32
  - Home range ........................................................... 33

**SUMMARY** .............................................................. 36
### CHAPTER 3: SPACE USE AND SOCIAL STRUCTURE IN THE LEAST CHIPMUNK

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>37</td>
</tr>
<tr>
<td>METHODS</td>
<td>39</td>
</tr>
<tr>
<td>Behavioural observation</td>
<td>39</td>
</tr>
<tr>
<td>Encounter avoidance</td>
<td>41</td>
</tr>
<tr>
<td>RESULTS</td>
<td>45</td>
</tr>
<tr>
<td>Home range overlap</td>
<td>45</td>
</tr>
<tr>
<td>Behavioural observation</td>
<td>51</td>
</tr>
<tr>
<td>Encounter avoidance</td>
<td>53</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>54</td>
</tr>
</tbody>
</table>

### CHAPTER 4: THE INFLUENCE OF GRID-TRAPPING ON SPACE USE AND HOME RANGE IN THE LEAST CHIPMUNK

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>60</td>
</tr>
<tr>
<td>Predictions</td>
<td>60</td>
</tr>
<tr>
<td>METHODS</td>
<td>61</td>
</tr>
<tr>
<td>Experimental design</td>
<td>62</td>
</tr>
<tr>
<td>Home range calculations</td>
<td>62</td>
</tr>
<tr>
<td>Effect of data source on home range estimate</td>
<td>63</td>
</tr>
<tr>
<td>RESULTS</td>
<td>64</td>
</tr>
<tr>
<td>Effects of grid-trapping on home range</td>
<td>65</td>
</tr>
<tr>
<td>Effects of data source on home range</td>
<td>65</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>67</td>
</tr>
<tr>
<td>Effects of grid-trapping on home range</td>
<td>67</td>
</tr>
</tbody>
</table>
List of Tables

Table 2.1—Summary of grid-trapping changes .................. 8
Table 2.2—Habitat classifications ................................. 10
Table 2.3—Population means ......................................... 15
Table 2.4—Mean Minimum Survival Rates ......................... 16
Table 2.5—Minimum over-winter survival ......................... 17
Table 2.6—Means (and ranges) of chipmunk weights (in g) ...... 18
Table 2.7—Summary of habitat preferences from trapping data. ......................................................... 25
Table 2.8—Chipmunk home ranges from this and previous studies ....................................................... 34
Table 3.1—Mean home range overlap ................................. 46
Table 3.2—Mean distances from interaction to home ............ 52
Table 3.3—Mean encounter frequency on grid H vs. simulation 54
Table 4.1—Telemetry-based home range estimates ................ 65
List of Figures

Fig. 2.1 -- The study area ........................................... 6
Fig. 2.2 -- Jolly-Seber population estimates for Grids X and H .................................................... 13
Fig. 2.3 -- Habitat maps: (a) Grid X, (b) Grid H .................. 21
Fig. 2.4 -- Observed and expected number of telemetry locations vs. vegetation type. ......................... 26
Fig. 2.5 -- Habitat use index for adults and juveniles vs. habitat type. .................................................. 29
Fig. 3.1 -- Flowchart of random-encounter simulation model. 43
Fig. 3.2 -- Telemetry-based home range map of Grid H ........ 47
Fig. 3.3 -- Telemetry-based home range map of Grid X ........ 49
ACKNOWLEDGEMENTS

I would like to thank my supervisor, Charles Krebs and my research committee, Jamie Smith, Lee Gass and Tony Sinclair for their advice and support. Jamie Smith's amazingly prompt and thorough comments on the rough draft were greatly appreciated.

Inhabitants of Kluane Research Station all provided help of various kinds. The friendship and encouragement of Andy and Carole Williams made the field work possible. Sian and Megan Williams, Andrew Lawrence, Shielia Fox, Garth Mowat, Sally Wright, Patty Harris, and Lisa McIntyre provided field assistance.

During the writing-up stage, Peter Watts provided innumerable suggestions, constant brow-beating, and invaluable help with programming, figures, proof-reading, formatting, and in writing these acknowledgements. Without his help the chipmunk data would still be locked inside the computer.

I thank Alistair Blachford and Susan Ertis for programming assistance, Chris Foote (who once saved my life), Simon Courtenay, Gordon Haas, Rob Powell and Don Robinson for advice and for bolstering morale.

I thank my mother for being endlessly supportive even while convinced of the utter lunacy of this endeavor.

My field work was funded by Northern Studies Training Grants, and NSERC grants to Dr. Krebs. I was supported by teaching assistantships while at U.B.C.

This thesis is dedicated to Cygnus and Zombie.
CHAPTER 1: GENERAL INTRODUCTION

This study investigates factors affecting space use in a population of least chipmunks (Tamias minimus) at Kluane Lake in the southwest Yukon.

Forbes (1966), Sheppard (1969), and Meredith (1972) remarked on the paucity of data available on western species of chipmunk. Since that time, a number of studies have investigated patterns of space use, habitat preference and social dominance in the group of western chipmunks formerly known as Eutamias. Five of these have included Tamias minimus among the species studied (Heller, 1971; Sheppard, 1971; Meredith, 1976; States, 1976; Chappell, 1978). These studies assessed the influence of competition with other chipmunk species and of differences in habitat preference on altitudinal zonation in the distribution of the least chipmunk and its geographically sympatric congeners. This study presents the first data on space use, habitat preference and social dominance for the least chipmunk in isolation from its congeners.

Chapter 2 provides an overview of demography and home range in the population. It describes the habitat and investigates the animals' habitat use patterns. Population levels, home range and habitat use are then compared to those reported in previous studies of the genus.

Chapter 3 examines the relationship between social spacing
and space use. To determine whether social spacing occurs, I ask whether chipmunks defend exclusive areas, whether social dominance is affected by ownership of space, and whether chipmunks avoid encountering each other.

Chapter 4 evaluates whether the provision of food and cover resulting from trapping and pre-baiting increases the availability of these resources enough to affect home range. I then compare trap and telemetry based methods of estimating home range.
CHAPTER 2: DEMOGRAPHY, HABITAT USE, AND HOME RANGE OF THE LEAST CHIPMUNK IN THE SOUTHWEST YUKON

INTRODUCTION

This chapter presents data collected during the summers of 1985 and 1986 on the demography and home range movements of a population of least chipmunks (*Tamias minimus*) near Kluane Lake in the southwest Yukon. The home range data are used to assess habitat preferences of chipmunks, and the home ranges, demographic patterns and derived habitat preferences are compared with those previously reported.

Published estimates of home range and habitat associations of the least chipmunk are relatively common in the literature, since several studies have used such estimates in assessing competitive interactions with congeners (Heller, 1971; Sheppard, 1971; Meredith, 1976; States, 1976; Chappell, 1978). This provides ample opportunity for comparison.

The few studies of the least chipmunk that have not focussed on competition describe morphological traits and life-history characteristics rather than demography (Criddle, 1943; Sheppard, 1969; Skryja, 1974). However, studies of the demography of other chipmunk populations are more numerous (Gashwiler, 1970; Tryon and Snyder, 1973; Sullivan et al, 1983). The chipmunk population
near my study area at Kluane has been monitored since 1980 in demographic studies of other small mammals (Gilbert and Krebs, 1984; Gilbert, unpublished data). Although my field work covered too short a period to permit robust conclusions about demographic patterns, densities in this study can be compared to those reported in previous studies of chipmunks, and with those previously found near my study area at Kluane.

METHODS

Study area

The study area was located just east of Kluane Lake (61° N, 138° W). Two trapping grids were established approximately 2 and 3 km from the lake on an old alluvial fan, bounded by Silver Creek on the north-east and partially bounded by the Alaska Highway on the south. Vegetation cover ranged from closed spruce forest (Picea glauca), to open spruce - soapberry (Shepherdia canadensis) shrub-land, to open meadows dominated by Dryas drummondii.

Live-trapping

Population size and home ranges were monitored using live trapping. In 1985 I set up two rectangular trapping grids, 6 ha
in size and 500 m apart. Animals were captured in Longworth traps at stations 21 m apart. Traps were baited with a mixture of oats and sunflower seeds, and were locked open and left pre-baited between trapping sessions. I trapped each grid every 2 to 3 weeks. During trapping sessions, I set traps during the morning of day 1 and locked them open on the morning of day 3. Traps were generally checked in the afternoon and evening of day 1, morning, afternoon and evening of day 2, and in the morning of day 3 for a total of 6 checks per session. Captured chipmunks were permanently marked by toe-clipping and their pelage was marked with Nyanzol D for visual identification. I recorded capture location, weight, sex, age class (adult or juvenile) and breeding condition of each chipmunk. I assessed breeding condition of females according to nipple size (small, medium or large) and whether they were obviously pregnant. Males were classified as breeding or non-breeding according to the position of the testes (scrotal or abdominal) respectively.

I trapped grids from early May to late August, 1985, and from early May to mid-September, 1986. In mid-July, 1985, I expanded the western-most grid (grid X) from 6 ha to 8 ha so that it would contain most nest sites when juveniles first entered the traps (Figure 2.1). In May, 1986, I expanded both grids to 18 ha in order to completely encompass most local home ranges. I also increased the distance between grids to 1 km to eliminate movement between grids (Chapter 4). I removed traps from the eastern third of grid X and expanded it westward. Home range
Fig. 2.1 — The study area, showing location of trapping grids H and X. Shading indicates extent of grids at different times (see text for details).
estimates from 1985 were high enough to warrant a coarser level of sampling, so trap-spacing was increased to 42 m.

In 1986 the two grids were trapped for only half the season (see Chapter 4). Both grids were trapped in early May and mid-September, the easternmost grid (grid H) alone was trapped from May to mid-July, and grid X alone was trapped from mid-July to September. The sizes, locations, trap-spacing, and trapping periods of the two grids are summarized in Table 2.1.

Table 2.1--Summary of grid-trapping changes

<table>
<thead>
<tr>
<th>YEAR</th>
<th>SPACING TRAPS</th>
<th>GRID SIZE</th>
<th>PERIOD OF OPERATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>21 m .5 km</td>
<td>H 6 ha</td>
<td>H May thru Aug.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>X 6 ha to July 17, then 8 ha</td>
<td>X May thru Aug.</td>
</tr>
<tr>
<td>1986</td>
<td>42 m 1 km</td>
<td>H 18 ha</td>
<td>H May thru July 16 and mid-Sept.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>X 18 ha</td>
<td>X early May and July 16 thru Sept.</td>
</tr>
</tbody>
</table>

Radio-telemetry

Radio-telemetry was used to locate nest-sites of most adult residents in both years. In 1986 I used telemetry to provide continuous estimates of home range. Radio-transmitters were collar-mounted; each package weighed 2 - 2.5 g, less than 5% of
mean 1986 adult body weight (51 g). Signal strength was too low to permit triangulation of animal locations, so home range data were collected using scan sampling. I walked a regular census route on each grid, leaving the route to track each signal to its source and record its location. Chipmunks readily grew accustomed to my presence and remained apparently undisturbed as long as I did not approach within 5 m. Upon locating an undisturbed animal, I recorded the location, substrate, behaviour over a 1 minute period and food type of those animals which were eating. Location only was recorded if the animal was disturbed, if an assistant was doing the tracking, or if more than one person was present.

Habitat classification

In order to evaluate the association between the home range movements of chipmunks and their habitat, I classified each 30 m by 30 m grid quadrat according to the dominant cover type and substrate. Open and closed forest communities were distinguished from each other according to percent cover of the dominant tree species. Percent cover was recorded as the mean of visual estimates by two different observers, taken over a circle of radius 10 m measured from the grid stake at the centre of each quadrat. Where estimates differed by more than 20 percentage points, percent cover was reassessed by different observers. Quadrats with mean percent cover less than 25% were classed as
open forest; those with cover of over 25%, and in which tree canopies overlapped, were classed as closed forest.

I recognized eight different habitat types (Table 2.2).

<table>
<thead>
<tr>
<th>HABITAT TYPE</th>
<th>SPECIES</th>
<th>SUBSTRATE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Closed spruce -soapberry</td>
<td><em>Picea glauca</em>, <em>Shepherdia canadensis</em>, <em>Hedysarum boreale</em>, <em>Arctostaphylos uva-ursi</em></td>
<td>Fine till</td>
</tr>
<tr>
<td>2. Closed spruce -moss</td>
<td><em>Picea glauca</em>, <em>Shepherdia canadensis</em>, <em>Hedysarum boreale</em>, <em>Arctostaphylos rubra</em>, <em>A. uva-ursi</em>, <em>Lupinus arcticus</em></td>
<td>Soil, moss</td>
</tr>
<tr>
<td>3. Ecotone between open and closed habitats</td>
<td><em>Shepherdia canadensis</em>, <em>Salix spp.</em>, <em>Eleagnus commutata</em>, <em>Arctostaphylos uva-ursi</em>, <em>Hedysarum boreale</em></td>
<td>Fine till</td>
</tr>
<tr>
<td>4. Open poplar, soapberry, spruce</td>
<td><em>Populus balsamifera</em>, <em>Shepherdia canadensis</em>, <em>Picea glauca</em>, <em>Dryas drummondi</em>, <em>Arctostaphylos rubra</em>, <em>A. uva-ursi</em>, <em>Oxytropis campestris</em></td>
<td>Coarser till</td>
</tr>
<tr>
<td>5. Open dryas</td>
<td><em>Dryas drummondi</em></td>
<td>Coarser till</td>
</tr>
<tr>
<td>6. Open spruce -soapberry</td>
<td><em>Picea glauca</em>, <em>Shepherdia canadensis</em>, <em>Dryas drummondi</em>, <em>Arctostaphylos rubra</em>, <em>A. uva-ursi</em>, <em>Oxytropis campestris</em></td>
<td>Coarser till</td>
</tr>
<tr>
<td>7. Dead spruce</td>
<td><em>Picea glauca</em></td>
<td>Very coarse till</td>
</tr>
<tr>
<td>8. Coarse till, soapberry</td>
<td><em>Shepherdia canadensis</em></td>
<td>Very coarse till</td>
</tr>
</tbody>
</table>
Five of these conformed to the habitat classifications of Krebs and Wingate (1976). These were: two closed forest communities, spruce (Picea glauca) -moss and spruce-soapberry (Shepherdia canadensis); two open forest communities, spruce-soapberry and balsam poplar (Populus balsamifera) - soapberry; and Dryas drummondii flats. The spruce-moss community has a sparse herb layer of licorice root (Hedysarum boreale) and bearberry (Arctostaphylos rubra and A. uva-ursi), some sparse soapberry shrub, and almost complete moss cover. The closed spruce-soapberry community has a sparser herb layer, a denser layer of soapberry shrub, and a stony substrate with little moss. The open spruce-soapberry has a substrate of coarser till, and a herb layer dominated by bearberry, Dryas, and locoweed (Oxytropis campestris), that is similar to the herb layer of the open poplar-soapberry community. Three additional habitat types were: bare alluvial till with sparse soapberry, bare alluvial till with dead (drowned) spruce, and an ecotone between the closed and open forest communities characterised by soapberry, willow (Salix glauca), and sometimes silver berry (Eleagnus commutata).
RESULTS

Demography

Jolly-Seber estimation was used to calculate population sizes from the capture-recapture data (Seber, 1982). These results are plotted in Figure 2.2. In 1985, the mean number of animals did not differ significantly between grid H and grid X ($t=2.00$, $p=.10$). On pooled data from both grids, a t-test revealed no significant difference in the number of animals between years ($t=1.91$, $p=.07$). There was an average of 22.6 chipmunks per grid present on both grids over both years. The number of adults on each grid remained stable through the spring and summer season on both grids, although in 1985 the number of males dropped slightly after May, coincident with the end of the mating season. There were more adults on grid H in 1986 (23.4) than in 1985 (13.7) or on grid X in either year (17.2 in 1985, 16.2 in 1986). Since there was a three-fold increase in the size of the grids from one year to the next, numbers of adults should have been higher on both grids in 1986. The asymmetry in the number of new animals occupying the expanded grids could be due to the fact that the expansion of grid H included more favourable habitat types than the expansion of grid X.

The mid-summer population peak evident in Figure 2.2 is the result of juvenile emergence. No population peak is shown for grid H in 1986 since trapping stopped before juveniles were old
Fig. 2.2 -- Jolly-Seber population estimates for Grids X and H
enough to enter traps. The appearance of juveniles in July was consistent from year to year. Chipmunks, including Tamias minimus, breed only once a year in Canada (Criddle, 1943; Forbes, 1966; Sheppard, 1969). Mating tends to occur all at once in late April-early May, birth in late May-early June, and juvenile emergence in July. That there is some variation in this is indicated by the fact that weights of juveniles captured in the same session have a range of approximately 10 g. From Table 2.3 it appears that more juveniles emerged on grid X than on grid H in 1985, but this difference is not significant (t=1.03, p>.50).

![Table 2.3--Population means](image)

Among adults, the sex ratio was consistently biased toward males (1.57 males/female) on grid X. On grid H it was biased toward males in 1985 (1.50 males/female) but was nearly even in
1986 (0.95 males/female). Among juveniles, more females than males were captured on both grids.

Mean minimum survival rates between-sessions (three-weeks) are presented in Table 2.4. Jolly-Seber survival estimates consistently exceeded unity and are therefore not biologically meaningful (Boonstra, 1985).

<table>
<thead>
<tr>
<th>GRID</th>
<th>YEAR</th>
<th>AGE</th>
<th>SEX</th>
<th>SURVIVAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>x</td>
<td>1985</td>
<td>adult</td>
<td>male</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>1986</td>
<td>adult</td>
<td>male</td>
<td>0.82</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>adult</td>
<td>female</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td>1986</td>
<td>adult</td>
<td>female</td>
<td>0.86</td>
</tr>
<tr>
<td>h</td>
<td>1985</td>
<td>adult</td>
<td>male</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td>1986</td>
<td>adult</td>
<td>male</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>adult</td>
<td>female</td>
<td>0.95</td>
</tr>
<tr>
<td></td>
<td>1986</td>
<td>adult</td>
<td>female</td>
<td>0.86</td>
</tr>
<tr>
<td>x</td>
<td>1985</td>
<td>juvenile</td>
<td>male</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>1986</td>
<td>juvenile</td>
<td>male</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>juvenile</td>
<td>female</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>1986</td>
<td>juvenile</td>
<td>female</td>
<td>0.87</td>
</tr>
<tr>
<td>h</td>
<td>1985</td>
<td>juvenile</td>
<td>male</td>
<td>0.67</td>
</tr>
<tr>
<td></td>
<td>1985</td>
<td>juvenile</td>
<td>female</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Adult survival remained high over the summer, averaging 0.89. There were no differences in adult survival between grids or between the sexes. Juvenile survival averaged 0.6, but was generally lower for males (0.44) than for females (0.84).
1985, the year with the most data, juvenile survival was much lower on grid X than on grid H. Nearly twice as many juveniles were captured on grid X in 1985 as on grid H (22 vs. 13), consistent with the different number of breeding females. Seven breeding females were resident on grid X, while 4 were resident on grid H in 1985.

Minimum overwinter survival is listed in Table 2.5. Females survived better than males on both grids, both for adults and for juveniles. On grid H, adults survived better than juveniles, while on grid X the reverse was true.

<table>
<thead>
<tr>
<th>GRID</th>
<th>AGE</th>
<th>SEX</th>
<th>SURVIVAL (N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>h</td>
<td>adult</td>
<td>male</td>
<td>0.75 (8)</td>
</tr>
<tr>
<td>h</td>
<td>adult</td>
<td>female</td>
<td>1.00 (5)</td>
</tr>
<tr>
<td>h</td>
<td>juvenile</td>
<td>male</td>
<td>0.60 (5)</td>
</tr>
<tr>
<td>h</td>
<td>juvenile</td>
<td>female</td>
<td>1.00 (7)</td>
</tr>
<tr>
<td>x</td>
<td>adult</td>
<td>male</td>
<td>0.56 (9)</td>
</tr>
<tr>
<td>x</td>
<td>adult</td>
<td>female</td>
<td>0.75 (4)</td>
</tr>
<tr>
<td>x</td>
<td>juvenile</td>
<td>male</td>
<td>0.67 (3)</td>
</tr>
<tr>
<td>x</td>
<td>juvenile</td>
<td>female</td>
<td>1.00 (6)</td>
</tr>
</tbody>
</table>

Adult weight averaged 50.4 g over both grids and both years (Table 2.6) and did not differ significantly between years. Weights were low when animals were first trapped in May (mean = 44.9 g), and increased to an average of over 50 g by early June. From this point, male weight remained relatively stable over the summer, while female weight increased. Females were heavier by 5 g on average while lactating than during pregnancy. The smallest
juveniles to enter traps weighed 29 g, but rapidly grew to adult weight. By September, mean juvenile weight (49.7 g) did not differ from mean adult weight (50.4 g).

Weights used to calculate means in Table 2.6 were obtained by weighing each captured animal once per trap-session. There are up to seven repeated weighings per animal per year, so the means are not derived from entirely independent measurements.

<table>
<thead>
<tr>
<th>YEAR</th>
<th>ADULT MALES</th>
<th>ADULT FEMALES</th>
<th>JUVENILES</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>47.2</td>
<td>53.1</td>
<td>44.3</td>
</tr>
<tr>
<td></td>
<td>(37 - 57)</td>
<td>(40 - 65)</td>
<td>(31 - 52)</td>
</tr>
<tr>
<td>1986</td>
<td>47.8</td>
<td>52.6</td>
<td>48.0</td>
</tr>
<tr>
<td></td>
<td>(39 - 57)</td>
<td>(39 - 64)</td>
<td>(29 - 53)</td>
</tr>
</tbody>
</table>

When live-trapping began in May, males were already in breeding condition and remained so until the end of May. In 1986, breeding was underway by late April. I observed several mating chases at the end of April when the traps were still buried in snow. In both years, all males captured in May were in breeding condition. Females began lactating in late May in 1985 and in early June in 1986. They had finished lactating by the beginning of August. This agrees with Criddle's (1943) estimate of a 30-day gestation period for Tamias minimus borealis. In 1985, each grid had one resident female that did not breed. In 1986, the same resident female on grid H was the only female that did not breed. For both sexes, all of the yearlings captured on
the grids bred during their first breeding season. This contrasts with Sheppard (1969) who found that Tamias minimus oreocetes in western Alberta did not breed in the spring following their birth.

Juveniles were first observed on the study area on June 29, 1985 and on June 30, 1986. Juveniles first entered traps on July 10 in both years. This supports Hirshfeld and Bradley's (1977) estimate of juvenile emergence at 5 weeks of age for Tamias panamintinus and T. palmeri. No estimates of recruitment are presented here because the expansion of grids and low trappability of young juveniles precluded that analysis.

Home Range

Home range was estimated from the telemetry data for 23 animals in 1986. Twenty-five chipmunks were fitted with radio-collars, but two (both females from grid H) were excluded from home range calculations. Female 60 was excluded because nearly half of her telemetry locations were across Silver Creek from the grid. Female 108 was excluded from all analysis because she developed a severe eye infection that might have been caused by an infection on her neck due to the tightness of her collar. She became trap-shy until the end of the summer, when I was finally able to remove the collar. Except in early May when some of the other collars were too tight and caused chafing around the neck (and for which the data were also excluded), the other chipmunks
did not appear to suffer adverse effects from wearing radio-collars.

A total of 1238 telemetry locations, collected from May through September, were used to estimate home ranges. Home range sizes were calculated by the minimum convex polygon method, based on a minimum of 20 locations, with an average of 54 points per home range. Mares et al (1980) found that 20 captures was the minimum number necessary to accurately estimate home range of the eastern chipmunk. Home range areas range from 0.97 ha to 9.65 ha with a mean area of 4.86 ha (S.D.=2.35). Home ranges of males (mean=6.13 ha, S.D.=1.96) were significantly larger than those of females (mean=2.89 ha, S.D.=1.331), t=4.34, p<.001. Analysis of other aspects of chipmunk home range appear in Chapters 3 and 4.

**Habitat preference**

To assess habitat preference, I used the habitat classification data to construct a habitat map for each grid (Fig 2.3). Habitat types are listed in Table 2.2.

On grid X, all 8 habitat types are represented, while on grid H only 4 of them occur: closed spruce-soapberry, ecotone, open poplar-soapberry and Dryas flats. Both the live-trapping and the telemetry location data were plotted on this map to test for associations between habitat type and frequency of use. For the live-trapping data, I used a G test to compare the frequency
Fig. 2.3 -- Habitat maps: (a) Grid X, (b) Grid H

1. Closed spruce soapberry
2. Closed spruce moss
3. Ecotone
4. Open poplar soapberry
5. Dryas flats
6. Open spruce soapberry
7. Dead spruce
8. Open till soapberry
of capture in each vegetative community with that expected from the proportion of traps set in that community. Tests were performed separately for the two grids and for each size of each grid, since the distribution of traps in the habitat differed after each expansion.

For grid H, use differed significantly from trap distribution in both years: $G=23.578$ for 1985; for 1986 $G=22.945$, $p<.001$ in both years. In both years, chipmunks were captured less frequently in closed spruce-shepherdia habitat and more frequently in open poplar-shepherdia habitat than expected from trap distribution. Observed and expected frequencies were equal for the ecotone, but chipmunks were captured less often than expected on Dryas meadow in 1985, but more often than expected in 1986. Dryas meadow was the only habitat type not represented in the expansion of grid H. Changes between years were therefore due to changes in the sampling distribution.

For grid X, G tests comparing frequency of capture in each habitat type with relative number of traps set there were significant on all three grid sizes. For the smaller 1985 grid from which the poplar-soapberry and dead spruce habitats were absent, $G=12.107$, $df=5$ and $.025<p<.05$. For the expanded 1985 grid on which all eight habitat types occurred, $G=22.107$, $df=7$ and $.001<p<.005$. For the 1986 grid from which closed spruce-soapberry habitat was absent, $G=198.2$, $df=6$ and $p<.001$.

When closed spruce-shepherdia habitat occurred on grid X fewer captures were located there than expected. For the closed
spruce-moss habitat, observed number of captures was nearly equal to the number expected on the smallest grid X. After the grid was expanded, more of it was in spruce-moss habitat, and far fewer captures than expected occurred there. For all three sizes of the grid, the number of captures in open spruce-soapberry and in Dryas habitat was greater than expected. The number of captures in ecotone was less than expected in the small and medium versions of the grid, but greater than expected in the large version of the grid. The till-soapberry habitat had a greater than expected number of captures, while the till-dead spruce had fewer captures than expected for the medium grid and more than expected for the large grid. These results are summarized in Table 2.7. A "+" indicates that number of captures observed is greater than expected, a "-" indicates that observed number of captures is less than expected, "0" means that observed number of captures equalled expected number, and the absence of data is indicated by a ".". Trapping results show that chipmunks prefer open habitat types (4, 5, 6, and 8) over closed spruce forest (habitats 1 and 2). Results are inconclusive for the ecotone and dead spruce habitats (3 and 7).
Table 2.7—Summary of habitat preferences from trapping data.

<table>
<thead>
<tr>
<th>HABITAT TYPE</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>H 85</td>
<td>-</td>
<td>.</td>
<td>0</td>
<td>+</td>
<td>-</td>
<td>.</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>H 86</td>
<td>-</td>
<td>.</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>.</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>X 85, 6ha</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>.</td>
<td>+</td>
<td>+</td>
<td>.</td>
<td>+</td>
</tr>
<tr>
<td>X 85, 8ha</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>X 86</td>
<td>.</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

The same tests were performed on telemetry locations inside trapping grids. Habitat types were used non-randomly on both grids (p<.001). Observed and expected numbers of locations are plotted in Figure 2.4. For grid H the telemetry results were similar to the trapping results for 1986. The telemetry results for grid X were less consistent with the trapping results. Grid X trapping and telemetry results both show a positive association with open spruce-soapberry and open till-soapberry (types 6 and 8) and a negative association with closed spruce-moss (type 2). However, telemetry data were positively associated with ecotone (type 3), while trapping results were inconclusive. There is a strong positive association with Dryas flats and open poplar-soapberry (types 4 and 5) in the trapping data, but for telemetry data observed locations do not differ from the number expected.
Fig. 2.4 — Observed and expected number of telemetry locations vs. vegetation type.

1. Closed spruce soapberry
2. Closed spruce moss
3. Ecotone
4. Open poplar soapberry
5. Dryas flats
6. Open spruce soapberry
7. Dead spruce
8. Open till soapberry
I compared the habitat preferences of adults and juveniles using the recapture data for 1985, when juvenile recapture data were most numerous (Figure 2.5). The habitat use index was calculated by dividing the percent of captures observed in a given habitat by the percent of captures expected in that habitat. Juveniles had a greater proportion of captures in habitat types such as dead spruce, soapberry and till, spruce-moss and closed spruce-soapberry than adults.

**DISCUSSION**

*Demography*

I found no evidence of pronounced year-to-year fluctuation in numbers of least chipmunks at Kluane contrary to Callahan (1950) who asserts that wide population fluctuations are typical of western chipmunks. This contrasts with Tryon and Snyder (1973) who reported a 3-4 year population cycle in eastern chipmunks. Their data did not support their claim, however, since peak populations were only 2-3 times the size of the lowest populations. Two demographic studies of Tamias townsendii found evidence only of 2- to 3-fold annual fluctuations (Gashwiler, 1970; Sullivan et al, 1983).
Fig. 2.5 — Habitat use index for adults and juveniles vs. habitat type. Value of index for each habitat type = % captures observed / % captures expected.

1. Closed spruce soapberry
2. Closed spruce moss
3. Ecotone
4. Open poplar soapberry
5. Dryas flats
6. Open spruce soapberry
7. Dead spruce
8. Open till soapberry
present study it is impossible to tell whether chipmunks select ecotone, avoid ecotone or are indifferent to it. This probably reflects a problem with my habitat classification scheme, rather than indecision on the part of chipmunks. Results may have been more consistent if I had divided ecotone further into categories according to the habitat types that bordered it.

Home range

The home range sizes of least chipmunks in the Yukon were 4 to 120 times size of least chipmunk home ranges in other areas (Table 2.8). Different methods used complicate these comparisons, since the minimum area method and grid squares square area method generally yield smaller home range estimates than does the minimum convex polygon method used in the present study. In most of these studies, capture points were sufficiently clumped that use of the convex polygon method would have added only a fraction of the estimated area to the figure listed here, so this does not preclude comparison. Sample size presents more of a problem, since the methods used here are all dependent on sample size. Feldhamer (1979) was the only study in which sample sizes were low enough to severely underestimate home range.

In most cases, home range areas listed are the means for adults only, as in the present study. For studies in which home range areas were reported during the course of an experimental manipulation, home ranges listed here are for the control area.
<table>
<thead>
<tr>
<th>STUDY / LOCATION</th>
<th>SPECIES</th>
<th>METHOD</th>
<th>HOME RANGE (ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blair 1942 Michigan</td>
<td>Tamias striatus</td>
<td>Trapping. Minimum convex polygon (MCP).</td>
<td>0.90</td>
</tr>
<tr>
<td>Broadbrooks 1970 Washington</td>
<td>T. amoenus</td>
<td>Trapping. No. traps used * trap-unit area.</td>
<td>1.20</td>
</tr>
<tr>
<td>Burt 1940 Michigan</td>
<td>T. striatus</td>
<td>Trapping. MCP.</td>
<td>0.62</td>
</tr>
<tr>
<td>Chappell 1978 California</td>
<td>T. minimus T. amoenus T. speciosus</td>
<td>Trapping. No. traps used * trap-unit area.</td>
<td>1.05 1.31 1.39</td>
</tr>
<tr>
<td>Elliott 1978 New York</td>
<td>T. striatus</td>
<td>Observation. No. quad. used * area.</td>
<td>0.17</td>
</tr>
<tr>
<td>Feldhamer 1979 Oregon</td>
<td>T. minimus</td>
<td>Trapping. Standard diameter.</td>
<td>0.04</td>
</tr>
<tr>
<td>Forsyth and Smith 1973, Ont.</td>
<td>T. striatus</td>
<td>Trapping. Minimum area.</td>
<td>0.18</td>
</tr>
<tr>
<td>Glennie, 1988 Yukon</td>
<td>T. minimus</td>
<td>Telemetry. MCP.</td>
<td>4.86</td>
</tr>
<tr>
<td>Mares et al 1976, Penn.</td>
<td>T. striatus</td>
<td>Trapping. MCP.</td>
<td>0.11</td>
</tr>
<tr>
<td>Mares et al 1982, Penn</td>
<td>T. striatus</td>
<td>Trapping. Minimum area.</td>
<td>0.09</td>
</tr>
<tr>
<td>Martinsen 1968 Montana</td>
<td>T. minimus T. amoenus</td>
<td>Trapping. MCP.</td>
<td>1.14 0.86</td>
</tr>
<tr>
<td>Sheppard 1972 Alberta</td>
<td>T. minimus T. amoenus</td>
<td>Trapping. Minimum area.</td>
<td>0.85 0.99</td>
</tr>
<tr>
<td>States 1976 Oregon</td>
<td>T. amoenus</td>
<td>Trapping. Boundary strip.</td>
<td>0.75</td>
</tr>
<tr>
<td>Yerger 1953 New York</td>
<td>T. striatus</td>
<td>Observation and Trapping. MCP.</td>
<td>0.07</td>
</tr>
</tbody>
</table>
There have been several attempts to predict life-history parameters on the basis of body size (Blueweiss et al, 1978; Eisenberg, 1981; Peters, 1983; Western, 1979). Much of this work was inspired by an early paper by McNab (1963) in which he reported that home range was related to body mass: A=2.70M0.63 (where area is expressed in hectares, mass in kilograms). Mace and Harvey (1983) have derived allometric equations for the relation of home range to body size for rodents. They separated taxa into three trophic groups: herbivores, granivores, and omnivores. Yukon chipmunks are largely granivorous so their predicted home range size (in ha) scales as 0.007M1.12 (where mass is in grams). The home range size of Tamias minimus at Kluane is 4.86 ha, 12 times that predicted by McNab's equation for a 50 g animal, 0.409 ha, and it is 8.8 times that predicted by Mace and Harvey's equation for granivores, 0.56 ha.

Examining Table 2.6 reveals that Tamias does not follow the allometric principle that larger animals should have larger home ranges. Of all the chipmunk species listed, the eastern chipmunk, Tamias striatus, has the smallest home range, but it is also the heaviest (about 100 g). Home range size predictions from the allometric equations, 0.63 ha from McNab, 1.23 ha from Mace and Harvey for granivores, generally exceed the home range sizes listed here. Western chipmunks listed here have larger home ranges than their eastern congeners, usually over 1 ha, but only weigh about 50 g, so that the allometric equations provide underestimates of home range. These discrepancies indicate that
factors such as latitude, food availability, and population density outweigh the influence of body size. For this genus the McNab approach has little predictive value, and this is likely to be generally true at the taxonomic level of the genus where more detailed information is needed to account for differences in life-history characteristics.

SUMMARY

I compared demography, habitat choice and home range of a population of least chipmunks at Kluane Lake with previous studies of chipmunks. Population size is lower than in most previous studies of this and other chipmunk species, but the year-to-year stability of the population is similar to that found in other chipmunk species. Home range sizes are at least 4 times greater than any reported for the genus. Habitat use comparison with previous studies is limited by the fact that they were conducted in different habitat at distant locations (Sierra Nevada, California; the central Rocky Mountains in Alberta; and the mountains of Oregon). I found that Yukon chipmunks prefer shrub-land and open forest to closed canopy forest, which is generally consistent with the findings of previous studies.
There have been several attempts to predict life-history parameters on the basis of body size (Blueweiss et al, 1978; Eisenberg, 1981; Peters, 1983; Western, 1979). Much of this work was inspired by an early paper by McNab (1963) in which he reported that home range was related to body mass: \( A = 2.70M^{0.62} \) (where area is expressed in hectares, mass in kilograms). Mace and Harvey (1983) have derived allometric equations for the relation of home range to body size for rodents. They separated taxa into three trophic groups: herbivores, granivores, and omnivores. Yukon chipmunks are largely granivorous so their predicted home range size (in ha) scales as \( 0.007M^{1.12} \) (where mass is in grams). The home range size of *Tamias minimus* at Kluane is 4.86 ha, 12 times that predicted by McNab's equation for a 50 g animal, 0.409 ha, and it is 8.8 times that predicted by Mace and Harvey's equation for granivores, 0.56 ha.

Examining Table 2.6 reveals that *Tamias* does not follow the allometric principle that larger animals should have larger home ranges. Of all the chipmunk species listed, the eastern chipmunk, *Tamias striatus*, has the smallest home range, but it is also the heaviest (about 100 g). Home range size predictions from the allometric equations, 0.63 ha from McNab, 1.23 ha from Mace and Harvey for granivores, generally exceed the home range sizes listed here. Western chipmunks listed here have larger home ranges than their eastern congeners, usually over 1 ha, but only weigh about 50 g, so that the allometric equations provide underestimates of home range. These discrepancies indicate that
factors such as latitude, food availability, and population density outweigh the influence of body size. For this genus the McNab approach has little predictive value, and this is likely to be generally true at the taxonomic level of the genus where more detailed information is needed to account for differences in life-history characteristics.

SUMMARY

I compared demography, habitat choice and home range of a population of least chipmunks at Kluane Lake with previous studies of chipmunks. Population size is lower than in most previous studies of this and other chipmunk species, but the year-to-year stability of the population is similar to that found in other chipmunk species. Home range sizes are at least 4 times greater than any reported for the genus. Habitat use comparison with previous studies is limited by the fact that they were conducted in different habitat at distant locations (Sierra Nevada, California; the central Rocky Mountains in Alberta; and the mountains of Oregon). I found that Yukon chipmunks prefer shrub-land and open forest to closed canopy forest, which is generally consistent with the findings of previous studies.
CHAPTER 3: SPACE USE AND SOCIAL STRUCTURE IN THE LEAST CHIMPUNK

INTRODUCTION

This chapter discusses the effects of social structure on the use of space in a population of least chipmunks (*Tamias minimus*) in the southwest Yukon. Chipmunk populations exhibit stability (Chapter 2) compared to populations of other small rodents which experience marked multi-annual fluctuations (Taitt and Krebs, 1985). For example, in my study area, *Clethrionomys rutilus* and *Microtus pennsylvanicus* fluctuate widely in numbers (Krebs and Wingate, 1985).

Social spacing has long been associated with the regulation of population density (Calhoun, 1949; Wynne-Edwards, 1962; Watson and Moss, 1970). Social interactions affecting space use can limit an animal's access to food, shelter, mates, travel routes, or bar it completely from certain areas. Explanations based on spacing behaviour have been used to explain both cyclic (Christian, 1950; Chitty, 1967) and stable populations (Healy, 1967).

This study set out to establish if, and in what form social spacing occurs in the least chipmunk at Kluane Lake. Three types of social spacing were considered: territoriality, space-related dominance and encounter avoidance. These types of social structure have each been previously documented for *Tamias*.

Of these three types, territoriality is the most restrictive. In a territorial system, animals have fixed, defended core areas from which others are excluded. Definitions of ter-
ritoriality vary, emphasizing either exclusive occupancy (e.g. Pitelka, 1959; Schoener, 1968) or defense (Noble, 1939). In studies of Tamias striatus, Burt (1940), Yerger (1953), and Yahner (1978) claimed that these chipmunks were territorial. Broadbrooks (1970) found evidence of territorial behaviour in Tamias amoenus, and Brand (1976) suggested territoriality was typical for western chipmunks.

Space-related dominance is similar to territoriality, but an exclusively defended core area is lacking. Individuals do not patrol territories and exclude all intruders, but are dominant in agonistic interactions within their core areas and have prior access to resources there. Numerous studies on chipmunks (e.g. Dunford, 1970; Elliott, 1978) have reported the existence of this social system.

Encounter avoidance was first documented in chipmunks by Getty (1981). Space is partitioned in time, either by spacing at regular intervals at a given time, or by maintenance of a minimum distance between neighbours. Spacing is not actively maintained by aggressive behaviour, but by avoiding interactions.

I tested to see which of these 3 systems of space use applied to the least chipmunk at Kluane Lake. Territorial animals will have home ranges with minimal overlap and maintain non-overlapping core areas. A systematic monitoring of home ranges would be sufficient to detect this.

Space-related dominance does not predict exclusive core areas, but predicts aggressive defense of core areas. Encounters
should result in agonistic interactions in which dominance is determined by the location of the encounter. This prediction can be tested by observing and comparing outcomes of interactions at different locations on the study site.

Encounter avoidance predicts that encounters will be less frequent than would be expected based on the degree of home range overlap and random movement within home ranges. This can be tested by comparing the frequency of encounters measured by telemetry with encounter frequency from a simulation model constructed using real home range parameters and random movement patterns. I define an encounter as an event in which two chipmunks are close enough to each other that each is aware of the presence of the other. In my analysis I used an encounter radius of 30 m. An encounter does not necessarily involve a social interaction.

METHODS

The study area, trapping and telemetry techniques were described in Chapter 2. From the telemetry and recapture data I calculated the home range area and overlap for each animal using the minimum convex polygon method (Southwood, 1966, p.262). This method is simple to use, statistically stable (Jennrich and Turner, 1969) and facilitates comparison with previous studies.
Behavioural observation

During the summer of 1985 I investigated the occurrence and rates of behavioural interactions. Population density and activity levels of chipmunks were too low for natural interaction rates to provide sufficient data to assess spacing behaviour. I therefore provoked interactions by placing piles of sunflower seeds at sites spaced systematically over the grids in open areas where chipmunk activity was highest. From a distance of 5 m I observed interactions among pelage-marked chipmunks which were attracted to the seed piles.

Observations were divided into bouts. A bout began when two or more chipmunks began an interaction, and ended when one or more of them was displaced, or when a new animal appeared. For each bout the identities of the participants were recorded and the bout was scored as either a win-loss, a draw, or tolerance. A win-loss was defined as an interaction in which the winner displaced the loser from the seed pile by means of aggressive behaviours such as threats, lunges, chases and fights. Similar behaviours have been described by Aniskowicz and Vaillancourt (1979) for the eastern chipmunk. A draw occurred when animals behaved aggressively but neither displaced the other. Tolerance occurred when animals showed no aggressive behaviour, but behaved amicably or ignored each other.
Encounter avoidance

In 1986 telemetry was used to determine whether animals were avoiding encounters. Actual encounter frequencies were compared with encounter frequencies generated by a simulation model of random movement within home ranges (program listing in Appendix 1). I obtained estimates of encounter frequency from the telemetry data using sampling windows 90 minutes in length. In each sampling window distances among positions of all animals are calculated and compared against an encounter radius of 30 m. All inter-neighbour distances up to 30 m are classified as encounters. The telemetry data do not provide truly simultaneous positional estimates for all animals. Since the average elapsed time between locations of animals in encounters is 15 minutes, I do not consider this problem to be serious.

The number of animals wearing radio-collars at the same time on the same grid varied from 0 to 9. In this analysis I used only sampling windows in which four or more animals carried transmitters. For this reason I used only the grid H telemetry data. Due to the shortage of functioning radio-collars, there were rarely more than 4 chipmunks on grid X equipped with transmitters at the same time.

The random model (which generates encounter data to compare with actual encounter rates) utilizes the following home range attributes from the actual data. For each chipmunk whose movement is simulated, positions of nest site and centre of
activity were obtained from the trapping and telemetry data. The model also uses values for maximum distance from centre of activity, time active above ground, and probability of changing location that were derived from the data. Computer generated location data were mapped on the same coordinate system as the study grids to facilitate comparison.

The algorithm used in the model is illustrated in figure 3.1. Initial input includes the number and identity of chipmunks sampled and the month. When the run begins, each animal decides whether or not to move (probability is 50%). If it moves it leaves its nest site and moves 1 grid coordinate (15 m) in a randomly chosen direction: any of 360 degrees. Simulated chipmunks remain within the specified maximum distance from centre of activity (180 m for males, 90 m for females); movements beyond this boundary are preempted, and a new direction randomly chosen that keeps the animal within its maximum distance. This process repeats until the end of each time interval, when the distances among all chipmunk positions in the model are calculated. These distances are compared with the specified encounter radius to determine the number of simulated encounters. Each run simulates one day's activity. The number of encounters generated for the period that corresponds to the sampling window can then be compared with number of encounters recorded in the field.
Fig. 3.1 -- Flowchart of random-encounter simulation model.
# of chipmunks

chipmunk identities

Define:
- nest sites
- activity centre
- max. range

month

length of active day

snapshot interval

start

for each chipmunk

move?

more chipmunks?

set time

start day

choose direction

calc. new location

within bounds?

snapshot?

end of day?

N

Y

relocate

encounter statistics

encounter statistics

number of encounters

stop

end of day?

N

Y

snapshot?

N

Y

choose direction

within bounds?

relocate
RESULTS

Home range overlap

Home range overlap between neighbours was determined by measuring the percentage of spatial overlap of convex polygons. I calculated overlap separately using the trapping and telemetry data. For the trapping data, all chipmunks with more than 5 non-linear recaptures were included in calculation of home range overlap. Five captures is seldom sufficient to yield accurate estimates of home range area, but including these home ranges in the overlap analysis gives a better indication of the degree of crowding than could be obtained by excluding them.

According to trap-based estimates of home range, mean home range overlap was 94.3% for all animals combined. Each home range was overlapped by an average of 14.9 others (Table 3.1). Overlap on female home ranges by other females averaged 75.1%; this does not differ significantly from male-male home range overlap, 70.4%. Male home ranges were overlapped by more male neighbours than female home ranges are overlapped by female neighbours (6.5 vs.4.0). This is consistent with the male-biased sex ratio.

The telemetry-based estimate of home range overlap was 86.8%
for all individuals combined, lower than the trap-based estimate, since not all animals were radioed. In terms of intensity of use, the amount of home range overlap revealed by telemetry was substantially higher than 86.8%. Within a chipmunk home range, the area which does not overlap with any neighbouring home range contains an average of only 8% of the "owner's" radio-locations. These exclusive areas do not, therefore, correspond to core areas, as a core area is generally understood to be the part of its range which the animal frequents the most. Telemetry-based home range maps are presented in Figures 3.2 and 3.3.

<table>
<thead>
<tr>
<th>SOURCE</th>
<th>PERIOD</th>
<th>PERCENT OVERLAP</th>
<th>NO. NEIGHBOURS OVERLAPPED</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>ALL F M</td>
<td>F M</td>
<td>ALL F M</td>
</tr>
<tr>
<td>Trap</td>
<td>2.5 mo.</td>
<td>94.3 75.1 70.4</td>
<td>14.9 4.0 6.5</td>
</tr>
<tr>
<td>Telem</td>
<td>4.5 mo.</td>
<td>86.8 65.2 82.0</td>
<td>6* 3* 5.2*</td>
</tr>
<tr>
<td>Telem</td>
<td>12 May-10 June</td>
<td>80.1 60.0 73.6</td>
<td>5* 2.5* 4.7*</td>
</tr>
<tr>
<td>Telem</td>
<td>11 Jun-20 July</td>
<td>76.2 52.0 76.0</td>
<td>5* 2.5* 5*</td>
</tr>
<tr>
<td>Telem</td>
<td>21 Jul-12 Sept</td>
<td>83.0 62.6 78.8</td>
<td>6* 3* 5*</td>
</tr>
</tbody>
</table>

Home range shifts occurred between May and the end of September, especially among females that had just finished weaning their young. I therefore divided all of the telemetry data into three periods based on female breeding condition: pre-
Fig. 3.2 — Telemetry-based home range map of Grid H. Coordinates from 1 to 37 on the y-axis and from 1-29 on the x-axis are within the grid boundaries. One grid coordinate = 15 m.
Fig. 3.3 -- Telemetry-based home range map of Grid X. Coordinates from 1 to 29 on both axes are within grid boundaries. One grid coordinate = 15 m.
lactating (May 12 to June 10), lactating (June 11 to July 20) and post-lactating (July 21 to September 12). Home range overlap is less during these discrete periods than when calculated over the entire field season, but even for lactating females, who were most often located near their nest sites, overlap is always greater than 50%.

**Behavioural observation**

Behavioural observations during the summer of 1985 began after the mating season and provided interaction data on 35 chipmunks, 14 of them on grid H, the other 21 on grid X. During 240 hours of observation, 353 bouts were recorded, of which 315 (89%) were aggressive. Each bout involved two animals, so that an average of twenty bouts were recorded for each animal. Each animal interacted with an average of 6 neighbours. Thus, even if interactions were divided evenly among neighbours, the total of 353 bouts recorded would yield only 3.3 bouts per pair of neighbours. The data obtained are therefore too sparse to document dominance reversals for each individual with its neighbours.

However, the relationship between dominance and location can be explained by looking at the data on a bout-by-bout basis. For all win-loss bouts, there was no significant difference between winners and losers in the mean distance from the location at which the interaction occurred to the centre of the participant's
home range on either grid (grid X, paired samples $t = 1.32$, $p = .19$, $df = 109$; grid H, paired samples $t = .41$, $p = .68$, $df = 162$). Nor was there any significant difference when the same analysis was repeated for distance from interaction location to nest site (nest sites were known for 19 chipmunks). Using data from both grids, paired samples $t = .67$, $p = .51$, $df = 220$ (Table 3.2).

<table>
<thead>
<tr>
<th>Table 3.2 -- Mean distances from interaction to home</th>
</tr>
</thead>
<tbody>
<tr>
<td>GRID CATEGORY</td>
</tr>
<tr>
<td>----------------</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>X</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>H</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>

Only bouts between animals resident on the grid where the encounter occurred were included in the previous analysis, since estimates of burrow sites and home range centres were unavailable for non-residents. Twenty-eight bouts (8% of the total) occurred between residents and non-resident intruders. Twenty-four of these resulted from unprovoked interactions and included the only instances of fighting that I witnessed over the entire season. The intruders won only 7 of the 28 encounters. This frequency differs significantly from the frequency expected if intruders were as likely to dominate in interactions as residents ($X^2 = 7.0$, $p < 0.01$, $df = 1$). Bouts with intruders were usually
initiated by residents that were subordinate to other residents on the grid. Of the bouts lost by intruders, 71% were lost to non-breeding animals which were lighter than the intruders.

For all win-loss bouts, the mean weight of winners (50.9 g) was slightly but significantly higher than the mean weight of losers (49.3 g, t = 3.43, p = .001, df = 314). Chi-square tests were used to determine whether sex, age, and breeding condition were related to dominance. The sex of the participants did not affect the outcome of interactions ($X^2 = .72, p = .40, df = 1$). Adults won in all aggressive interactions with juveniles ($X^2 = 19.37, p < .001, df = 1$) which tended to be more aggressive than interactions with other adult residents. The effects of breeding condition were analyzed only for females, since most behavioural observation took place after May 20, at which point males were not in breeding condition. Breeding females won significantly more interactions than females which never bred ($X^2 = 15.51, p < .001, df = 2$). Bouts involving breeding females were divided into 3 categories according to whether they were pregnant, lactating, or post-lactating. Lactating females won interactions more often than pregnant and post-lactating females ($X^2= 5.12, p<.025, df=1$).

**Encounter avoidance**

If encounter avoidance occurs, it should be most apparent while females are lactating, since their movements are more
restricted and they win a greater proportion of interactions at that time. Therefore, encounter frequencies during pre-lactating, lactating, and post-lactating periods were compared separately with the model's output. The results are presented in Table 3.3. For the pre-lactating and lactating periods, encounter frequency was significantly less than that generated by the random model, so the samples were pooled \( (t=2.41, \ p = .02, \ df=45) \). For the post-lactating period, encounter frequency did not differ significantly from the model \( (t=1.30, \ p=0.20, \ df=42) \).

<table>
<thead>
<tr>
<th>PERIOD</th>
<th>MEAN ENCOUNTERS</th>
<th>MEAN ENCOUNTERS GENERATED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-lactating</td>
<td>0.48</td>
<td>1.16</td>
</tr>
<tr>
<td>Lactating</td>
<td>0.86</td>
<td>1.19</td>
</tr>
<tr>
<td>Post-lactating</td>
<td>1.37</td>
<td>1.23</td>
</tr>
</tbody>
</table>

**DISCUSSION**

From the home range data presented here, the hypothesis that least chipmunks at Kluane Lake are territorial can be conclusively rejected. Both trap and telemetry-based estimates of home range overlap demonstrate that exclusive core areas do not exist.
Territoriality can also be rejected using Noble's (1939) definition of territory, which emphasizes defense rather than exclusivity as diagnostic of territoriality. Home ranges are too large to be patrolled and defended. Intensive use is centred on the same grid areas for all animals whose home ranges overlap these areas; they cannot be defending core areas.

The absence of territoriality in Tamias minimus at Kluane Lake does not specifically contradict previous studies. Territoriality in chipmunks has been reported for dense populations of Tamias striatus and Tamias amoenus. The social system of the least chipmunk has never been specifically examined, previous studies have considered agonistic behaviour in least chipmunks only in order to evaluate the importance of competition among species of western chipmunks (Heller, 1971; Sheppard, 1971; States, 1976; Chappell, 1978).

Little evidence was found for space-related dominance. Social dominance appears to be based on individual characteristics such as size and age rather than ownership of space. Size, age and breeding condition are typically related to dominance in studies of social dominance that lack any spatial component. An exception to the apparently space-independent pattern of social dominance was evident in the interactions between residents and non-residents. Non-residents were generally heavier than the residents which defeated them, which is contrary to the trend reported above. Three of the intruders were resident on another grid where each of them was socially dominant. These three
There is another factor which casts doubt on the apparently agonistic social structure revealed here. Six of the located nests were within 15 m of another chipmunk nest. In addition, a group of three males were repeatedly observed sharing a nest, as were a male and female pair after juveniles were weaned at the end of August. These animals behaved amicably while sharing nests, yet interacted aggressively at seed piles on the grids. Brown (1964) suggested that territorial behaviour is only adaptive where the contested resource is distributed so that it is economically defendable. My sunflower seed piles constituted a rich, discrete, defendable resource, and their presence resulted in behaviours which were not typical of the normal behaviours of chipmunks at Kluane. In August 1986, chipmunks were frequently observed feeding on seasonally abundant Shepherdia berries at inter-individual distances of less than three meters without any sign of aggressive behaviour. In 1985, inter-individual distances of 7 m at seed piles were often sufficient to provoke aggressive interactions.

Previous studies of chipmunk social behaviour that have reported aggressively maintained spacing mechanisms, especially studies of western chipmunks, have relied either on lab trials or provoked interactions. I believe that aggressively maintained social spacing was absent at Kluane for the reasons given above. However, the relationship between the frequency of artificially provoked interactions and naturally occurring interactions needs
to be studied before this conclusions can be confirmed.

On the basis of the difference between encounter rates in the data and the random model, I conclude that encounter avoidance occurred. The comparison is limited by the fact that the data were not gathered simultaneously, and by the length of the defined encounter radius. Automatic scan sampling would have provided simultaneous data, but for an area as large as an average chipmunk home range, and with the forested habitat causing signal bounce, this was not feasible.

These results suggest that the social structure of low-density populations of Tamias minimus is determined by ecological constraints such as the restriction of movements during lactation, and the necessity of harvesting seasonally-abundant food resources, rather than by space-related interactions. The fact that spacing in the post-lactating period did not differ from random may have resulted from chipmunks harvesting Shepherdia berries in the month of August. Mutual tolerance while feeding and the sharing of nests among adults indicate that naturally occurring aggression was relatively rare among least chipmunks at Kluane. This suggests that encounter avoidance is maintained passively.

It is also possible that observed instances of amicable behaviour occurred among chipmunks which were related to each other. Relatively high survival rates (Chapter 2) and the longevity of the species (up to 6 years according to Criddle, 1943) could result in a high degree of relatedness among neigh-
Heller (1971) and States (1976) found that least chipmunks were less aggressive than congeners living in adjacent habitat, although this contradicted other studies of the same congeners (Sheppard, 1971; Chappell, 1978). Heller invokes the concept of economic defendability (Brown, 1964) and suggests that aggressive behaviour is metabolically infeasible in the least chipmunk due to the physiological stress that would ensue in the sage-brush desert habitat the species occupies. Aggressive behaviour may also have been inhibited by coexistence with larger and aggressively dominant congeners. Isolated from congeneric species, least chipmunks in the Yukon are near the northern limit of their range where different metabolic constraints apply. They may have little need for aggressively maintained spacing behaviour because of their constant, low, population density, and very large home ranges. Aggressive defense of resources may in fact be prohibited by the requirement of hoarding sufficient food for winter during the short snow-free season.
CHAPTER 4: THE INFLUENCE OF GRID-TRAPPING ON SPACE USE AND HOME RANGE IN THE LEAST CHIPMUNK

INTRODUCTION

This chapter investigates two possible effects of grid-trapping on home range. Firstly, it asks whether the presence of a trapping grid changes the actual home ranges of the animals that live there. The presence of traps could increase the availability of two resources: food and cover. Are these changes sufficient to distort home range? Secondly, it asks how trapping affects the measurement of home range. Does it provide an accurate measure of home range compared to that afforded by telemetry?

Criticisms of grid-trapping as a method for home range estimation are common (Hayne, 1950; Sanderson and Sanderson, 1964; Banks et al, 1975; Cranford, 1977), but points of criticism are confined to properties of grid-trapping such as low numbers of recaptures, the amount of time required to accumulate sufficient captures, assumptions about travel distance between traps and lack of continuous data. Home range is often underestimated by grid-trapping because grids are not sufficiently large to contain the movements of animals that inhabit them (Broome and McMahon, 1986). These aspects of grid-trapping affect the measurement of home range rather than the home range itself.
Previous studies of chipmunk home range, especially experimental studies (Mares et al., 1976; Mares et al., 1982; Sullivan et al., 1983; Lacki et al., 1984; Trombulak, 1985), have generally employed trapping to estimate home range. The value of such studies would be severely compromised if their methodologies affect the very parameter they are intended to measure.

My own observations from the summer of 1985 suggest that trapping and leaving traps pre-baited between sessions added enough food or cover to the chipmunks' environment to affect movement patterns. I repeatedly observed animals "trap-lining" (visiting one trap after another along a grid row, filling cheek pouches with bait and bedding, and pausing only to scatter-hoard as their pouches filled) both during and between trapping sessions, and found that it was generally easier to attract chipmunks to food piles placed at trap-stations than elsewhere.

Predictions

Providing supplemental food to small mammal home ranges is generally thought to decrease home range area. Numerous correlational studies have shown a negative relationship between food availability and home range size (Blair, 1943; O'Farrell et al., 1975), and food addition experiments have resulted in home range reductions (Mares et al., 1976; Taitt et al., 1981). If grid-trapping is equivalent to small scale food addition, telemetry-revealed home range areas should decrease after grid-trapping is
instituted on an area, and increase after grid-trapping ceases.

Another possible response to grid-trapping is a shift or expansion of home ranges to include areas supplied with traps that were not previously within those home ranges. This predicts immigration onto trapping grids and home range shifts inward from the edge of the grid while the grid is operating.

Animals that live on the grid area should respond to grid-trapping with a change in use distribution. Once trapping has begun, animals on the grid periphery should use the food-enriched part of their home range, the part which overlaps the grid, more intensively than the part which does not. If trap-lining is occurring, then animals inside the grid should be located near trap stations more frequently than would be expected by chance.

METHODS

Procedures used in the collection of trapping and telemetry data have been described extensively in previous chapters and will not be repeated here.

Experimental design

In April 1986 two 18 ha grids, approximately 1 km apart, were surveyed in similar habitat. From early May to mid-July, grid H (the southernmost grid) was operated as a trapping grid. On July 16, I removed all traps from grid H and transferred them
to grid X (the northern grid). From mid-July to late September, grid X alone was treated as a trapping grid (Figure 2.1, Table 2.1). I used radio-telemetry to monitor home ranges of resident adults throughout the summer.

On each grid, trapping was used as a treatment, and home range sizes during the non-trapping period were taken as control values for that grid. The sequence of treatment and control were reversed on grid X with respect to grid H in order to account for seasonal effects. Chipmunk home ranges are known to vary according to season, especially for females, whose movements are restricted during late pregnancy and early lactation (Martinsen, 1968; Broadbrooks, 1970). If grid-trapping effects on food availability determine home range size, grid H residents should have smaller home ranges in early summer than in late summer, while for grid X residents the reverse should be true. If seasonal effects determine home range size then seasonal changes in home range size should be consistent for both grids. Restriction of movements during lactation would result in larger home ranges in late than in early summer on both grids.

**Home range calculations**

Home range size was calculated using the minimum convex polygon method (Southwood, 1966). It is well-known that the minimum convex polygon (MCP) increases with sample size until it reaches an asymptote at the actual home range size (Stickel, 1954;
Jennrich and Turner, 1969). Mares et al. (1980) showed that for the eastern chipmunk, home range area leveled off after 20 captures. Therefore, in order to standardize home range measurements to sample size, I used MCP calculated at 20 radio locations for all comparisons. For all radio-collared chipmunks in this study an average of 87.18% (SD=13.96) of home range is revealed after 20 locations. In the majority of studies for which such estimates are calculated, 90% or 95% home range is used. I calculate MCP after 20 captures instead of at 90% home range because I used Mares et al. (1980) estimate for the home range limit as a field target for minimum number of locations. For most animals I collected more than 20 location points in each part of the summer, but due to logistic problems I could only collect the minimum number of locations in some cases. I chose not to exclude these from the analysis.

**Effect of data source on home range estimate**

In order to compare trap-based home range estimates with telemetry-based estimates, MCP calculated using the first 20 location points is used as above. Since, for each chipmunk, trapping data only exist for half of the summer, trap-based estimates are compared with telemetry data collected during the same period (early or late summer).
RESULTS

Effects of grid-trapping on home range

Table 4.1 presents the mean telemetry-based home range size for early and late summer on grid H and grid X. The mean home range sizes listed in Table 4.1 suggest a trend in home range opposite to that predicted for a grid-trapping food addition effect, but this trend is not statistically significant: grid H paired samples \( t = .37, p = .72 \); grid X paired samples \( t = .41, p = .69 \).

<table>
<thead>
<tr>
<th>GRID</th>
<th>EARLY SUMMER</th>
<th>LATE SUMMER</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MEAN(N)</td>
<td>S.D.</td>
</tr>
<tr>
<td>H</td>
<td>2.8 ha (11)</td>
<td>1.9</td>
</tr>
<tr>
<td>X</td>
<td>2.2 ha (8)</td>
<td>0.9</td>
</tr>
</tbody>
</table>

There is no detectable food addition effect due to grid-trapping on the amount of immigration occurring on the two grids. Three adult chipmunks immigrated onto each grid during early summer while I was trapping on grid H. In late summer, while I was trapping on grid X, 2 adults immigrated onto grid X and 1 adult immigrated onto grid H. Measurement of immigration was not
as reliable for the non-trapping grid as it was for the trapping grid, since it was not monitored systematically. The number of sightings of unmarked adults corroborates the absence of a causal relationship between trapping and immigration. In early summer I recorded 5 sightings of unmarked adults on grid H and 3 sightings on grid X. In late summer there were 2 sightings on each grid.

For 9 of the 24 chipmunks equipped with radio-collars, 10% to 50% of locations were outside the grids. On grid H, the number of off-grid locations is less than the expected number in early summer, while in late summer, off-grid locations exceed the expected number ($X^2=7.0$, df=1, $p<.01$). On grid X, the trend is reversed, which is consistent with a grid-trapping effect since the treatment is reversed, but it is not statistically significant ($X^2=2.5$, df=1, $p>.10$).

For telemetry locations inside the grids I classified all locations within 7.5 m of a trap station as "trap-associated", and all locations greater than 7.5 m from a trap station as "not trap-associated". I chose a distance of 7.5 m because it is the smallest distance I could discern based on the grid system. Locations classified as "trap-associated" must be close enough to a trap-station that I can assume that a chipmunk is at least aware of the presence of the trap. For grid X, locations are associated with trap stations less frequently than expected in early summer and more frequently than expected in late summer ($X^2=16.7$, df=1, $p<.001$). This coincides with the trapping regime. On grid H, the trend is the same, although it is not
significant ($X^2=2.95$, df=1, $p>.10$). This does not coincide with the trapping regime, which was the reverse of that on grid X.

**Effects of data source on home range**

For the 19 animals for which both trapping and telemetry data are available for the same part of the summer, there is no significant difference between mean home range size (at $n=20$) derived from trapping and that derived by telemetry. Mean trap-revealed home range is 2.4 ha, mean telemetry revealed home range is 3.0 ha (paired samples $t=1.63$, $p=.121$).

**DISCUSSION**

**Effects of grid-trapping on home range**

Grid-trapping does not measurably change the size of chipmunk home ranges. Chipmunks continued to trap-line during trap-sessions as they did in 1985, and continued to empty pre-baited traps of bait and cotton between trap-sessions. Grid-trapping certainly increased the availability of food, bedding material, and cover, but not enough to affect telemetry-based estimates of home range that were independent of trapping. This indicates that for experimental studies of chipmunk home range, grid-trapping provides an adequate estimate of home range. There
is no evidence that grid-trapping distorts home range in a way that would invalidate conclusions about home range response to food and density manipulations.

Another typical response to experiments which increase the availability of food is a density increase caused by immigration onto the grid (Mares et al., 1976; Gilbert and Krebs, 1981). Immigration occurred at approximately the same rate on both grids over the season. Immigration of adults was higher in early than in late summer, and there was an increase in the density of juveniles on both grids at juvenile emergence in which immigration was indistinguishable from recruitment. Grid-trapping had no effect on the amount of immigration.

Tests for changes in use distribution as a result of grid-trapping were inconclusive. It is possible that chipmunks whose home ranges lie partially outside the grids change their movement patterns so that they frequent grids that are being trapped more than grids that are not being trapped. The trend is significant on one grid only. This inconsistency suggests that factors other than the presence or absence of grid-trapping, such as home range shifts of females after juvenile emergence or availability of seasonally abundant patches of food, may explain distribution of use.

For radio-locations inside the grids, only the inhabitants of grid X show a change in use concentration in response to trapping. This suggests that trap-lining behaviour occurred on grid X but not on grid H. Since grid X contained a greater
proportion of poor habitat than grid H (Chapter 2), it is possible that the food provided by traps on grid X was a more significant resource than on grid H.

The mean home range sizes listed in Table 4.1 are slightly greater than half the mean home range size of 4.86 ha for both grids over the entire season which I reported in Chapter 2. This discrepancy is the result of two factors. Firstly, 3 of the male chipmunks with the largest home ranges died or dispersed before the grid-trapping treatment was switched and are therefore excluded from this analysis. Secondly, most lactating females shifted their home ranges after their young had emerged. Since the data used in Chapter 2 to calculate mean home range for the entire summer include both pre- and post-emergence periods, they yield higher estimates of home range than the data for either period alone.

Effects of data source on home range

Trapping and telemetry provide statistically indistinguishable estimates of home range size using the minimum convex polygon method of home range calculation, provided the sample sizes are equal. This is consistent with the findings of Jones and Sherman (1983) who compared eight different methods of home range calculation and showed that trap- and telemetry-revealed home range estimates were most comparable to one another with the minimum convex polygon method.
At very low sample sizes, trap- and telemetry-revealed home range estimates would differ, because as numerous authors have observed (Hayne, 1949; Stickel, 1954; Jones and Sherman, 1983), captures often occur in a straight line due to the placement of traps, yielding MCP home range estimates of zero. Since very low sample sizes yield inaccurate MCP home range estimates regardless of the data source, this does not argue against the use of trapping for estimating home range. However, accumulating sufficient data to provide accurate home range estimates is more rapid and less labour-intensive using telemetry than using trapping.

Another difficulty that is frequently encountered in grid-trapping studies of home range is that grids are too small to contain the majority of home ranges of animals that inhabit them, so that home range estimation is impossible (Broome and McMahon, 1986). When these problems can be avoided, grid-trapping is an adequate means of home range estimation if the researcher is only interested in the size of home ranges. When other aspects of home range, such as use distribution are of interest, telemetry is the superior method.
LITERATURE CITED


APPENDIX:

SOURCE CODE LISTING (in BASIC) OF RANDOM CHIPMUNK ENCOUNTER SIMULATION MODEL

10 TR=0
20 DIM NA(13,1),NO(13,4),SC(9,2)
30 FOR A=5 TO 9:FOR B=0 TO 2:READ SC(A,B):NEXT:BEXT
40 DATA 10,15,18,9,26,17,8,21,5,21,9,21,9.5,20.5,20.5
50 FOR A=1 TO 13:FOR B=0 TO 1:READ NA(A,B):NEXT:BEXT:MEXT
60 DATA 102,1,12,44,13,33: DATA 12,1,11.5,27.5,14,20
70 DATA 52,1,1,22.5,1,15: DATA 7,1,2.5,10.5,21,11
80 DATA 10,0,0,30,7,32: DATA 101,0,0,1.5,5,20
100 DATA 102,1,12,44,13,33: DATA 12,1,11.5,27.5,14,20
110 DIM SW(NC,4),SH(NC,1),T(NC),TGC(NC)
120 FOR I=1 TO NC:PRINT "Name chipmunk ":STR$(A);:INPUT NN
130 FOR B=1 TO 13:IF RECNA(B,0) THEN 100
140 IF NA(A,1)=1 THEN SS(A,0)=SC(NO,0):SS(A,1)=SC(NO,1):SH(A,0)=7: SH(A,1)=6
150 IF NA(A,1)=0 THEN SS(A,0)=SC(NO,0):SS(A,1)=SC(NO,1):SH(A,0)=6: SH(A,1)=0
160 FOR C=1 TO 4:SH(A,C)=RO(B,C):NEXT
170 NEXT:BEXT
180 IF INPUT "Output frequency? ",FR
190 IF INPUT "Output file name? ",FS
200 OPEN FS FOR OUTPUT AS 11
210 XM=2:INPUT "Encounter radius? ":XM:PRINT
220 REM now initial parameters have been distilled into:
230 REM sk: 0=maximum radius, 1=nest x, 2=nest y, 3=centre x, 4=centre y
240 REM ss: 0=active time, 1=retire. All selections account for sex.
250 REM SS(1,1):FOR A=2 TO NC:IF SS(A,1)>80 THEN SS(A,1)=80
260 NEXT:BEXT
270 FOR T=SS(1,0) TO 11 STEP .04
280 IF T>SS(1,0) THEN FOR A=1 TO NC:XI(A)=SH(A,1):Y(A)=SH(A,2):NEXT
290 FOR CH=1 TO NC:TGC(CH)=" ":NEXT
300 REM will I move?
310 IF (XM*.25) THEN 370
320 IF (XM*.25) THEN 370
330 REM test for range constraints
340 XI=COS(DI):YI=SIN(DI)
350 IF SQRT((Y(CH)+XI-SH(CH,3))^2+(X(CH)+YI-SH(CH,4))^2)>SH(CH,0) THEN XN=XN+1:GO
TO 320
360 X(CH)=X(CH)+XI:Y(CH)=Y(CH)+YI
370 NEXT
380 NC=-(Y-SH(1,0))/YR
390 IF ABS(NC-(INT(NC)))>0.000000002 THEN 580
400 XN=0:PRINT "Time is ":PRINT T:FOR CH=1 TO NC
410 PRINT X(CH),Y(CH);
450 PRINT "ENCOUNTER";
460 NEXT:PRINT TC$(CH):NEXT:EN=EN/2:TE=TE+EN
480 PRINT BU,EN:PRINT
500 NEXT
505 PRINT "Total encounters=";PRINT TE
510 CLOSE