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HABITAT SELECTION AND INTERSPECIFIC AGONISM IN TWO PARAPATRIC SPECIES OF CHIPMUNKS (EUTAMIAS)

by

DON HOWARD MEREDITH

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Habitat Selection and Interspecific Agonism in Two Parapatric Species of Chipmunks (Eutamias)," submitted by Don Howard Meredith in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Date 21 February, 1975

To the high country,

"Walk away quietly in any direction and taste the freedom of the mountaineer."

--John Muir

ABSTRACT

Eutamias minimus and *E. amoenus* are altitudinally parapatric in the southern Alberta Rocky Mountains, *E. m. oreocetes* occupying the alpine and *E. a. luteiventris* occupying the forest. I investigated the roles of habitat selection and interspecific agonism in the parapatric relationship between the two species in southern Alberta.

Although both species were observed to utilize tree islands in the narrow subalpine zones on the steep slopes of a valley, neither species was observed in the broad subalpine on the valley floor.

Field-experienced individuals of both species selected rock over trees during habitat selection experiments in the laboratory. Laboratory-raised *minimus* selected rock over trees, while laboratory-raised *amoenus* had no significant preferences. I conclude that *minimus* has evolved an innate preference for the cover quality of talus because talus is the only continuous cover with vertical depth available in the alpine. *Amoenus* may learn to select talus because of its cover quality, but does not inherit such a preference because of the variety of cover types available in the forest.

Amoenus was aggressively dominant over *minimus* in simultaneous introductions of one individual of each species into artificial habitats. In agonistic tests where

minimus was in residence for one day prior to the introduction of *amoenus*, both species won the same number of matches, but *minimus* won a significantly larger number of total encounters. Thus, the residency of a chipmunk may be important in the outcome of agonistic encounters, and may explain the apparent exclusion of *amoenus* from the alpine.

North of the Bow River in the Rocky Mountains of Alberta, *minimus* and *amoenus* are geographically parapatric, *E. m. borealis* and *E. a. ludibundus* both occupying forest habitats. In habitat selection experiments using field-experienced individuals, *minimus* selected rock, whereas *amoenus* selected neither habitat during the day and rock during the night. The lack of preference by *E. a. ludibundus* during the day may be related to behavioral adaptations of that subspecies to the closed canopies of its forest habitat.

Again, *E. a. ludibundus* was dominant over *E. m. borealis* in laboratory agonistic tests. The relationships of interspecific aggressive dominance to competitive exclusion and habitats occupied by potentially competing species are discussed.

The probable routes of dispersal into Alberta of the four subspecies are discussed. The origin of *E. m. oreocetes* is considered in relation to its zoogeography and the results of the habitat selection and interspecific agonism experiments.

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INTRODUCTION

The role of habitat selection in competitive exclusion has not been documented for chipmunks. Harris (1952) reported the effect of habitat selection on the habitat segregation between two subspecies of the deer mouse, Peromyscus maniculatus. Murie (1969) tested two species of Microtus for wet or dry soil preferences in relation to habitat segregation. Rosenzweig (1973) examined the effects of habitat selection on the coexistence of two species of heteromyid rodents. My study examines the roles of habitat selection behavior and interspecific agonism in the apparent competitive exclusion between two species of chipmunks with contiguous distributions in Alberta.

Montane chipmunks present interesting problems of competition. Of the 16 species of Eutamias recognized in North America (Hall and Kelson 1959), all are present in the west, while only one resides in the east. This large number of western species reflects the large scale fragmentation of habitats and resultant isolation of populations in the mountainous west (MacArthur 1972). Sympatry occurs among some of these species in mountainous areas (Merriam 1897). Ingles (1965) listed nine species of Eutamias in one east--west transect of the Sierra Nevada in California. Although each is geographically sympatric with its neighbors, the species are altitudinally zoned and seemingly parapatric, each associated with a particular plant life-zone (Johnson 1943).

Several recent studies dealt with interspecific competition in chipmunks. Brown (1971), Heller (1971), and Sheppard (1971) studied possible effects of interspecific aggression between contiguous species and concluded that interspecific dominance relationships were important in confining each species to its respective habitat. The above authors, however, indicated that habitat selection may play a more proximate role in habitat utilization. Heller and Gates (1971), and Heller and Poulson (1972) studied possible physiological differences between contiguous species in California, to determine if such differences were related to habitat segregation.

Heller (1971) and Sheppard (1971) separately studied two groups of chipmunks, each with one species living solely in the alpine, and came to different conclusions concerning the alpine species and their relationships to their congeneric neighbors and their habitats. On the east slope of the Sierra Nevada, four species of chipmunks are parapatric and altitudinally zoned according to major plant life-zones. Heller (1971) tested the four species for interspecific aggressive dominance in the laboratory. He found that the alpine species, *E. alpinus*, was dominant over its neighbor, *E. speciosus* of the lodgepole pine zone; and that

E. amoenus, of the pinon pine--sagebrush zone, was dominant over both its neighbors, E. minimus of the sagebrush zone and E. speciosus. He attributed the dominance of alpinus to its habitat, postulating that an aggressive species, in order to secure feeding areas for individuals, would evolve in a habitat of little vegetative cover and sparse food supply. Heller also attributed the dominance of amoenus to its habitat, postulating that aggression was favored in this species for defending a sparse food source of pinon pine nuts and suitable cover (shade) from the heat (Heller and Poulson 1972).

In the southern Alberta Rocky Mountains, E. minimus is largely restricted to alpine habitat, but its distribution narrowly overlaps that of E. amoenus in the "subalpine forest." Eutamias amoenus is found in open forests and clearings in the valleys (Sheppard 1971). Sheppard demonstrated that amoenus was dominant over minimus in tests of aggression in the laboratory. He postulated that the forest was the optimum habitat for both species, but amoenus prevented minimus from establishing in the forest through aggressive encounters. This contrasts with Heller's (1971) conclusion that alpine chipmunks would be more aggressive than species in the lower forest habitat.

In Alberta, Soper (1964) reported two subspecies each of the yellow-pine chipmunk, E. amoenus (Allen), and the least chipmunk, E. minimus (Bachman) (Fig. 1). North of the Bow River, Hollister's chipmunk, E. amoenus

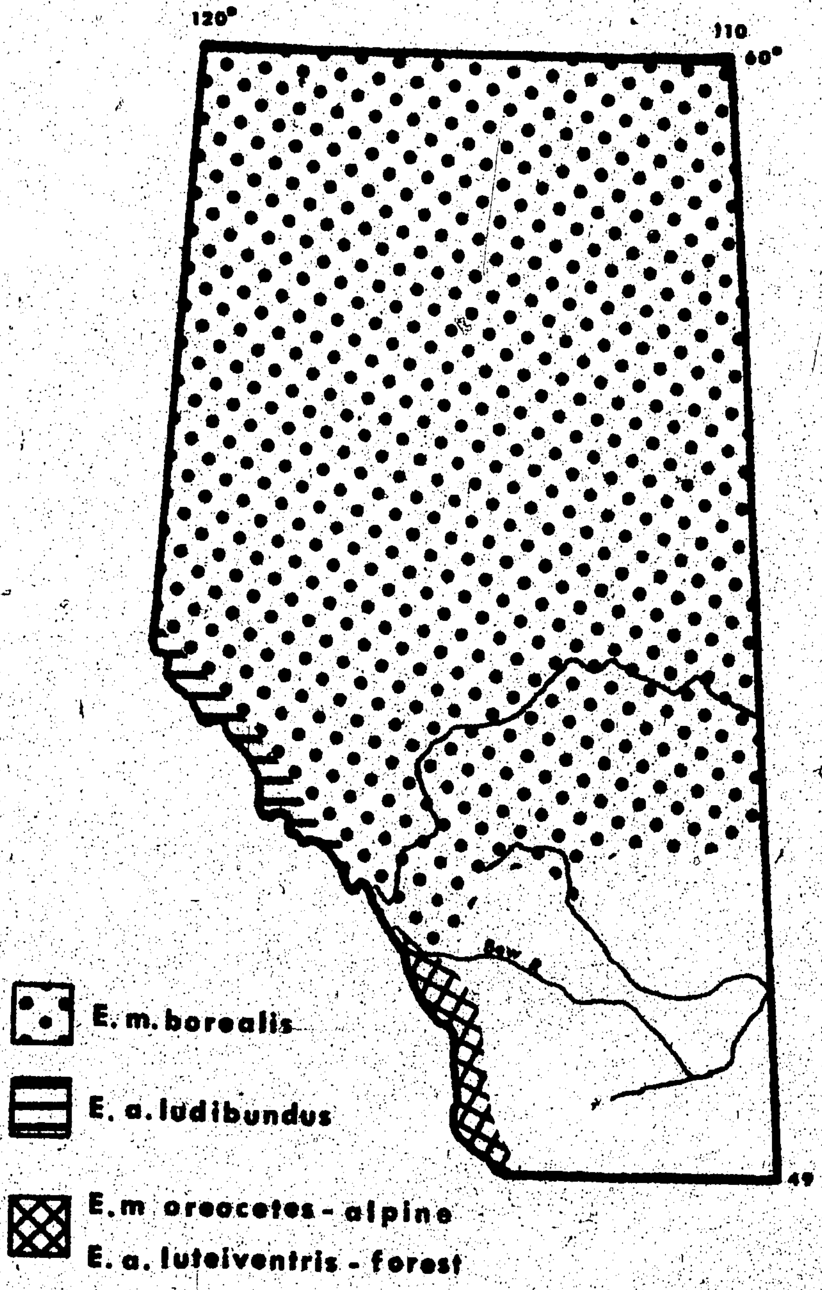

Fig. 1. *Eutamias amoenus* and *E. minimus* subspecific ranges in Alberta (Soper 1964). Subspecies north of the Bow River are geographically parapatric. Subspecies south of the Bow River are altitudinally parapatric.

ludibundus, is found in the forest of the mountains along the Continental Divide, while the little northern chipmunk, E. minimus borealis (Allen), is found in the forest of the mountains east of the range of E. a. ludibundus and in the boreal forest. The subspecies studied by Sheppard (1971) are present south of the Bow River and are altitudinally parapatric: the buff-bellied chipmunk, E. a. luteiventris (Allen) in the forest, and the timberline chipmunk, E. m. oreocetes Merriam, in the alpine. If interspecific dominance relationships in the north are similar to those south of the Bow River, the change in habitat relationships between the northern and southern subspecies suggests that aggressive interaction may not be the only factor defining the habitat utilized by each species. The habitat utilized may be determined more proximately by habitat selection and its relationship to the evolutionary and geographic history of the species.

In this study I define the term habitat selection as the behavior of selecting a preferred habitat. I distinguish habitat selection from habitat utilization, the occupation and use of a habitat. The habitat utilized by a species may not be the habitat that is preferred by that species. A competitor may prevent a species from occupying its preferred habitat.

However, the behavior of selecting a preferred habitat may be the result of a competitive relationship. By learning or inheriting a selective response to habitat, individuals may avoid habitats where interspecific competitors are present, and thereby avoid interaction. As Grant (1972:99) pointed out "if permitted by the environmental resources, the relationship evolves towards an absence of interaction, as this is the most conservative of energy."

Thorpe (1945), Klopfer (1963, 1965), Wecker (1963) and Hilden (1965) have discussed the role of inheritance in habitat selection behavior. Wecker (1963) evaluated the role of early experience in the habitat preference of the prairie deer mouse, Peromyscus maniculatus bairdi, and concluded that both heredity and learning are involved in habitat selection behavior. Early experience can reinforce innate habitat preferences.

To examine habitat selection behavior, I conducted experiments in the laboratory rather than in the field. The time available to construct an enclosure in the field, capture and test hibernators in Alberta is limited. Also, many factors in the field may be responsible for the outcome of an experiment, whereas in the laboratory more variables can be controlled. In discussing behavioral experiments in the field, King (1973:124) stated that "most natural conditions are so unique that generalizations from one time and place to another may be less valid than generalizations from laboratory experiment to the field."

Wecker (1963) and Rosenzweig (1973) determined that habitat structure is at least one cue in habitat selection by the animals they studied. Reilly (1971) tested E. minimus from Upper Michigan, in a 3 m diameter enclosure, for its preferences for restricted vertical and horizontal visibility and two different perching heights. His animals preferred unrestricted horizontal visibility and high perches. No preferences for restricted or unrestricted vertical visibility were found. I tested each species with two habitat types, determined from field data as being basic components of the respective habitats of E. a. luteiventris and E. m. oreocetes, trees in the forest, and rock in the alpine. These habitats were artificially constructed in the laboratory. Differences in habitat structure (e.g. perch height, horizontal and vertical cover) between the two habitats were the primary selection cues available.

I attempted to evaluate the roles of habitat selection and interspecific agonism in the parapatric relationship between E. amoenus luteiventris and E. minimus oreocetes in Southern Alberta. Approaches included investigation of the habitats of both species, particularly in the higher elevations where the ranges of the two species abut; laboratory habitat selection experiments on field-experienced and laboratory-raised individuals; and laboratory experiments to determine the influence of large structurally complicated arenas on interspecific behavioral interactions. I also investigated the two northern subspecies, *E. a. ludibundus* and *E. m. borealis* to compare their distributions, habitats, habitat selection, and interspecific agonism with the southern subspecies.

Habitat Utilization by the Southern Subspecies

I began my study in the Rocky Mountains of southern Alberta, in the summer of 1971, to determine if there is an overlap in the range of E. amoenus luteiventris and E. minimus oreocetes in the subalpine tree island habitat, as described for E. amoenus and E. townsendii in Washington (Meredith 1972); and to evaluate the actual and potential range of habitat use for each species. I selected Goat Valley, at the head of the Elbow River in the Opal Range of the Rocky Mountains (115°01'W, 50°41'N), as a study area because of its gradual altitudinal gradient (from 2040 to 2440 m in about 3.5 km) which produced a broad subalpine zone (as defined by Löve 1970).

Description of Study Area. A continuous forest (montane forest, Löve 1970) of Englemann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa) follows the valley floor up to about 2200 m in elevation, about 1.5 km from the valley mouth (Fig. 2). At that point the forest breaks up into tree islands and interspersed meadows, (subalpine belt, Löve 1970). Subalpine larch (Larix lyalli) is found with spruce and fir in some islands. The upper limit of the subalpine is reached at about 2300 m in elevation, where the trees are stunted and give way above to continuous meadow and rock (alpine belt, Löve 1970).

The subalpine is broad along the valley floor (about 600 m wide, Fig. 2) where the altitudinal gradient is gradual. The subalpine is also present all along the steep valley slopes but is only 50 to 100 m wide.

Methods. From 20 June to 26 August 1971, chipmunks were live-trapped (7.6 x 7.6 x 23 cm Sherman live-traps, baited with oats and sunflower seeds) using transect trap lines. Traps were placed in three parallel lines running up and down the slope, about 300 m apart with 15 m spacing. Each line consisted of 20 to 25 traps, and passed from bare rock in the alpine down to Goat Creek in the valley floor. The line closest to the valley mouth was set on the first trapping day, followed by the next two lines on days two and three, respectively. Each following day, the line closest to the valley mouth was moved upward, ahead of the furthest line, so that the system gradually moved up the valley. Thus, each line was set for three trapping days. One set of three lines was started at the valley mouth and another set of three was started in the broad subalpine near camp. A total of 13 lines were set on the east side of the creek (9 below and 4 above camp) and 7 lines were set on the west side (2 below and 5 above camp), for a total of 423 stations trapped and 1269 trap days. Animals were marked with numbered ear tags, enclosing colored plastic discs for field identification with binoculars (7 x 35). Weight of captured animals to the nearest gram (Pesola spring scale, 0-100 g), sex, reproductive condition, and habitat were recorded. Observations of unmarked chipmunks were recorded as to species and habitats occupied.

In the hope of determining the potential range of each species, Sheppard (1971) transplanted *amoenus* into areas occupied solely by *minimus* and vice versa. One pair of *minimus* survived in *amoenus* habitat for at least one year. Sheppard felt that one reason *amoenus* may not have established in *minimus* habitat was that its familiar forest habitat was too easily accessible, being a few m downslope. To repeat Sheppard's experiment and reduce the problem of easy forest access, I released 17 *amoenus* adults (10 males, 7 females) in alpine habitat near the head of Goat Valley, 2 to 3 km from where they were caught (near the valley mouth), and 1 km from the nearest tree island, on 8 and 14 August 1971.

In July and August of 1972, I continued the study. Individuals of both species were live-trapped and their movements and habitats monitored, using transect trap lines. To more accurately measure the long distance movements of individuals along the valley, three trap lines were set parallel to and east of the creek, from the valley mouth to camp, from 14 July to 17 August 1972. The three lines were about 300 m apart and each consisted of 22 to 25 traps (15 m spacing). Starting at the valley mouth, one line was set in the continuous forest on the first trapping day, one in the narrow subalpine on the second day, and one in the alpine on the third day. On the fourth day the forest line was moved ahead, continuing that line up the valley. On the fifth and sixth days the subalpine and alpine lines were moved ahead, respectively. This procedure was repeated until the three lines reached the vicinity of camp and the limit of the continuous forest. The alpine line included a total of 103 trap stations; the subalpine line, 110 stations; and the forest line, 115 stations. Each station was trapped for three days, yielding a total of 984 trap days. The alpine in the upper valley (above camp) was trapped using nine up-slope transect lines, yielding a total of 675 trap days.

Results. In 1971, 28 captures and 3 observations of 10 *amoenus* (6 males, 4 females), and 59 captures and 9 observations of 19 *minimus* (12 males, 7 females) were made in Goat Valley. In 1972, 151 captures and 6 observations of 25 *amoenus* (16 males, 9 females), and 76 captures and 3 observations of 13 *minimus* (8 males, 5 females) were made. In 1972, only 4 individuals (3 *amoenus* and 1 *minimus*) were captured from the previous year. Two had lost both ear tags and were identified as recaptures from the previous year by slits in their ears. In 1971, 7 unmarked *amoenus* and 5 unmarked *minimus* were observed. In 1972, 12 unmarked *amoenus* and 4 unmarked *minimus* were observed.

The distributions of the two species determined from capture and observation data are illustrated in Fig. 3. As described by Sheppard (1971), amoenus was caught mainly in the forest while minimus was caught most frequently in the alpine and talus slides (Fig. 2 and 3). Neither species was caught nor observed in the broad subalpine region of the mid-valley, except minimus where talus penetrated from the slopes. The ranges of both species overlapped slightly in the narrow subalpine of the steep valley slopes.

I observed several long distance movements by individuals of both species (Meredith 1974). Some amoenus individuals appear to migrate from the lower valley to the limit of the continuous forest in the upper valley in August. The long distance movements of minimus were both up and down the valley, throughout the season.

Fig. 4 illustrates the habitat use by the two species in Goat Valley for the two years, based on trapping records. A use index was derived by dividing the number of traps set in each habitat type into the percent captures of each species in each habitat type. Closed forest was defined as a stand of trees with canopies overlapping. Open forest was defined as a stand of trees with canopies not overlapping. The captures of both species in tree islands of the subalpine were made in the narrow subalpine on the steep slopes and not in the

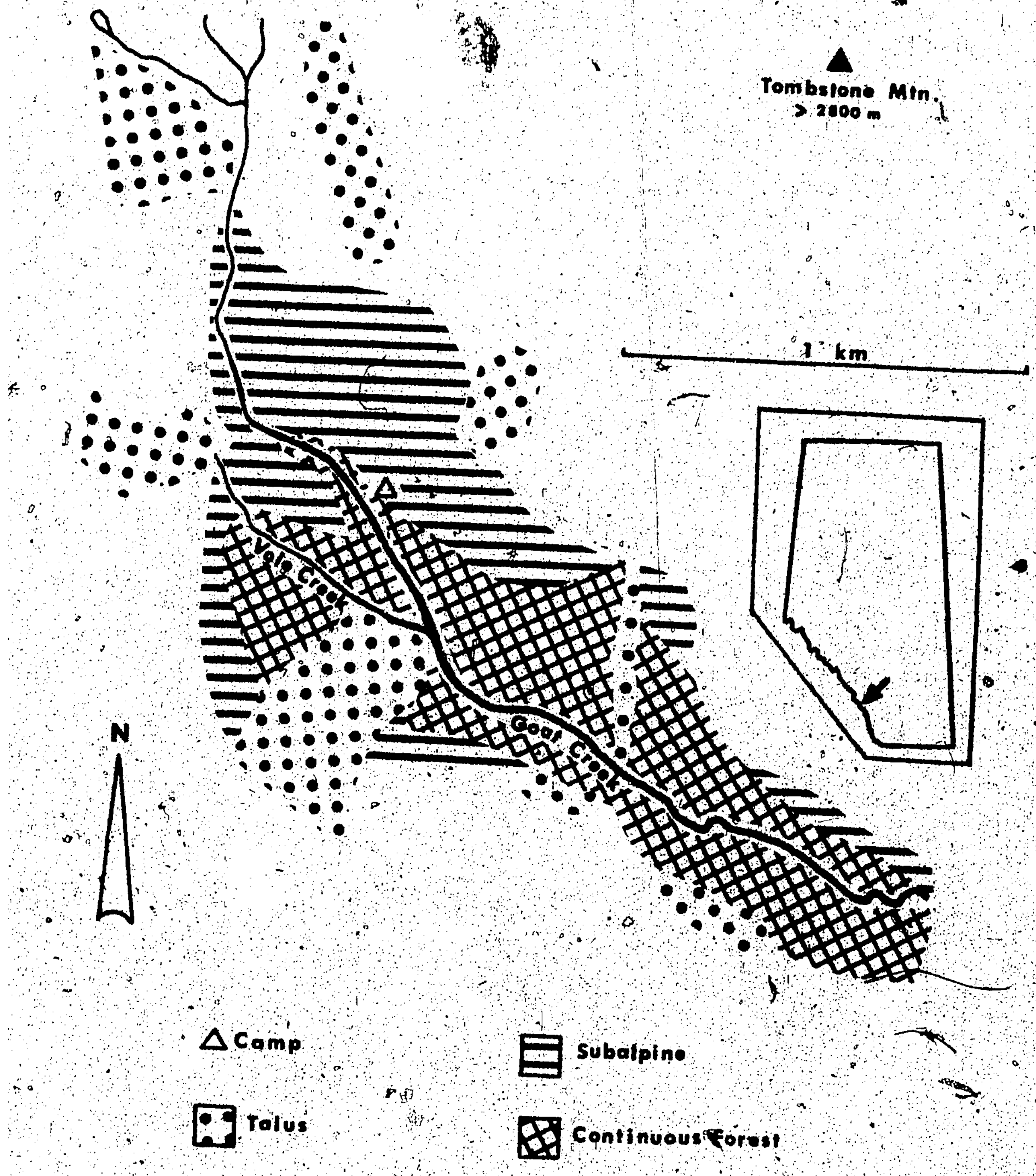

Fig. 2. Vegetation zones and major talus slides in Goat Valley.

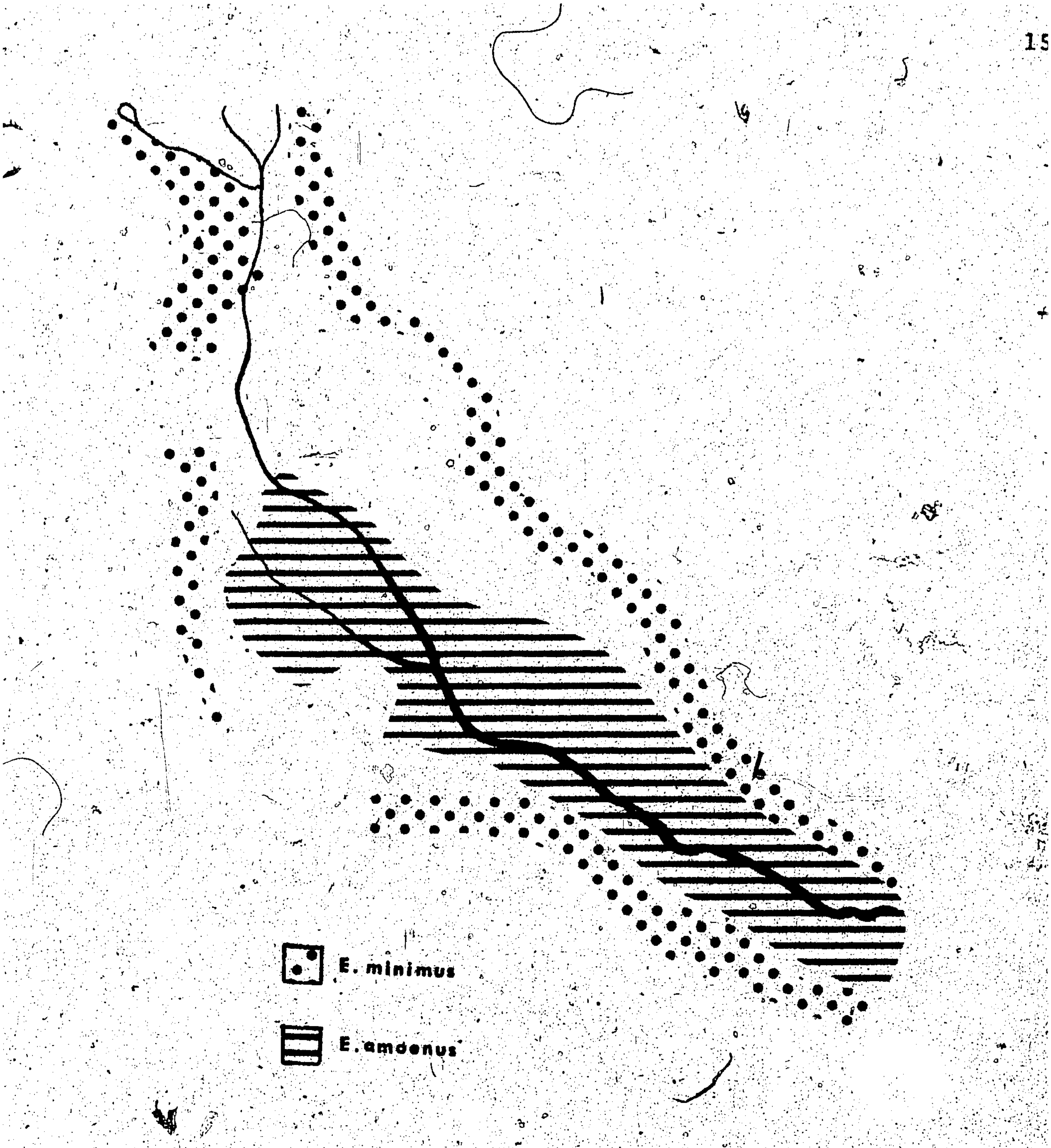

Fig. 3. Distributions of the two species of chipmunks in Goat Valley.

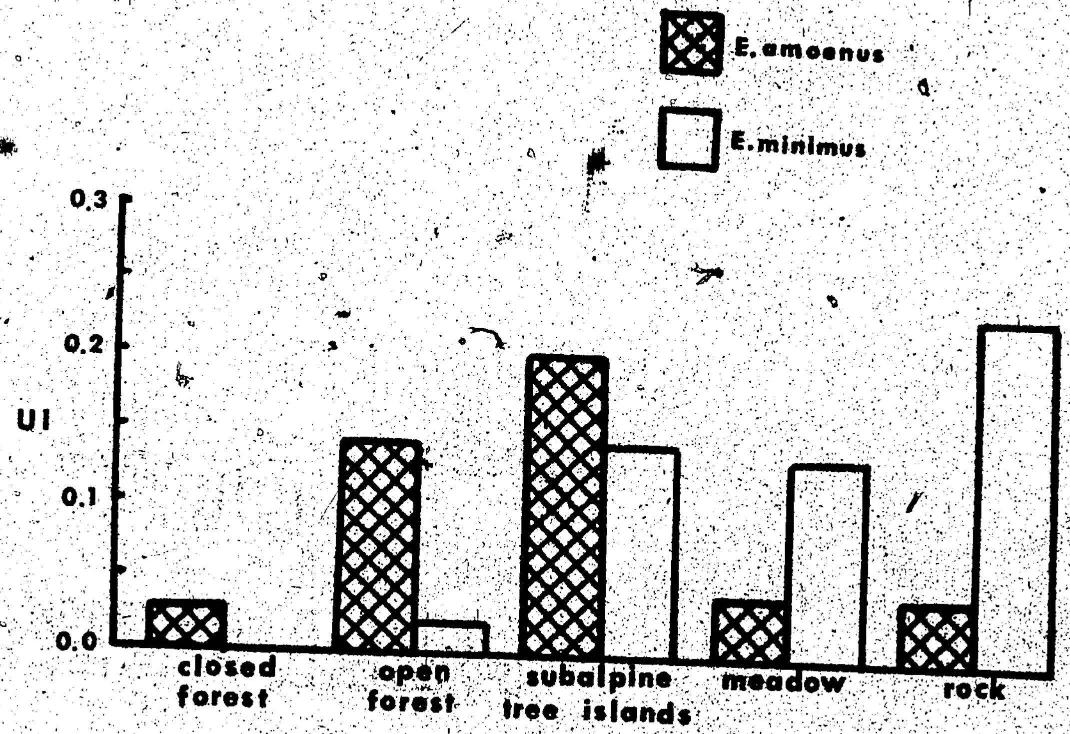

Fig. 4. Habitat use by the two species in Goat Valley, 1971-72. UI is a habitat use index (% capture/trap).

broad subalpine above camp (Fig. 3). Most of these captures were made in 1972, when one continuous line of 110 trap stations was set in the narrow subalpine belt.

Of the 17 amoenus released in the alpine in 1971, 6 (5 males, 1 female) were recaptured in the open forest within one week of their release. Two had returned to their original areas, about 3 km from the release point. In 1972, two of these individuals (1 male, 1 female) were recaptured in the open forest on the west side of Goat Creek. They were not captured in the original areas at the valley mouth, but were caught in the same area in which they had been recaptured in 1971, after the transplant. Although the alpine was extensively trapped in 1972, no amoenus were captured there.

Summary. In Goat Valley amoenus occupies the continuous forest, and minimus occupies the alpine and talus slides that penetrate from the alpine. The distributions of both species marginally overlap in the narrow subalpine zone on the steep valley slopes. Although the tree islands in the narrow subalpine are extensively used by both species, neither species occupies the broad subalpine on the valley floor. Amoenus was captured and observed in or near tree habitats, whereas minimus was captured and observed in or near talus. Six of 17 amoenus transplanted to the alpine in 1971 returned to the open forest. None of the 17 were captured in the alpine in 1972.

Removal Experiment

I have observed E. a. luteiventris in rockslides that are surrounded by forest and not connected to the alpine. Yet, E. m. oreocetes descends to low elevations in rockslides that are connected to the alpine, but otherwise surrounded by forest (Sheppard 1971). If amoenus is aggressively dominant over minimus, why does amoenus not exclude minimus from talus that penetrates the forest from the alpine? Does minimus somehow interfere with the ability of amoenus to exploit talus and its limited vegetation as either cover or a source of food? To attempt to answer these questions I removed the resident population of minimus near the terminus of a large rockslide that descends from an alpine area on Volcano Ridge, in the Ware Creek drainage of the Sheep River (114° 42'W, 50°42'N), and penetrates a lodgepole pine (Pinus contorta) forest inhabitated by amoenus.

Description of Study Area. The southeast facing slide drops from an elevation of about 1980 m to well within the continuous forest, its terminus being at about 1680 m in elevation. It is made up of large boulders, many greater than 3 m in diameter. It does not show signs of recent physical activity, as evidenced by large individual lichens on the rocks, large single lodgepole pine and white spruce (<u>Picea glauca</u>), and well developed shrub communities dominated by common juniper (<u>Juniperus communis</u>) growing at various locations within it.

<u>Methods</u>. In early May 1972 a trapping grid of 56 stations was set on the terminus of the slide (Fig. 5). The stations were set at 30 m intervals, with two Sherman live-traps per station. From 19 to 26 May, the grid was trapped for 6 days to monitor movements of both species. Animals were marked and recorded in 1972 as in Goat Valley, and were toe-clipped in 1973, as ear tags had been lost in many individuals over winter. Observations of individuals, with binoculars, provided additional information on location of activity.

To test for possible active competitive exclusion of <u>amoenus</u> by <u>minimus</u>, 16 <u>minimus</u> (all that were captured; 12 males, 4 females) were removed from the trapping grid, from 27 May to 16 July 1972. These individuals were used later for habitat selection experiments in the laboratory. The grid was monitored for <u>amoenus</u> movements for 6 days during each of the following periods, from 21 to 27 August 1972; 15 to 21 May, and 13 to 23 June 1973. No <u>minimus</u> were captured on the grid after 16 July 1972, or they would have been removed.

<u>Results</u>. Fig. 5 is a map of the terminus of the rockslide, showing the trapping grid and the ranges of the two species, as determined by captures and observations

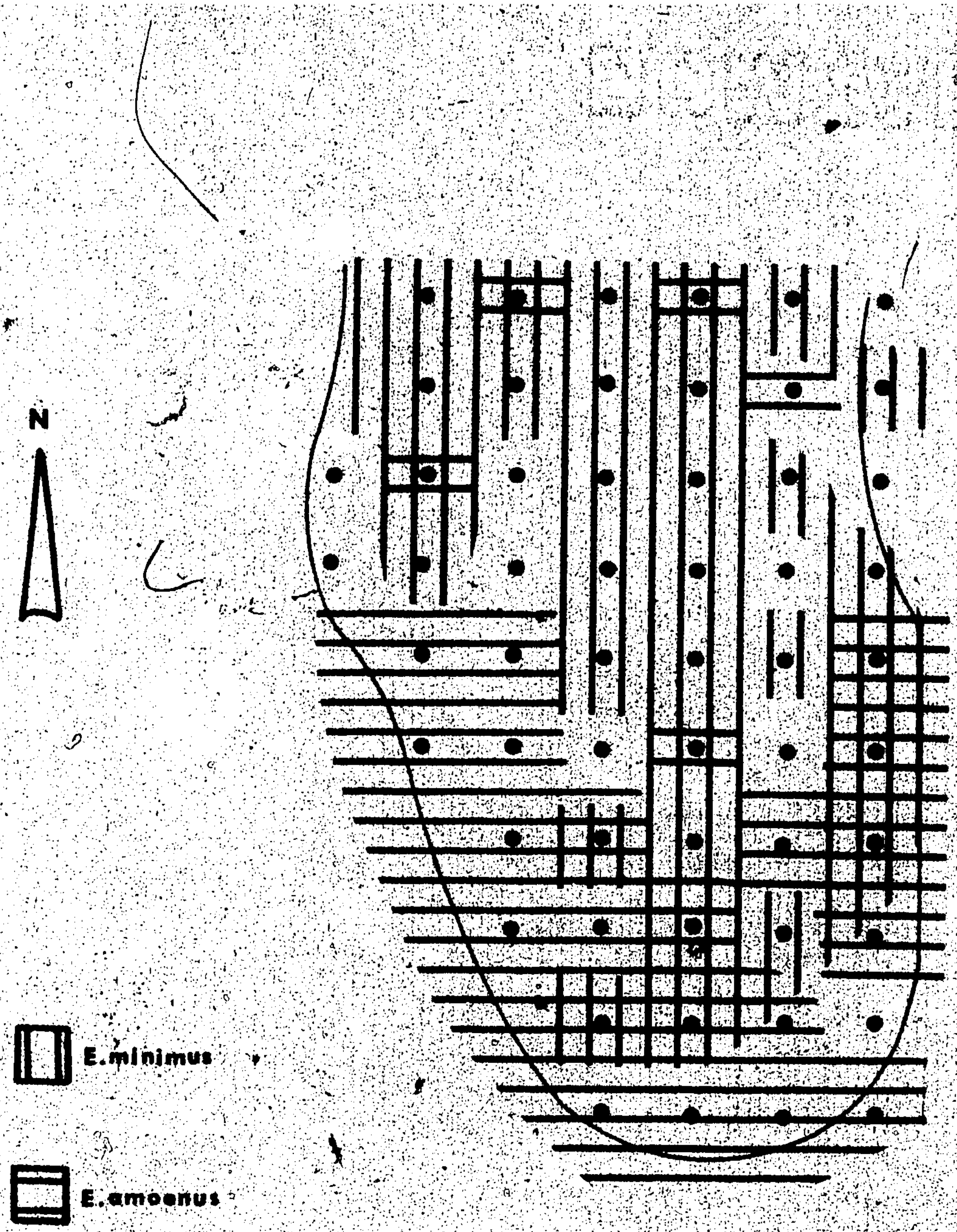

Fig. 5. Trapping grid on Volcano Ridge rockslide showing the ranges of captures and observations of the two species in May 1972. Trap station interval was 30 m.

made during the 6 day trapping period in May 1972. During that time, 5 male minimus adults and 9 amoenus adults (4 males, 5 females) were captured and their movements plotted.

From 21 to 27 August 1972, five amoenus adults (3 males, 2 females), two juveniles (male and female), and several unmarked juveniles were caught or observed on the grid, after the removal of minimus. All, but one adult male, were different from those individuals trapped in May 1972.

In May 1973 only two adult amoenus (male and female) were caught on the slide during the 6 day trapping period, although a group of at least six unmarked amoenus individuals had been previously observed (8 May) on the slide. The female had been tagged in 1971, but had not been captured or observed in 1972. No other chipmunks were seen during the 6 day period.

Because there were so few animals monitored in May, I returned to the slide for a 6 day period in June 1973. At that time 10 amoenus adults (6 males, 4 females) were caught and observed. All but three were caught for the first time. The male and female, caught in May 1973, were again caught in June, along with a female tagged in 1972. Fig. 6 illustrates the range of captures and observations of amoenus during June of 1973.

No minimus were captured during May or June of 1973. Two observations of minimus were made just north of

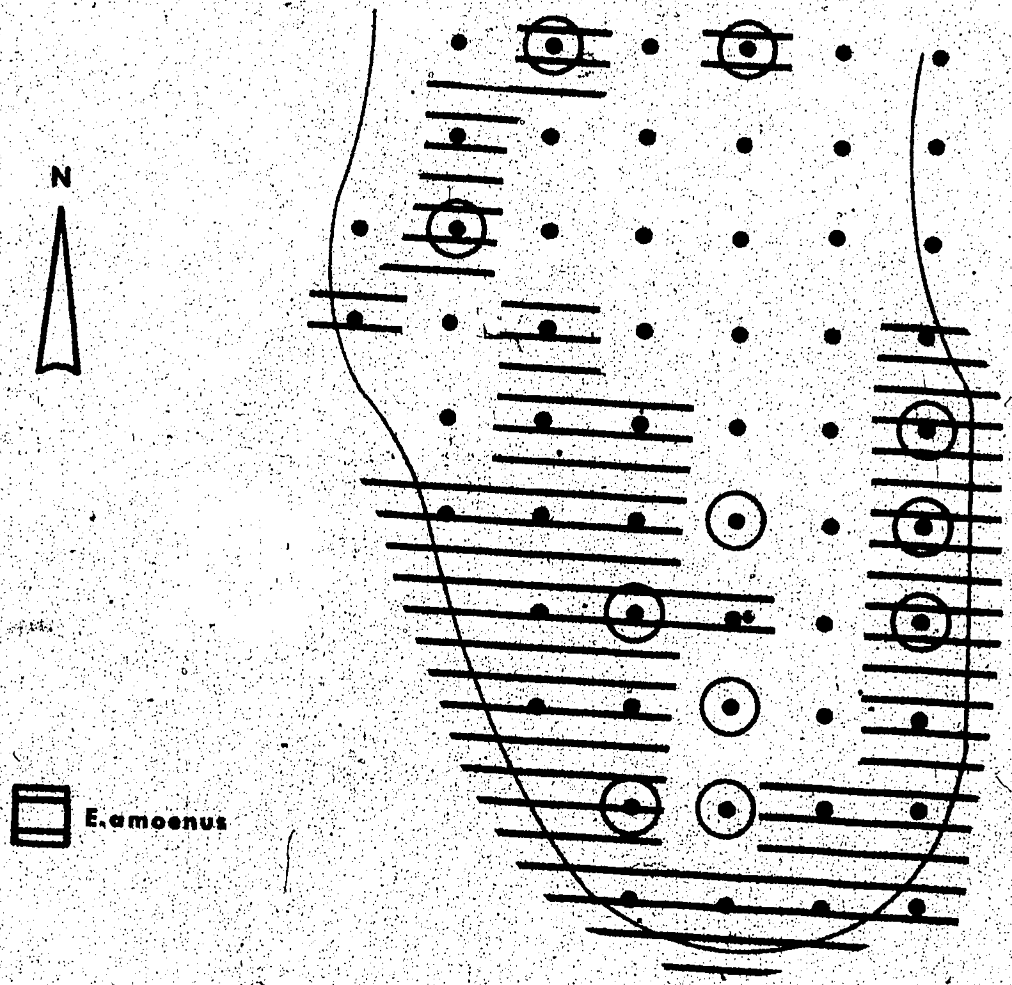

Fig. 6. Trapping grid on Volcano Ridge rockslide, showing the range of captures and observations of E. amoenus in June 1973. Trap stations where both species were caught or observed in May 1972 are circled.

the grid in June.

The number of trap sites where both species were captured or observed in May 1972, and the number of sites where amoenus was captured or observed on former minimus sites in August 1972 and June 1973 are shown in Table 1. The number of former minimus sites used by amoenus in August 1972 and June 1973 was compared to the number of minimus sites used by amoenus in May 1972, using the chi-square test. No significant differences were found ($P>0.1$).

In August 1972 juveniles of the year were on the slide with the adults. If the data from both juveniles and adults are combined, amoenus used 36 sites on the grid, 18 of which were former minimus sites. This is a significant increase in the number of minimus sites used over May 1972 ($P<0.01$). However, juveniles may behave differently from established adults at that time of the year. Juveniles may enter the slide in large numbers in late summer regardless of the presence of minimus.

Summary. After the removal of minimus, adult amoenus did not make significant incursions into former minimus area on the rockslide.

Distributions of the Northern Subspecies

The two subspecies found in the mountains north of the Bow River, E. m. borealis and E. a. ludibundus, live

Table 1. Number of trap sites on Volcano Ridge rockslide where both species were captured or observed in May 1972, and where amoenus was captured or observed on former minimus sites in August 1972 and June 1973. N = number of individuals, n = number of captures and observations.

Species	N	n	Total Sites Captured or Observed	Number of minimus Sites
May 1972--all adults				
minimus	5	54	31	31
amoenus	9	62	26	11
August 1972				
amoenus adults	5	35	24	8
amoenus juveniles	2+*	53	25	12
June 1973--all adults				
amoenus	10	50	28	12

* Several unmarked juveniles observed.

in forest habitats and are geographically parapatric (Fig. 1). Neither subspecies appears to inhabit alpine regions. Soper (1970) and Banfield (1958) reported the altitudinal limit of each subspecies to be tree-line. Unlike the southern subspecies, there is no obvious habitat segregation between the northern subspecies. Why does the parapatric relationship between the two species differ north and south of the Bow River?

To answer this question I collected chipmunks of both subspecies in Jasper National Park and transported them to Edmonton to compare their habitat selection and interspecific agonism to those of the southern subspecies (see the following chapters) and to attempt to understand how the habitats occupied may affect, or be affected by, the interspecific relationships. Minimus were collected at Devona, near the confluence of the Snake Indian and Athabasca Rivers (Fig. 8), and amoenus were collected at Derr Creek, 6 km east of Yellowhead Pass on the Miette River (Fig. 8).

To understand how the present interspecific relationships of the four subspecies may have developed, I felt it necessary to document further the present distributions of the two northern subspecies in the mountains of Alberta. The resident species of chipmunk in several regions of Jasper National Park and northern Banff National Park have not been clearly documented in the literature (reviewed by Banfield 1958, and Soper 1970).

This is especially true near the Continental Divide where the ranges of subspecies in British Columbia abut those of subspecies in Alberta.

Species Identification. Identification of live individuals of these two subspecies is more difficult than with the southern subspecies, where differences in size and coloration are clear. Absolute identification of dead individuals can be made in the case of males, based on the shape of the baculum (White 1953). However, I found that individuals of the northern subspecies can be identified, in the hand, on the basis of pelage characters (as described by Soper 1970). Pelage color was one criterion used. After examining study skins of the two subspecies at the Museum of Zoology, University of Alberta, I determined that the best character to separate individuals was the length of the dorsal, median, dark stripe on the head. As shown in Fig. 7, this stripe extends 5 to 10 mm anterior to a line drawn between the anterior bases of the ears in minimus. The stripe terminates at the anterior bases of the ears in amoenus. This extension of the stripe is less distinct in individuals of minimus from the boreal forest, east of the mountains. It is interesting that E. m. oreocetes also has this long stripe, while E. a. luteiventris does not. The median stripe facilitated identification of individuals with binoculars.

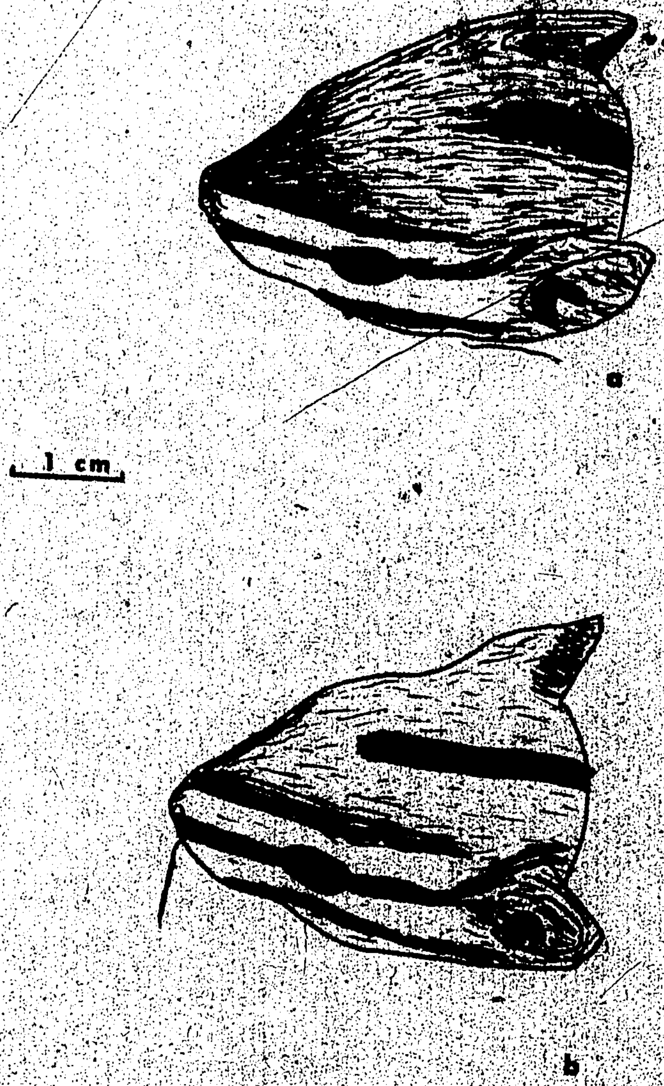

Fig. 7. Drawings of *E. a. ludibundus* (a) and *E. m. borealis* (b) heads showing longer mid-dorsal dark stripe of *E. m. borealis*. Drawings traced from 35 mm photographic slide of two individuals captured at Wilcox Pass, Jasper National Park.

Methods. I hiked into several regions of the parks to determine the species of chipmunk residing in each. I was only able to trap 2 to 5 days in any one area, limited by the amount of provisions carried. I set 30 to 50 Sherman folding live-traps in one or two lines to an area. Chipmunks captured were recorded as to subspecies, sex, reproductive condition, weight, and then released. Many chipmunks were also identified by observation with binoculars.

Results. In Jasper Park I trapped and observed E. a. ludibundus on the upper Smoky River (Adolphus Lake and Calumet Creek), the upper Athabasca River (Long Lake, above the confluence of that river with the Sunwapta River), and Wilcox Pass (Fig. 8); and E. m. borealis at Wilcox Pass. Fig. 8 summarizes the range data for each species in Jasper Park obtained from the literature and this study. Two areas remain in doubt, the lower Smoky River and the upper Snaring River. Two areas of overlap are evident, from the confluence of the Miette and Athabasca rivers north to the Snaring River (Soper 1970), and the Sunwapta Pass area.

In Banff Park I was interested in the possibility of E. a. ludibundus invading the park from either Sunwapta Pass or from the west. Banfield (1958) reported E. m. borealis at Saskatchewan Crossing and Sunwapta Pass, but not between those two locations. I trapped only E. m.

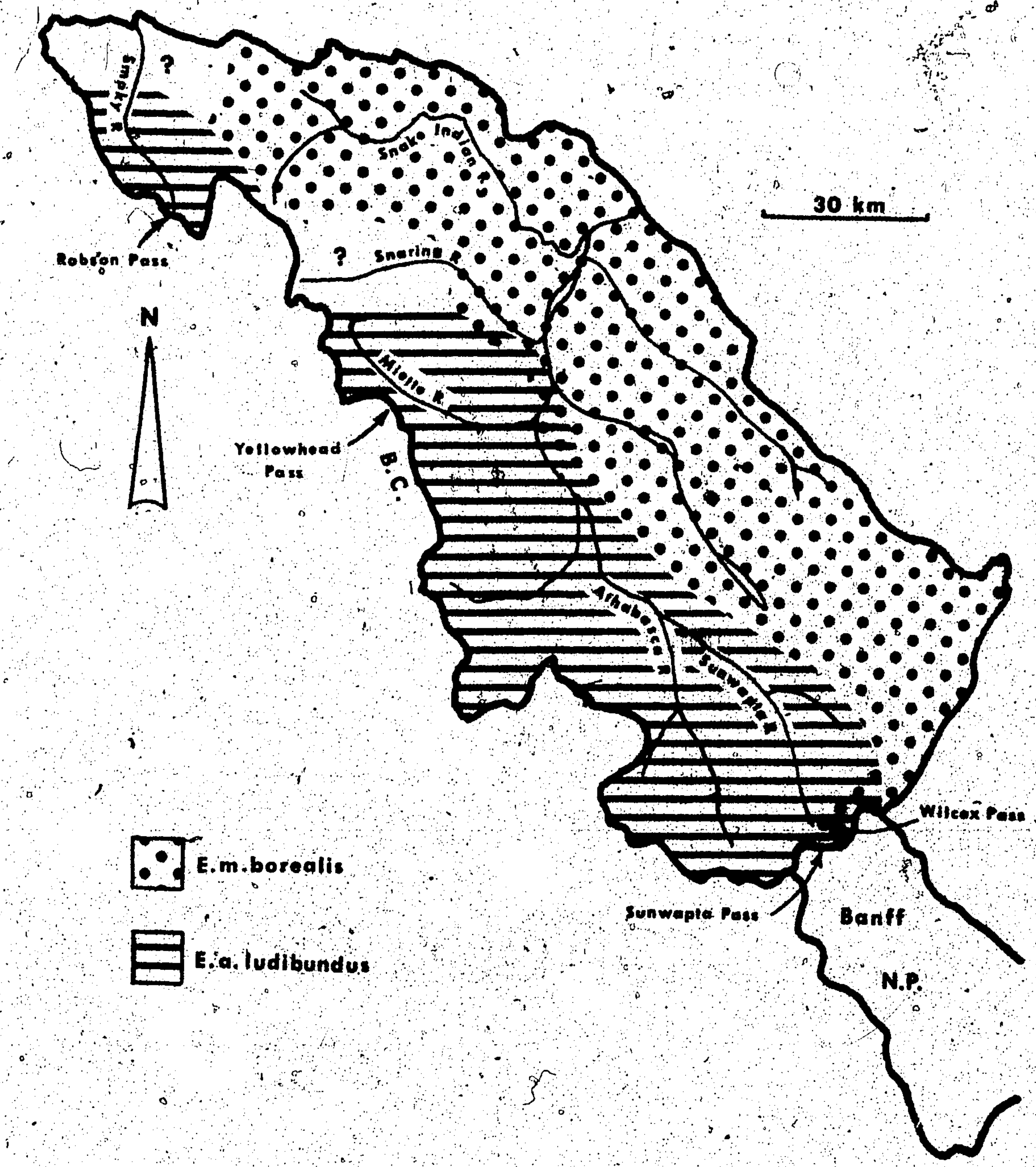

Fig. 8. Map of Jasper National Park showing the ranges of the two species of chipmunks (Soper 1970, and this study).

borealis near the confluence of the Alexandra and North Saskatchewan rivers, and near the confluence of the Howse and North Saskatchewan rivers. Fig. 9 summarizes the range data for each subspecies in Banff Park, obtained from the literature and this study. My data do not contradict the ranges reported by Banfield (1958).

At Robson Pass and Wilcox Pass in Jasper National Park (Fig. 8) I surveyed alpine regions to try and observe use of the alpine by either species. No chipmunks were observed in the alpine at either location.

Summary. North of the Bow River, the two species live in forest habitats, but inhabit distinct ranges only marginally overlapping along their contiguous boundaries. No chipmunks were observed in the alpine regions that I investigated. South of the Bow River, E. m. oreocetes lives exclusively in the alpine, the northern limit of its range (Egypt Lake, Banfield 1958) being a distance of at least 15 km from the range of its nearest conspecific, E. m. borealis, north of the Bow River.

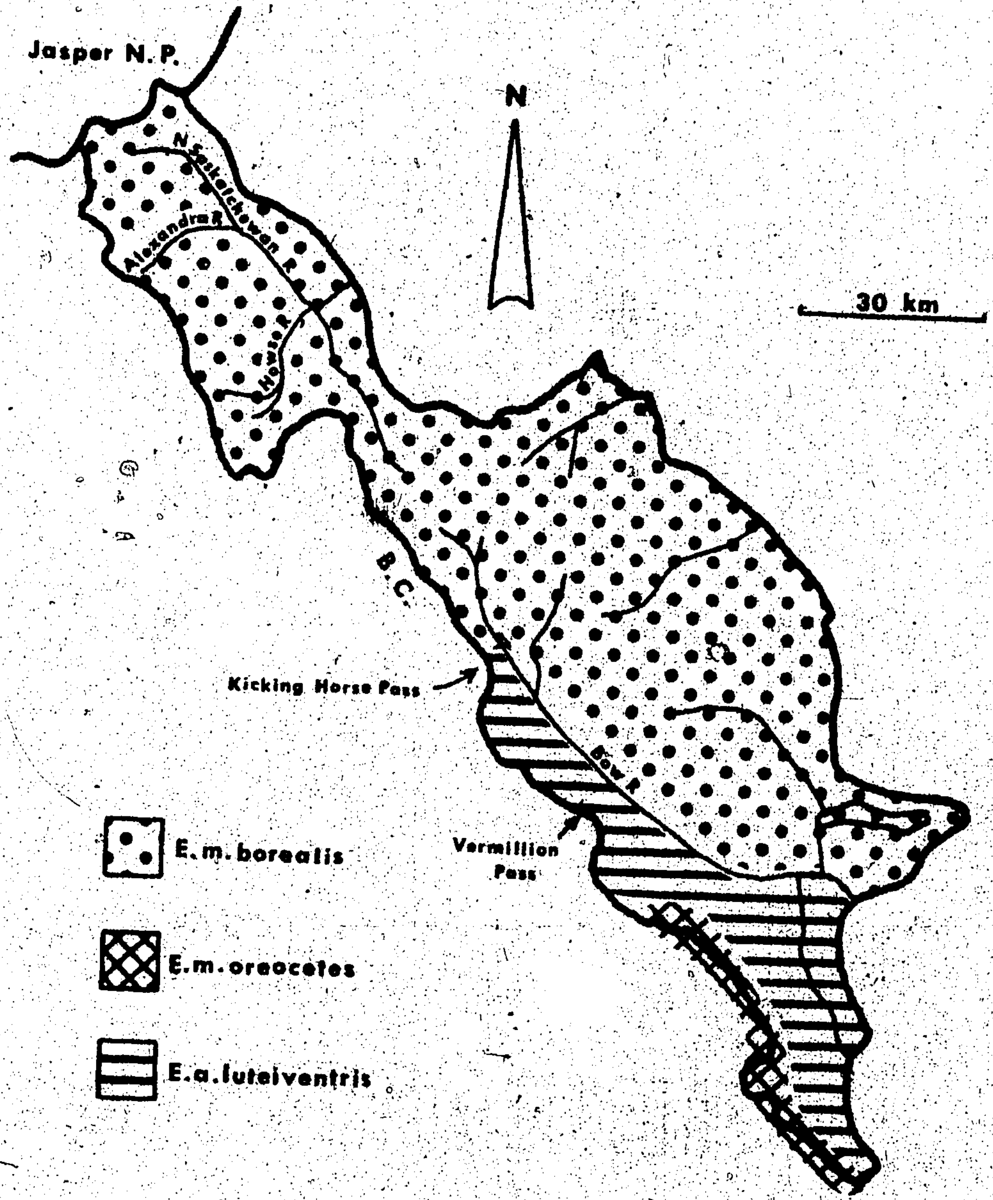

Fig. 9. Map of Banff National Park showing the ranges of the two chipmunk species (Banfield 1958).

HABITAT SELECTION

In the winters of 1972-73 and 1973-74, I tested chipmunks of the two southern subspecies (_E. m. oreocetes_ and _E. a. luteiventris_) in habitat selection experiments in the laboratory. The two northern subspecies (_E. m. borealis_ and _E. a. ludibundus_) were tested during the winter of 1973-74 only.

Methods

Two artificial habitats, each 8.8 m^2 in area, were constructed in a behavioral observation room equipped with one-way glass at the Biological Sciences Center, University of Alberta (Fig. 10). The two habitats represented rock and trees. Soil was placed at a depth of about 6 cm in each sector and covered with grass-sod. In sector A (Fig. 10) rocks, collected from the field, were piled to a height of about 0.8 m and about 0.3 m from all walls and dividers (Fig. 11). The rocks varied from 0.1 m to 0.8 m in diameter. In sector B, five dead spruce and pine trees, cut to about 1.5 m in height, were mounted on wooden stands and placed on the sod (Fig. 12). Two brush piles, of dead spruce and aspen cuttings, were also placed in this habitat in locations where upright trees might have facilitated escape over the dividers. A canopy of black plastic, with holes cut 5 to 10 cm in diameter, was suspended over the

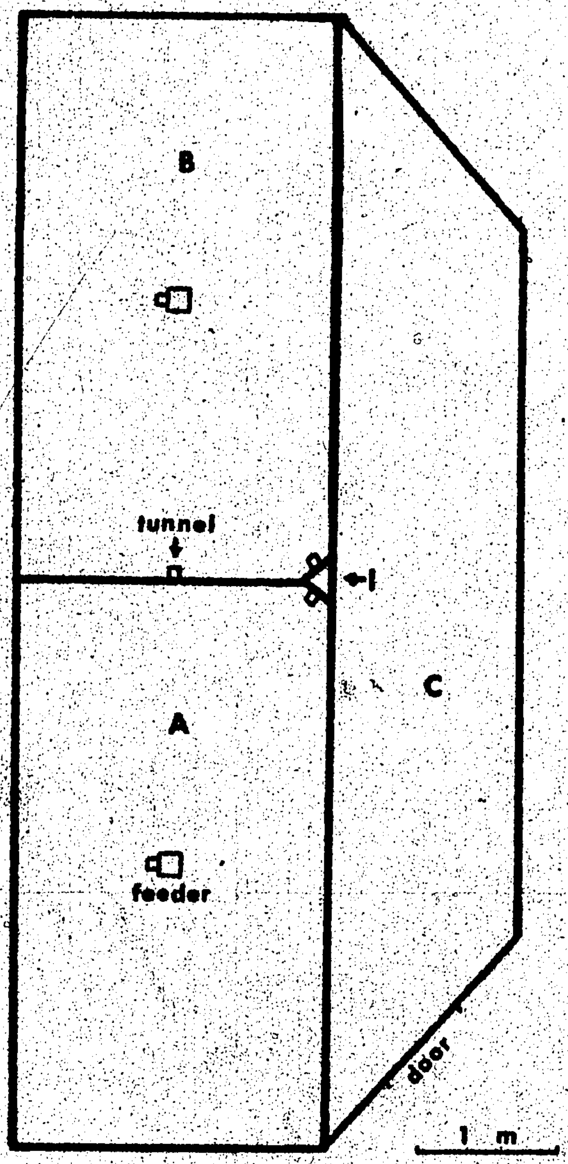

Fig. 10. Diagram of behavior observation room, divided into three sectors (A-C) and an introductory compartment (I).

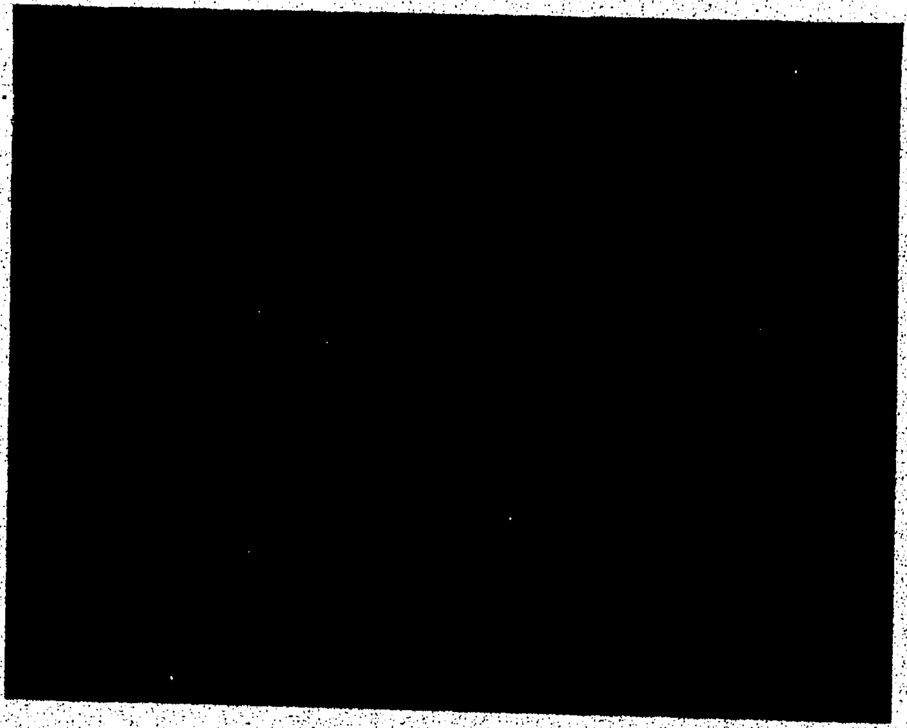

Fig. 11. The rock habitat, showing the dividers and tunnels.

Fig. 12. The tree habitat.

tree habitat, about 2.5 m above the sod, simulating overhead tree canopies (Fig. 13). Dividers 1.45 m high (0.55 m of plexiglass at the bottom and 0.90 m of metal above) separated the habitats from each other (Fig. 11). The chipmunks had access from one habitat to another only through tunnels (7 cm high x 5.5 cm wide x 10.5 cm long), each with a door attached to two mercury switches (Friesen 1972). The switches were connected to an event recorder (Esterline Angus) to monitor movements between habitats and record the number of minutes spent by individuals in each habitat. Each habitat contained a feeder, with a tunnel entrance wired to the event recorder. The photoperiod in the observation room was set at 12 L/12 D, with 0600 to 1800 hr MST as the light period. The temperature in the observation room varied from 19 to 22 C. Time spent in each habitat was chosen, a priori, as the prime criterion for habitat selection.

Chipmunks were introduced singly in the observation room through a small central compartment (0.15 m^2, I in Fig. 10), between 0900 to 1400 hr MST on Day 1 (depending on when the previous animal was captured and removed). Movements for analysis were monitored from 0000 to 2400 hr of Day 2. This allowed each animal time to explore and familiarize itself with the habitats and apparatus prior to activity being recorded. Daytime activity (light) was analyzed separately from nighttime activity (dark).

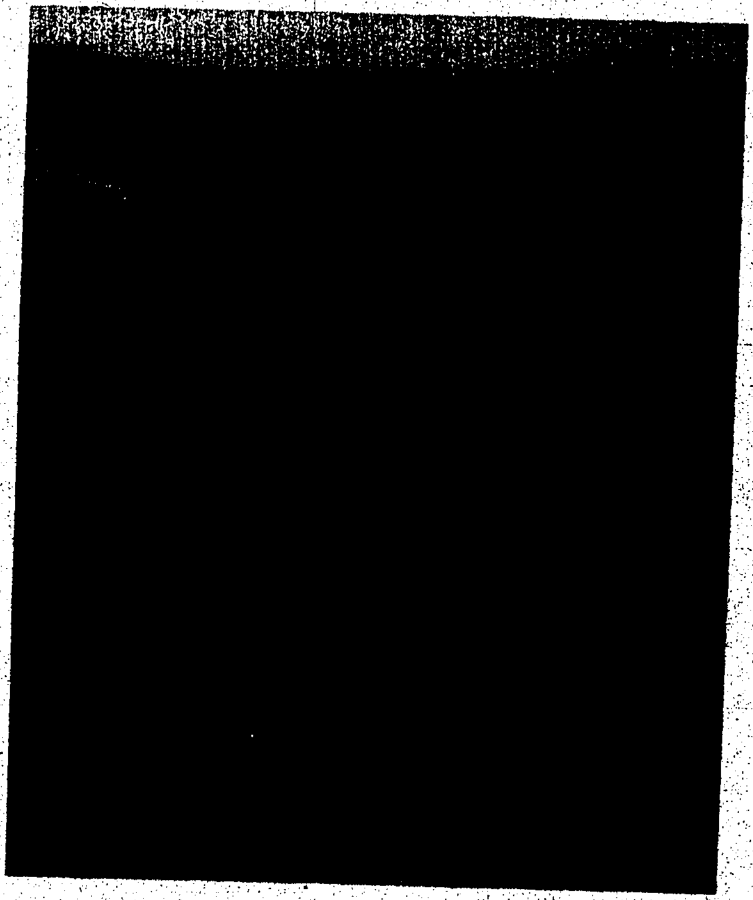

Fig. 13. Plastic canopy over tree habitat.

About 200 g of Vita-mite laboratory food and about 200 ml of water were provided in each feeder to each individual tested. To neutralize the possible effects of scent in the feeders, wood chips placed in both feeders were collected after each test, thoroughly mixed and returned to the feeders. The habitats were dampened with water before introducing a new animal.

During the winter of 1972-73, 18 E. a. luteiventris and 20 E. m. oreocetes were tested in the observation room with the rock and tree habitats, and with a third, meadow habitat. This involved the use of sector C which is also 8.8 m^2, but oblong in shape (Fig. 10). The meadow habitat was tested because it is one type found in both the alpine and the forest. The "meadow" was simply the soil and sod without vertical structure present.

To determine whether or not the shape of the sector had an extraneous effect on the outcome of the experiments, the habitats were rotated from one sector to another, after ten animals of each species had been tested (i.e. rock and meadow were each tested in oblong sector C and sector A or B). I found that individuals of both species significantly avoided sector C regardless of habitat present. Since sector C introduced an artificial bias to the experiment, I decided to discontinue its use and only test two different habitats in the winter of 1973-74. Since both species significantly avoided the meadow, I decided to test the two habitats that appeared fundamental to the separation of the two southern subspecies in the field, rock and trees.

Adults of the two southern subspecies were caught in May and June of 1973 in the Sheep River drainage and were tested in the artificial habitats in September and October of 1973. They were classified as "habitat-experienced" individuals (i.e. they had field experience).

Five pregnant _E. a._ _luteiventris_ females were caught in May of 1972 and were allowed to raise their litters in the laboratory, providing "habitat-naive" individuals (i.e. they had no field experience) that were tested in the artificial habitats in August and September of 1973. Nine pregnant _E. m._ _oreocetes_ females were caught in May of 1973, and were similarly treated. The habitat-naive chipmunks from these litters were tested in February and March of 1974.

Adults of the two northern subspecies were caught in July of 1973 in Jasper National Park. They were tested in the artificial habitats from October to December of 1973.

All chipmunks were transported to Edmonton and maintained individually in cages (50 cm long x 40 cm wide x 20 cm high) in Bioscience Animal Service Facilities at the University of Alberta. They were prevented from hibernating during winter by being kept at about 20 C with a 12 L/12 D photoperiod (Heller and Poulson 1970).

Individuals of each subspecies were tested consecutively in groups of six to ten animals. That is, 10 E. a. luteiventris were followed by 10 E. m. oreocetes, etc. Animals making up each group were drawn at random from the laboratory population.

Statistical Procedures

I used nonparametric statistical methods to compare the habitat selection data because of the heterogeneity between the variances of some of the compared samples (determined by the F-test, Sokal and Rohlf 1969) and the non-normal distribution of the sample variates (Sokal and Rohlf 1969), especially during the dark time periods.

The minutes spent in each habitat by each individual during the light and dark periods were converted to percentage, and a mean was calculated for each sample. Because the number of minutes spent by an individual in one habitat was inversely related to the number spent in the other habitat, the Wilcoxon's signed-ranks test for paired data (Sokal and Rohlf 1969) was used to compare habitat use within a subspecies group (Wecker 1963). The Mann-Whitney U-test (Sokal and Rohlf 1969) was used to compare habitat use between subspecies, and between experienced and naive groups within a subspecies. A probability level of 5% or less ($P \leq 0.05$) was considered to be statistically significant.

Results

Southern Subspecies. Nine male and 11 female habitat-experienced E. m. oreocetes, and 8 male and 9 female habitat-experienced E. a. luteiventris were tested. Results from these tests are compared in Table 2. Both species spent significantly greater time in the rock habitat in both the light and dark time periods. No significant differences were found between species, within each habitat.

The light period included daytime activity, in which there was much interhabitat movement (Appendix II) as would be expected from diurnal rodents. The dark time period included time spent in the nest. There were some interhabitat movements in the dark, but they were rare. Most occurred between 0400 to 0600, and 1800 to 2000 hr (Appendix II).

Nine male and 11 female habitat-naive E. m. oreocetes, and 6 male and 10 female habitat-naive E. a. luteiventris were tested. Naive minimus spent significantly greater time in the rock habitat in both time periods (Table 3). However, naive amoenus did not significantly select one habitat over the other in the light or dark period. More time was spent in the rock by amoenus during the dark, but this was not statistically significant due to the large variance of the sample.

Northern Subspecies. Five male and 6 female E. m. borealis, and 5 male and 5 female E. a. ludibundus were

Table 2. Mean ($\bar{X}$) and standard error (SE) of percent time spent in each habitat by experienced individuals of the two southern subspecies during Light and Dark time periods.

	N		Light			Dark	
			$\bar{X}$	SE		$\bar{X}$	SE
<u>E</u>. <u>m</u>. <u>oreocetes</u>							
rock	20	*	57.9	4.0	***	93.3	2.6
trees			42.1	4.0		6.7	2.6
<u>E</u>. <u>a</u>. <u>luteiventris</u>							
rock	17	***	63.4	3.3	***	92.2	3.8
trees			36.6	3.3		7.8	3.8

* Significant difference in habitat use, $P<0.05$

*** Significant difference in habitat use, $P<0.005$

Table 3. Mean ($\bar{X}$) and standard error (SE) of percent time spent in each habitat by naive individuals of the two southern subspecies during Light and Dark time periods.

	N	Light		Dark	
		$\bar{X}$	SE	$\bar{X}$	SE
E. m. oreocetes					
rock		58.8	5.4	85.8	6.1
	20	**		***	
trees		41.2	5.4	14.2	6.1
E. a. luteiventris					
rock		51.8	4.1	64.9	11.5
	16				
trees		48.2	4.1	35.1	11.5

** Significant difference in habitat use, $P<0.01$

*** Significant difference in habitat use, $P<0.005$

tested. All were habitat-experienced individuals. As shown in Table 4, minimus spent significantly greater time in the rock habitat in both time periods, with no use of the tree habitat for nesting sites. Although amoenus spent a significant amount of its nesting time in the rock, it did not significantly select one habitat over the other during the light period.

The habitat use by the two subspecies was significantly different in both time periods. However, the difference in the dark time period is probably more related to the lack of interhabitat movements by minimus during the dark period (Appendix II) than to any greater degree of selection of rock for nesting sites by minimus, since all individuals of both subspecies nested in the rock.

Summary

Experienced individuals of both southern subspecies selected the rock habitat. Naive E. m. oreocetes spent more time in the rock habitat, whereas naive E. a. luteiventris did not select one habitat over the other.

Experienced E. m. borealis selected the rock habitat. Experienced E. a. ludibundus spent more time in the rock habitat during the dark period, but did not select one habitat over the other during the light period.

Table 4. Mean ($\bar{X}$) and standard error (SE) of percent time spent in each habitat by experienced individuals of the two northern subspecies during Light and Dark time periods.

			Light			Dark	
	N		$\bar{X}$	SE		$\bar{X}$	SE
E. m. borealis							
rock	11	***	76.6	2.8	***	100.0	0.0
trees			23.4	2.8		0.0	0.0
E. a. ludibundus							
rock	10		50.6	3.7	***	97.4	1.5
trees			49.4	3.7		2.6	1.5

*** Significant difference in habitat use, $P<0.005$. Interspecific differences (intrahabitat) are significant, $P<0.005$, in both time periods.

INTERSPECIFIC AGONISM

In his study of aggressive behavior between *E. a. luteiventris* and *E. m. oreocetes*, Sheppard (1971) used two arenas to test his animals; one 1.5 m^2 in area and 2.4 m high (I assume the arena was square or rectangular), and one 3.7 m long, 8 cm wide and 10 cm high. Individual *amoenus* were matched simultaneously with individual *minimus*. He observed the animals for 30 to 60 min after introduction.

Although Sheppard determined that *amoenus* was aggressively dominant over *minimus*, the results from his simultaneous introductions do not explain why *amoenus* has not successfully occupied *minimus* habitat, unless *amoenus* is excluded by other environmental effects. Perhaps the small arenas and lack of habitat structure prevented some of the field relationships from occurring. Individuals probably had little chance to seek cover from their antagonists. In the field, an encounter between individuals may be of short duration, individuals being able to leave the immediate area and thus avoid further interaction.

To determine the effect of a larger, more structurally complicated arena on the outcome of interspecific interactions, I tested individuals of the two southern subspecies in the behavior observation room

(Fig. 10) with the rock and tree habitats present. Two individuals, one of each species, were introduced simultaneously. The two southern subspecies were tested in March and April of 1973. I tested the two northern subspecies in April and May of 1974 to compare with the southern subspecies.

In another experiment Sheppard (1971) allowed one chipmunk to familiarize itself with the arena for 3 to 5 days before the second chipmunk was introduced. Resident *amoenus* were dominant in significantly more matches (67.5% of 40 matches) than resident *minimus* (25% of 40 matches). If Sheppard's resident chipmunk data are compared to his simultaneous introduction data (48.5% of 68 matches dominated by *amoenus*; 1.5% dominated by *minimus*), it is seen that *minimus* was dominant in a significantly larger number of resident matches than simultaneous matches (chi-square two-way table, $P<0.001$), and *amoenus* was also dominant in larger number of resident matches ($0.1>P>0.05$).

Therefore, it appears that familiarity with a "home area" does have an effect on the outcome of an encounter with a rival that is unfamiliar with that area. In the field, a resident animal may be able to dominate a nonresident by using the structure of the habitat to its advantage. In this way, perhaps *minimus* is able to prevent *amoenus* from entering the alpine.

In March and April of 1974, I match[illegible] individuals of the two southern subspecies to test the outcome of interspecific encounters in the artificial habitat with minimus in residence. Similar tests with amoenus in residence were not done because I assumed from my results of the simultaneous matches that resident amoenus would be dominant over invading minimus.

Methods

Simultaneous Introductions. All animals used in these experiments had been tested in the habitat selection experiments and were familiar with the habitats and apparatus in the observation room. Only field-caught individuals were used. Each pair of animals tested was of the same sex. Otherwise, pairings were made at random from the laboratory population. Animals were matched only once to avoid any effect of prior experience. Food and water were provided as in the habitat selection experiments.

Each pair of chipmunks was placed simultaneously in the introduction compartment (I in Fig. 10) between 0900 and 1100 hr MST of Day 1. After the introduction, the observer immediately took a position in the upper level of the observation room, which is separated from the arena by a sound-proof wall and windows of one-way glass. The observer recorded interactions for 2 hr immediately following the introduction, 1 hr in the early afternoon of that day, and 2 hr after lights-on at 0530 to 0600 hr of Day 2. This provided 300 minutes of observation of each pair of animals. The animals were allowed to interact for nearly 24 hr to determine whether cohesive relationships, or perhaps reversals in dominance, would develop during a relatively long match. Time spent in each habitat by each individual was also recorded.

Sheppard (1971) recorded two kinds of aggressive encounters, fights and chases. Fights were recorded as lost by the animal that first ran away from the fight. Chases were recorded as the dominant chasing the subordinate. I recorded the same encounters plus what I call an <u>attack</u>, in which the dominant animal rushed the subordinate and made physical contact with it. This usually resulted in a chase; but, on occasion after an attack, both animals would mutually avoid or circle each other with flared tails. Although not included as aggressive behavior, mutual avoidance and various forms of cohesive behavior (Sheppard 1965) were also recorded.

<u>Intraspecific Agonism</u>. In May and June of 1973, individuals of the two southern subspecies, that had been previously matched interspecifically, were matched intraspecifically to obtain a relative index of aggressiveness for each species (Heller 1971). The procedures were the same as in the simultaneous interspecific introductions, except that male-female pairings were also used, and each individual was fur-clipped in distinct patterns across the back for individual identification.

Resident *minimus* Introductions. Again, all animals used in these experiments were field-caught and had previous experience with the artificial habitats, but not with agonistic experiments. They were matched only once. One minimus was introduced into the arena in mid-morning of Day 1. An amoenus individual was introduced between 0900 and 1100 hr of Day 2, and interactions and movements were recorded for 300 minutes as in the simultaneous introductions.

Statistical Procedures

The chi-square test for goodness of fit and two-way contingency tables (Sokal and Rohlf 1969) were used to compare the number of matches dominated by each species and the total encounters won by each species.

As in the habitat selection experiments, the observed times spent in each habitat by interacting individuals of both species were compared using Wilcoxon's signed ranks test and the Mann-Whitney U-test (Sokal and Rohlf 1969).

Results--Southern Subspecies

I define an encounter as one agonistic interaction between a pair of animals. A match is the pairing of two individuals over the 24 hr period that encounters were recorded.

Simultaneous Introductions. Fourteen individuals of each of the two southern subspecies were matched. The results from these matches are presented in Table 5. Amoenus was dominant in 8 of the 14 matches, while minimus was dominant in 4 matches. These differ from Sheppard's (1971) results in that the number of dominant amoenus matches is not significantly larger than the number of dominant minimus matches (P>0.1); although this may be due to small sample size. However, the total number of encounters won by amoenus (895) is significantly greater than those won by minimus (322) (P<0.001).

In Table 5 the encounters won-lost by the dominant individuals of each species are presented to illustrate the contribution by these individuals to the total encounters won-lost by each species (i.e. 4 dominant minimus contributed 73.0% of the total encounters won by all 14 minimus; and 8 dominant amoenus contributed 87.3% of the total encounters won by 14 amoenus).

Individual dominance was usually determined early in a match. A dominant individual was arbitrarily defined as an animal that won at least 50% more encounters than its opponent. In most matches the dominant won several times the number of matches won by the subordinate (see Appendices III and IV). However, in two male matches dominance was never clearly determined. In one match the dominance shifted from one individual to another throughout the match, with amoenus observed to dominate 33

Table 5. Agonistic encounters between the two southern subspecies introduced simultaneously.

	N	Total encounters won-lost	Individuals dominant*	Encounters won-lost by dominant individuals
<u>E</u>. <u>m</u>. <u>oreocetes</u>				
males	7	193-397	1	109-0
females	<u>7</u>	<u>129-498</u>	<u>3</u>**	<u>126-29</u>
Total	14	322-895	4	235-29
<u>E</u>. <u>a</u>. <u>luteiventris</u>				
males	7	397-193	4	312-11
females	<u>7</u>	<u>498-129</u>	<u>4</u>	<u>469-3</u>
Total	14	895-322	8	781-14

* Unclear dominance in 2 male matches**.
** Including one dominance reversal.

encounters to 28 for minimus. In the other match amoenus was clearly dominant for the first 2 hr of observation. In the third hour of observation minimus became dominant and remained so until the end of the match. In this match amoenus dominated 51 encounters to 46 for minimus.

Another dominance reversal occurred in one female match, where amoenus was dominant in the first hr and minimus was dominant in the last 3 hr. In this match minimus won 82% more matches than its opponent (42-23).

Interacting individuals of amoenus were observed to spend significantly more time in the trees ($\bar{X}$ 59.3%) than in the rocks ($P<0.005$). Although minimus spent slightly more time in the trees (54.1%), the difference was not significant ($P>0.1$)

Resident *minimus* Introductions. Twelve resident E. m. oreocetes were matched with 12 invading E. a. luteiventris. The results from these matches are presented in Table 6. Each species was dominant in half of the matches. However, the total number of encounters won by resident minimus (644) is significantly larger than that won by invading amoenus (572) ($P<0.05$).

These data differ from Sheppard's (1971) results in that his resident minimus won only 25% of their matches and only 28.5% (88-221) of their encounters.

The 6 dominant minimus contributed 88.8% of the total encounters won by all 12 minimus; and the 6 dominant

Table 6. Agonistic encounters between the two southern subspecies with _minimus_ in residence.

	N	Total encounters won-lost	Individuals dominant	Encounters won-lost by dominant individuals
Resident				
E. m. oreocetes				
males	8	465-431	4	412-26
females	4	179-141	2	160-1
Total	12	644-572	6	572-27
Invading				
E. a. luteiventris				
males	8	431-465	4*	405-53
females	4	141-179	2	140-19
Total	12	572-644	6	545-72

* Including one dominance reversal.

amoenus contributed 95.3% of the total encounters won by all 12 amoenus (Table 6). The total encounters won-lost by dominant minimus is significantly different from the total encounters won-lost by dominant amoenus (P<0.001).

In these matches there was only one dominance reversal, which occurred during a male match. Minimus was dominant at the start with a shift of dominance to amoenus occurring during the second hour of observation. The latter remained dominant until the end of the match.

Invading amoenus spent significantly more time in the trees ($\bar{X}$ 61.7%) than the rocks (P<0.005). Again, minimus spent more time in the trees (57.5%), but the difference was not significant (P>0.1).

The First Five Encounters. If animals in the field only interact for a short period (with one or both vacating the area afterward), then perhaps only the first few encounters between individuals in the laboratory are important in determining which animals will occupy an area. To analyze this effect, I picked the first five encounters between individuals of each match, and assigned dominance simply to the animal that won most of the five encounters.

In the simultaneous matches amoenus was dominant in nine matches and minimus was dominant in five. This difference is not significant (P>0.1). However, amoenus won significantly more total encounters (49) than minimus

(21) (P<0.001).

In the resident minimus matches minimus was dominant in nine matches, while amoenus was dominant in three. This difference is not quite significant (0.1>P>0.05). However, the number of matches dominated by resident minimus is significantly larger than the number of matches dominated by minimus during the simultaneous introductions (P<0.05). During the first five encounters, minimus won significantly more total encounters (44) than invading amoenus (16) (P<0.001).

Intraspecific Agonism. All 14 individuals of each southern subspecies used in the interspecific simultaneous introductions were used in the intraspecific simultaneous introductions. For each species there were three male-female matches, two male-male matches, and two female-female matches. The total number of aggressive encounters observed for the seven matches of amoenus (782) was significantly larger than the total number of aggressive encounters for the seven matches of minimus (405) (P<0.001). These data further support the observations of Sheppard (1971) that E. a. luteiventris is more aggressive than E. m. oreocetes. Although sample size was small, there was a trend in both species to use the trees more than the rocks during the interactions.

Results--Northern Subspecies

Ten individuals of each of the two northern subspecies were matched and the results are presented in Table 7. Amoenus was dominant in 8 of 10 matches. This is not a significant difference (0.1>P>0.05), although this may be due to small sample size. However, the total number of encounters won by amoenus (756) is significantly greater than those won by minimus (321) (P<0.001). The 2 dominant minimus contributed 99.3% of the total encounters won by all 10 minimus; and the 8 dominant amoenus contributed 100% of the total encounters won by all 10 amoenus. Interacting individuals of both species spent significantly more time in the trees (minimus: 57.2%, P<0.05; amoenus: 69.1%, P<0.001).

As is obvious from Table 7, an analysis of the first five encounters between individuals of the northern subspecies does not change the outcome of these matches.

Summary

In matches between the southern subspecies introduced simultaneously, amoenus failed to dominate a significantly larger number of matches than minimus, but won a significantly larger number of total encounters. In matches where minimus was placed in residence prior to the introduction of amoenus, each species was dominant in half of the matches. However, resident minimus won a

Table 7. Agonistic encounters between the two northern subspecies introduced simultaneously.

	N	Total encounters won-lost	Individuals dominant	Encounters won-lost by dominant individuals
E. m. borealis				
males	6	320-467	2	319-0
females	4	1-289	0	- -
Total	10	321-756	2	319-0
E. a. ludibundus				
males	6	467-320	4	467-1
females	4	289-1	4	289-1
Total	10	756-321	8	756-2

significantly larger number of encounters.

In matches between the northern subspecies introduced simultaneously, amoenus was dominant in a larger number of matches and a significantly larger number of encounters.

DISCUSSION

I placed the emphasis of this study on the southern subspecies, where minimus and amoenus are altitudinally zoned in the manner characteristic of many species of chipmunks in montane areas of western North America and where a previous study (Sheppard 1965, '68, '69, '71, '72) delineated much of the biology of the two species. The northern subspecies are not altitudinally zoned and were studied to compare their habitat relationships with those of the southern subspecies. For these reasons I have divided this chapter into three sections. In the first, I discuss the relationships of the southern subspecies. The northern subspecies are compared with the southern subspecies and other studies in the second section. In the third section I discuss the possible zoogeographic histories of the four subspecies that contributed to the development of their respective habitat relationships.

Southern Subspecies

Although the two species are altitudinally zoned in Goat Valley, they each have a wide variation in habitat use, as shown in Fig. 4. However, the data in Fig. 4 do not take tree-line into account. For example, captures of amoenus in rock were made along the edges of talus that penetrated the continuous forest, while captures of minimus in rock were made in the alpine or within talus that penetrated the forest. Captures of amoenus in meadow were made in forest meadows, while captures of minimus in meadow were made above tree-line, or in the subalpine.

All captures of the two species in the subalpine were made along the valley slope where the subalpine is a narrow belt, being only a few meters from the alpine and the continuous forest. A variety of food available in the subalpine and the proximity of that zone along the valley slope to talus and tree cover may explain the high use of that habitat by both species.

Most captures of minimus were made in or near talus. The absence of this chipmunk in the broad subalpine region of the valley may be explained by the lack of talus there.

Most captures of amoenus were made in or near trees. However, no amoenus were captured in the broad subalpine region, where presumably there is adequate habitat. It thus appears that conditions other than interspecific agonism are preventing either species from occupying the broad subalpine in Goat Valley.

Of the 17 amoenus transplanted to the alpine in 1971, none was found there in 1972. Sheppard (1971:526) stated, . . . "with introductions such as these, negative results are inconclusive because the animals may simply leave the area of introduction." Indeed, it appears that homing behavior may have played a significant role. Broadbooks (1970) reported one chipmunk in four (25%) returning to its home area when released one mile (1610 m) away. Of the animals released in Goat Valley, 12% returned to their original areas, some 3000 m away; and 35% were known to have reached the open forest, although at least two of these individuals established themselves in other than their original areas.

Whether *amoenus* is capable of living in the alpine remains to be established. However, the apparent seasonal migration of some individuals from lower Goat Valley to the lower limit of the broad subalpine in August, suggests that the upper valley may not be able to support a viable *amoenus* population throughout the season (Meredith 1974). Foraging in the alpine and broad subalpine may not be energetically feasible for *amoenus*, whereas *minimus* may be adapted in terms of size, physiology and behavior to survive in the alpine throughout the year (Sheppard 1971).

Small size may be an important adaptation of chipmunks that live solely in the alpine. In the Sierra Nevada *alpinus* lives solely in the alpine and is smaller (about 39 g) than its forest neighbor, *speciosus* (about 71 g) (Heller and Gates 1971). Like *alpinus*, *E. m. oreocetes* lives solely in the alpine and is smaller than its neighbor, *amoenus* (Sheppard 1968, and Appendix I). *Eutamias minimus oreocetes* is also smaller than its nearest conspecific neighbor, *E. m. borealis* (Appendix I), which lives in the forest. The question arises whether the two alpine chipmunks have evolved a small size to survive in the alpine. Why would small size be advantageous in the alpine?

In a reexamination of Bergmann's rule, McNab (1971:846) argued that "large individuals of a species lose more heat via their surface than small individuals, if all other factors (such as temperature differential between the body and the environment and the insulative value of the coat) are equal, because large individuals have larger surface areas than small individuals." Thus, large individuals require more energy than small individuals. Where the food supply is sparse, small body size may be advantageous.

Thus, it may be advantageous for an alpine chipmunk to be relatively small, as the growing season is shorter than in lower elevations, and food source patches are sparsely distributed. As pointed out by Vaughan (1974), animals that hibernate must take in a greater amount of energy than is required to sustain them during their active season (in the case of chipmunks, the energy required during the winter is stored as food in the burrow, Broadbooks 1958). Because of the shorter growing season, alpine chipmunks have less time during the active season to forage and store food than their counterparts at lower elevations. Because food source patches are sparsely distributed in the alpine (some not being available in

Goat Valley until late July as a result of late snow-melt), more energy may be expended by alpine individuals to gather food than is expended by individuals at lower elevations where food sources are presumably not as sparsely distributed and the snow-melt is earlier. Thus, a large individual with a large energy requirement may not be able to visit enough patches in a day to sustain itself and store food. This, combined with the shorter daily foraging time available, may account for the inability of *amoenus* to maintain a stable population in the alpine and successfully compete with *minimus* there.

The lack of significant incursion by adult *amoenus* into former *minimus* area on Volcano Ridge rockslide may be explained by this hypothesis. An inadequate food supply may be preventing *amoenus* from invading the interior of the slide. *Amoenus* may only utilize the edge of the slide to make nests and seek refuge from predation, while being close to the forest where the food supply is probably more abundant and varied (Sheppard 1965, 1971).

However, the data from Volcano Ridge may be the result of other factors. The experiment may have been terminated too early for a resident population of *amoenus* to become established in the absence of *minimus*. Different individuals at different times of the year are being compared without a control. Thus, the data do not support or deny the hypothesis that *minimus* excludes *amoenus* from alpine rockslides.

Is competitive exclusion occurring between the two species? From Sheppard's (1971) transplant and agonistic data it can be concluded that amoenus is preventing minimus from invading the forest. However, neither species occupied the broad subalpine in Goat Valley, suggesting that other factors may be involved. The negative results from Sheppard's (1971) transplants, the Goat Valley transplants, and the Volcano Ridge rockslide experiment fail to answer the question of whether minimus excludes amoenus from the alpine. As argued by Sheppard (1971) and myself, amoenus may not be adapted to the alpine environment; but this may be a result of its exclusion from that environment, and not being subjected to the selection pressures that would necessitate alpine adaptations. Hoffmann (in Sheppard 1965) observed that E. a. luteiventris lives in the alpine of western Montana when E. m. oreocetes is absent. Thus, competitive exclusion may be restricting each species to its respective habitat, or perhaps the relationship has evolved into one of mutual avoidance, in which each animal selects and remains in its optimal habitat. As argued by Sheppard (1971) the fundamental niches (Hutchinson 1957) of both species are quite similar, but through long association along a contiguous boundary their niches may have narrowed through competition, temperature tolerance, habitat selection, or some other specialization.

Habitat Selection. In the habitat selection experiments, habitat experienced individuals of both species significantly selected rock over trees in both day and night (Table 2). This lack of difference between the species may be explained in several ways.

First, habitat selection may not be a factor in the apparent competitive exclusion between these species. Both species are selecting the rockslide as the best habitat for nest site placement and foraging when food and water are available in both habitats. Rockslides provide continuous ground cover, which is probably important to a diurnal animal foraging in relatively open habitats where it may have to seek concealment from predation quickly. Selection of the rock habitat may not be a response to the rocks themselves, but to the quality of the cover provided by the habitat.

Reilly (1971) found that minimus from Upper Michigan preferred habitats with unrestricted horizontal visibility and high perches. Rockslides are good examples of a habitat with both of these factors. The relative lack of tree cover increases horizontal visibility. Large boulders positioned at high points on the slide provide high perches. Most of the chipmunks that I observed on rockslides were first seen on such boulders.

A second factor that may explain the lack of difference in selection behavior between the species is that the selection factors that I chose to test (structure of rock and trees) may not be the factors selected in the field. Chipmunks may select their habitats on the basis of food preference or microclimatic factors. Sheppard (1965, 1971) analyzed the contents of cheek pouches of collected animals and found the food habits of *amoenus* and *minimus* to be similar. "Such differences as exist can readily be explained in terms of seed availability and do not seem to reflect differences in food preference," (Sheppard 1971: 324).

Third, my representations of these habitats may not have been adequate. That is, the observation room may have been too small, the rock pile too shallow, or the trees too short. The plastic canopy over the tree habitat may have blocked too much light, making that habitat more like a closed forest than the open forests inhabited by *E. a. luteiventris*.

However, data from the naive individuals do show interspecific differences in selection behavior (Table 3). Naive *minimus* selected rock over trees in both time periods, while naive *amoenus* did not select one habitat over another. Thus, it appears that the response to the rock habitat by *minimus* is at least partly innate, and *amoenus* learns to select rock as optimal habitat. Indeed, in the southern Alberta Rocky Mountains, the few rockslides that are surrounded by forest are utilized by *amoenus*. If *amoenus* learns to select rock, why would an innate preference for rock be advantageous to *minimus*?

This question was addressed by Wecker (1963) concerning Peromyscus maniculatus bairdi and its innate selection response for the "field" habitat. He concluded that learned habitat selection behavior or habitat imprinting requires a "period of habituation" during a critical period of the life of an individual, probably shortly after the individual leaves the nest. If the environment remains relatively stable, an inherited response to an optimal habitat may be advantageous to an individual. If the environment is changing, such an inherited response may not be advantageous, and those animals that must learn which habitat is optimal may be more successful in surviving and producing offspring.

In the alpine, rockslides provide the only continuous cover that has vertical depth and is present throughout the year. Meadow plant communities provide seasonal cover, but with little vertical depth. A chipmunk being pursued by a predator would not have the variety of escape routes in a meadow community as it would in a rockslide. Because rockslides have vertical depth, they also provide better cover from weather than meadow communities. A young alpine chipmunk that innately selects the cover quality of a rockslide as a refuge from predation or weather, may have a higher probability of survival over a young chipmunk that must learn to select rockslides.

Amoenus may inherit a generalized response to habitats that provide cover. In the forest there are many cover types that provide vertical cover in depth (e.g. tree canopies, brushpiles, rockslides), and it may not be advantageous for a chipmunk to inherit a response for just one type of cover.

The habitat selection data suggest that *minimus* innately selects a cover type that is found frequently in the alpine and this may result in restriction to that zone, except where rockslides penetrate the forest from the alpine. However, the habitat selection data do not suggest that *amoenus* is restricted to the forest. If *amoenus* is dominant in agonistic encounters, and it is assumed that it can adapt to the alpine, why doesn't it invade and replace *minimus* in the alpine?

Interspecific Agonism. The results from the interspecific agonism experiments are inconclusive concerning the dominance of *amoenus*. In the simultaneous introductions *amoenus* won a significantly larger number of total encounters, but failed to dominate a significantly larger number of matches (Table 5). Since the dominant individuals can account for most of the encounters won by a species (Tables 5, 6 and 7), I feel that the number of individual matches won and lost is the important criterion to be considered when evaluating the aggressive dominance of a species. Although the dominance of *amoenus* might have been substantiated with a larger sample size, it is clear that the dominance of *amoenus* was not as conclusive as suggested in Sheppards' (1971) simultaneous introductions.

Sheppard (1971) used small arenas containing, at the most, only nest boxes and a hollow log. In his experiments individuals could only retreat to a nest box or the hollow log to avoid their opponents. In my tests the individuals could easily avoid each other's presence without having to seek a hiding place by simply moving to the other habitat. Sheppard's experimental design isolated aggression from the many other factors that are present in the field. My design introduced two more factors, large arena size, allowing avoidance, and habitat structure. These may have been responsible for the inconclusive dominance of amoenus in my results.

During matches, both species (including the northern subspecies) spent most of their time in the trees, which contrasts with their behavior in the habitat selection experiments. Likewise, the majority of encounters occurred in the trees (Appendices III and IV). When interacting, a chipmunk may prefer to be on the highest perches available to observe its opponent. When both individuals were in the trees the dominant chipmunk usually positioned itself at the top of a tree and intently watched its opponent below. The subordinate occasionally climbed the tree and attempted to solicit a cohesive interaction (naso-nasal or naso-anal, Sheppard 1965) which usually ended in the dominant chasing the subordinate from the tree. If dominance had not been established, the individual that was on a tree top was usually attacked by the other individual and a chase ensued.

In the rocks the pattern was similar, except that the dominant individual appeared less tolerant of the presence of the subordinate. If the subordinate was visible to the dominant, the dominant usually gave chase. The subordinate avoided such chases by going into the rocks or leaving the habitat. In the trees, however, the dominant appeared to be more tolerant of the subordinate, as long as the latter did not climb high in the trees.

From the above observations, I conclude that each individual was not as stressed as it would have been in a smaller, less complicated arena. It was not necessary for the subordinate to hide in its nest to avoid interaction. Indeed, subordinates initiated many interactions even though dominance appeared to be established.

As found by Sheppard (1971), minimus is more hesitant and less active than amoenus (Appendix II). In an arena where the individuals cannot avoid their antagonists, perhaps the initial reaction of minimus is to escape the bolder amoenus, and thus lose the first encounters. After such losses minimus may not be able to reverse the "aggressive momentum" established by amoenus. In a larger arena, minimus may be able to avoid interacting with amoenus until it is ready to approach its opponent on its own terms, when it may best be able to dominate an encounter. Of course, amoenus would benefit from the larger arena in the same way, but minimus may receive greater benefit, because of its more hesitant and generally cautious behavior.

The dominance reversals support the above contention. The two individuals in each of these matches were nearly equal in their aggressiveness. Because each individual was able to avoid the other when the encounters were not in its favor, a one-sided dominance was prevented.

When minimus was a resident of the artificial habitats for one day prior to the introduction of amoenus, neither species was conclusively dominant over the other. Indeed, minimus won significantly more total encounters than amoenus although both species won an equal number of matches (Table 6). If just the first five encounters of each match are analyzed, then minimus won a larger number of matches, as well as a significantly larger number of encounters. Thus, residency may play an important role in the outcome of an interaction between these two species.

When an amoenus was introduced into the artificial habitats, the resident minimus usually initiated the first encounter. This was followed by a large number of interactions that usually determined the dominance for the remainder of the match. However, if amoenus dominated a match, minimus would continue to initiate interactions and occasionally dominate them. As shown in Table 6, subordinate minimus won significantly more encounters than subordinate amoenus. It thus appeared that resident minimus were attempting to drive invading amoenus out of the arena. In the field an amoenus being unfamiliar with the home area of minimus, might leave the area after the first few encounters. A minimus that is subordinate to an invading amoenus may also be able to drive out the invader by continually harassing it, resulting in the invader spending too much time and energy chasing its antagonist to successfully occupy the habitat (i.e. aggressive neglect, Brown 1971).

Northern Subspecies

The northern subspecies, E. minimus borealis and E. amoenus ludibundus, are geographically (horizontally) parapatric in Alberta (Fig. 7), both living in forested areas. While both species reside in the mountains of Jasper Park, the majority of the range of E. m. borealis mainly occupies the boreal forest (taiga) to the east and north (Fig. 1, and Hall and Kelson 1959), and E. a. ludibundus occupies the mountains of interior British Columbia (Cowan and Guiguet 1965).

I observed amoenus in Jasper Park to be associated with closed forests (overlapping tree canopies), characteristic of the moist forests that cross from British Columbia into western Jasper Park. Minimus in Jasper Park tends to be associated with open forests (non-overlapping tree canopies) characteristic of many of the forests in the eastern front ranges of Jasper Park.

Habitat Selection. In the habitat selection experiments on the northern subspecies, I used only habitat-experienced individuals. Therefore, I tested the composite of innate and learned habitat selection behavior. Minimus significantly selected rock over trees in both time periods, while amoenus did not particularly select either habitat during the day and selected rock during the night (Table 4). Thus, three of the four subspecies studied prefer rock over trees during the day. One of these subspecies lives in the alpine where talus is the only continuous cover available with vertical depth. The other two live in open montane forests, where talus may be preferred over other types of cover, when available, because it provides continuous ground cover.

Eutamias amoenus ludibundus, however, lives in forests with relatively continuous tree canopies that reduce light penetration and thus the visibility of animals foraging beneath them. This chipmunk may be behaviorall adapted to the closed forest to reduce its exposure to predation. It may have selected either artificial habitat because both provided a continuous cover, on the ground in the rocks, and vertically in the trees. The other two forest dwelling subspecies, E. a. luteiventris and E. m. borealis, may not have selected the artificial tree habitat because the plastic canopy did not represent the tree canopies of the open forests. Their behavioral adaptation to the open forest may cause them to prefer a habitat with vertical visibility that was not provided in the artificial tree habitat.

All four subspecies preferred rock during the dark time period (Tables 2 and 4). Thus, I conclude that the rock habitat in the laboratory provided better cover for nest placement than did the tree habitat. Little is known about the distribution of nest sites in various types of cover in the field. Broadbooks (1958) and Smith (1973) have documented use of burrows by Eutamias in areas with little cover. Use of talus for nest placement has not been observed and would be difficult to confirm.

Interspecific Agonism. Heller (1971) postulated that interspecific aggressive dominance would evolve in chipmunk species that defend sparse, potentially limiting food supplies. Minimus is an exception to that hypothesis. Sheppard (1965) reported that where minimus is the only species of Eutamias, it is found in forested areas. In regions where other species of Eutamias may be potential competitors, minimus is restricted to non-forested habitats, e.g. alpine and sagebrush; while the other Eutamias species occupy the forest. Sheppard argued that the forest habitat is optimal in terms of food sources for Eutamias and that minimus is excluded from the forest by other species that it comes in contact with. As shown in Table 7, E. a. ludibundus was dominant over E. m. borealis in agonistic experiments in the artificial habitats. Therefore, in three studies of the interspecific aggressive dominance between potentially competing subspecies of *minimus* and *amoenus*, *minimus* was found to be subordinate to *amoenus* (*E. m. scrutator* and *E. a. monensis*, Heller 1971; *E. m. oreocetes* and *E. a. luteiventris*, Sheppard 1971; *E. m. borealis* and *E. a. ludibundus*, this study). In two cases the subordinate *minimus* occupies non-forested habitats (*E. m. scrutator* and *E. m. oreocetes*) while *amoenus* occupies the forest. In the third case both occupy the forest. Both species are wide ranging and occupy various habitats (Sheppard 1965), yet the dominance relationship seems to remain the same. Instead of the habitats occupied determining the dominance relationship, the dominance relationship appears to determine the habitats occupied.

As noted by King (1973) most studies of the ecological determinants of agonistic behavior in rodents have concentrated on population density. However, "density is only one correlated variable with these behavioral changes and need not be the causal mechanism," (King 1973: 119). The relationships of a species to its prey, predators, habitat, and the social structure of its population probably play a role in determining its aggressiveness. Heller's (1971) dominance hypothesis associating aggressiveness to sparse food sources may apply to the case of *alpinus*; but, I do not believe it can be applied to *minimus* and *amoenus*.

Zoogeographic Relationships

As described by Armstrong (1972), zoogeographers seek to explain the distribution of animals by the analysis of data from various systematic and ecological disciplines. "The ultimate problem of zoogeography is to ascertain the ongoing historical succession of ecological conditions responsible for the evolution of observed distributional patterns," (Armstrong 1972:318). The present distributions in Alberta of the two species of chipmunks I studied were probably affected by the interaction of changing climatic, geological and ecological conditions. I assume that their various behavioral, morphological, and physiological characteristics affected, and were affected by, their zoogeographic histories. I have attempted the following zoogeographic analysis of the four subspecies concerned to help explain how their parapatric relationships may have developed. The following discussion is speculative and based on little detailed information.

The ice sheets of the Pleistocene greatly affected floral and faunal dispersal patterns in North America. Because the Laurentide and Cordilleran Ice Sheets covered most of Alberta during the Wisconsin glaciation (Stelck 1967), the species of most plants and animals found in Alberta today have invaded the province since that glaciation. By examining the present day distribution of a species, one is able to suggest probably faunal origin (in a broad geographical area) and various routes of and barriers to its dispersal. Many small mammals are potentially vulnerable to climatic factors, because most cannot seasonally migrate large distances to avoid extremes in their environments.

Both minimus and amoenus are wide ranging species, probably originating somewhere in the western United States. From their range maps (Hall and Kelson 1959) it can be postulated that minimus followed the retreat of the Laurentide Ice Sheet north through eastern Montana to eastern and northern Alberta and Saskatchewan. From there it expanded east, as far as Quebec, and west into the Rocky Mountains.

Amoenus has a somewhat more restricted range than minimus, occupying the northwestern United States, British Columbia and Alberta (Hall and Kelson 1959). It probably followed the retreat of the Cordilleran Glacier Complex north into the mountains of British Columbia and Alberta.

The greater part of the range of E. a. ludibundus is in the mountains of interior British Columbia. Cowan (1946) interpreted its range in Jasper Park as representing an invasion from the west. Yellowhead (1131 m in elevation, Fig. 8) and Robson (1652 m in elevation, Fig. 8) passes were the most likely principle routes used. Both of these passes are forested and provide no ecological barriers to this species. From the Miette River this species probably invaded the forested areas to the south, along the Athabasca River. There are a few low elevation, forested passes along the Continental Divide south of Yellowhead Pass, but according to Cowan and Guiguet (1965), E. a. luteiventris occupies the forest to the west of the divide. Whether E. a. ludibundus intergrades with E. a. luteiventris in the vicinity of these passes is not known.

Both species may have invaded the Athabasca River valley in Jasper Park from the east and west, respectively, at relatively the same time; or minimus may have been excluded from the Miette River and upper Smoky River valleys by the aggressively dominant amoenus when the passes were freed of ice. Their parapatry along an environmentally continuous boundary (unlike the alpine--forest boundary) may be due to the prior residency of minimus combined with other unknown factors that allow that chipmunk to compete successfully with amoenus east of the boundary. The two known areas of marginal sympatry (Fig. 8) may represent particular habitat mosaics that allow the two species to divide the resources between themselves, without one species displacing the other (MacArthur and Wilson 1967). At Wilcox Pass (Fig. 8), I observed the range overlap to occur in the subalpine tree island--meadow mosaic, a condition similar to that found in the Washington Cascades where E. amoenus and E. townsendii coexist in subalpine areas (Meredith 1972). I did not investigate the area of sympatry north of the confluence of the Miette and Athabasca rivers (Fig. 8) reported by Soper (1970). However, the area appears to be a continuation of the grassland--forest mosaic that I found at Devona (confluence of Snake Indian and Athabasca rivers, Fig. 8). That amoenus does not occupy this habitat with minimus at Devona may be a result of the distance of Devona from the allopatric range of amoenus. To maintain a competitive population in these marginal sympatric areas, at least one species may have to recruit individuals from its allopatric population in order to match the number of reproducing females per female parent produced by its competitor's sympatric population (Debach 1966). Such an hypothesis awaits further study of the reproductive and general biology of these two subspecies in Jasper Park.

The North Saskatchewan River valley in Banff Park (Fig. 9) was probably invaded from the east by E. m. borealis. Valley glaciers at the head of the North Saskatchewan, Sunwapta and Athabasca rivers may have prevented E. a. ludibundus from invading the North Saskatchewan Valley prior to invasion by E. m. borealis.

In British Columbia E. a. luteiventris occupies all of the western slope of the Rocky Mountains from Mount Robson Provincial Park to beyond the U.S. border (Cowan and Guiguet 1965). It may have invaded Banff Park through Kicking Horse (1628 m in elevation, Fig. 9) and Vermillion (1651 m in elevation, Fig. 9) passes. These passes are forested and offer no ecological barrier. However, another invasion route may have been from the south. It is possible that the above passes were covered by ice (Reeves 1973) when *E. a. luteiventris* invaded the ice-free valleys of British Columbia. The Montana populations of this chipmunk may have followed the forest development north along the eastern slope of the Rocky Mountains, eventually invading the Bow Valley from the south and east.

Today, both *E. m. borealis* and *E. a. luteiventris* occupy the Bow Valley, but parapatrically along the Bow River. If the aggressive dominance relationship between these two subspecies is similar to the relationship between other subspecies of *minimus* and *amoenus*, and if interspecific aggressive dominance is an important competitive factor in this relationship, then the Bow River valley was probably initially invaded by *E. m. borealis*, as that chipmunk probably would not have excluded a resident *E. a. luteiventris* population. The valley south of the river was subsequently invaded by *E. a. luteiventris* which excluded *E. m. borealis* there. Why had *E. a. luteiventris* not successfully invaded north of the Bow River?

The Bow River is an effective barrier to small ammals during the non-winter months because of its width nd fast current. However, during the early spring when here is ice on the river and chipmunks are active, it would be conceivable for chipmunks to cross the river. Indeed, other rivers of similar size (e.g. North Saskatchewan and Athabasca rivers) have been readily crossed. Therefore, I doubt that the Bow River alone is responsible for the boundary between the two species.

Because the river forms an effective barrier during most of the active season for chipmunks, *E. a. luteiventris* may not have been able to establish a colonizing population north of the Bow River, where *E. m. borealis* was already present. If a few *E. a. luteiventris* individuals crossed the river into unfamiliar territory during the early spring, they may have been dominated by a superior number of resident *E. m. borealis* individuals. This would be unlike the condition of an invading population of chipmunks crossing a river into new territory unoccupied by another species of chipmunk, or a population of competitively dominant chipmunks continually invading (no seasonal barrier) the range of a subordinate species throughout the active season.

The origin of *E. m. oreocetes* presents an interesting zoogeographic problem. Cowan (1946) argued that *E. m. borealis* intergrades with *E. m. oreocetes* in the alpine of the Continental Divide in Banff Park. Banfield (1958), who investigated the Bow Valley, considered the *minimus* population on the Continental Divide to be *E. m. oreocetes*, since the chipmunks there are smaller and grayer than *E. m. borealis*, and are ecologically and geographically isolated from E. m. borealis.

The range of E. m. oreocetes is small, extending from southern Banff Park to northwestern Montana (Hall and Kelson 1959), solely in the alpine of the Rocky Mountains. If the progenitor of E. m. oreocetes was E. m. borealis (the closest conspecific neighbor) and if E. a. luteiventris is competitively dominant over E. m. borealis in the forest, then one can argue that E. m. borealis initially resided in the forested valleys of the east slope of the Rocky Mountains, south of the Bow River. The dominant E. a. luteiventris subsequently invaded those forested valleys and excluded the subordinate E. m. borealis from the forest. Because minimus had established a resident alpine population adapted to alpine conditions, E. a. luteiventris (not so adapted) was unable to exclude minimus from that habitat. However, a second hypothesis concerning the origin of E. m. oreocetes should be considered.

The Cordilleran Glacier Complex of the Wisconsin glaciation extended along the Rocky Mountains to just south of the Alberta-Montana border, where it broke up into discontinuous valley glaciers in the higher mountains (Alden 1953). It is conceivable that E. m. oreocetes may represent a population of minimus that was isolated in a mountain refugium south of the Cordilleran Glacier Complex. Although little is known about the environment in that area at that time, such an environment may have produced a population of chipmunks adapted to life in an arctic--alpine habitat. When the ice retreated and other species of chipmunks followed the forests into the mountains, _E_. _m_. _oreocetes_ may not have been a successful competitor in the forest, but was able to compete successfully in the alpine.

CONCLUSIONS

As pointed out by DeBach (1966:191), "most cases of competitive displacement in nature have already gone to completion." The altitudinal parapatry of minimus and amoenus in southern Alberta is probably the result of a competitive relationship that developed when the two species invaded the Rocky Mountains of southern Alberta. The aggressive dominance of amoenus over minimus may have been an important factor when the two species competed in a common habitat. It probably reinforces the habitat segregation that is evident today, although other factors may have developed to minimize the energy expended by individuals of both species in competitive interactions.

The origin of the alpine E. m. oreocetes possibly occurred through geographical isolation, or through isolation as a result of the invasion of a superior forest competitor. Amoenus may have been prevented from occupying the alpine by the presence of a resident species better adapted to alpine conditions.

Interspecific agonism appears to play a role in the maintenance of parapatry for both species, each defending its habitat from incursions by the other. "Aggressive neglect" might be an important factor in the restriction of amoenus to the forest, tree-line being the limit to which aggressiveness may be of benefit to amoenus.

This species possibly utilizes too much time and energy chasing its antagonists to successfully forage in the alpine.

Habitat selection may play a role in the maintenance of parapatry for minimus, but not for amoenus. Because minimus is restricted to the alpine by the presence of amoenus in the forest, and because cover is important to the survival of a diurnal small mammal, minimus seems to have developed an innate preference for the cover quality of talus, the one type of continuous cover with vertical depth available in the alpine. Because amoenus has a choice between several types of cover with vertical depth, it has not specialized its preference. Therefore, its habitat selection may not restrict it to the forest to the extent that minimus is so restricted to the alpine.

Of the two factors I investigated, only interspecific agonism appears to play a role in the restriction of amoenus to the forest. Both habitat selection and interspecific agonism probably play roles in the restriction of minimus to the alpine.

North of the Bow River, preference of E. a. ludibundus for closed forests might restrict it from occupying the open forests of the eastern front ranges. Presence of a resident minimus population in the open forest possibly reinforces this restriction. Similarly, preference of E. m. borealis for open forests might restrict it from occupying the closed forests of the

Continental Divide, especially when those forests are occupied by an aggressively dominant *amoenus* population.

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APPENDIX I

Table of mean weights ($\bar{X}$) and standard errors (SE) in grams of adults of the four subspecies of chipmunks weighed after capture at the following locations: *E. m. borealis* in July at Devona, Jasper N.P.; *E. a. ludibundus* in July at Derr Creek, J.N.P.; *E. m. oreocetes* in June at Sheep-Elbow Summit, Bow River Forest; and *E. a. luteiventris* in May and June in the Sheep River drainage, Bow River Forest. Data were treated with the t-Test (Sokal and Rohlf 1969).

	N	$\bar{X}$	SE
Northern Subspecies			
E. m. borealis	16	45.7	±1.6
		**	
E. a. ludibundus	20	51.3	±1.0
Southern Subspecies			
E. m. oreocetes	22	39.0	±0.8
		***	
E. a. luteiventris	20	47.5	±0.8

** Significant difference between means, $P<0.01$.
*** Significant difference between means, $P<0.001$.
Both intraspecific comparisons are significantly different: *E. minimus* $P<0.001$; *E. amoenus*, $P<0.01$.

APPENDIX II

Table of mean number of interhabitat movements in 2 hr intervals for individuals in all groups of chipmunks tested in habitat selection experiments. N = number of individuals. $\bar{X}/24$ = mean number of movements per individual over 24 hr. m.o. = *Eutamias minimus oreocetes*. a. ltv. = *E. amoenus luteiventris*. m.b. = *E. m. borealis*. a. ldb. = *E. a. ludibundus*. e = habitat-experienced. n = habitat-naive.

	N	Dark			Light						Dark			$\bar{X}/24$
		0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20	20-22	22-24	
m.o.-e.	20	0.1	0.9	4.0	10.9	7.2	6.8	6.3	3.7	1.3	0.7	0.2	0	41.8
-n	20	0	0.1	0.7	14.1	12.7	10.8	5.5	4.4	1.3	1.9	0	0	51.5[a]
a. ltv.-e.	17	0	0	2.8	27.6	9.7	10.8	8.3	6.7	4.1	0.4	0	0	70.4[b]
-n	16	0	0	1.3	32.9	39.8	27.2	11.1	7.6	6.9	7.6	0	0	134.8[a,b]
m.b.-e.	11	0	0	0	33.4	18.2	18.2	13.3	2.6	0.4	0	0	0	85.9
a. ldb.-e.	10	0	0	2.0	19.5	17.4	8.4	9.5	6.3	1.9	0	0	0	65.0

[a] Significant difference ($P<0.001$, Mann-Whitney U-test).
[b] Significant difference ($P<0.05$).

APPENDIX III

Number of agonistic encounters won by each individual in each match between the two southern subspecies of minimus (m) and amoenus (a).

A. Simultaneous Matches.

Sex of Pair	Rock m	Rock a	Trees m	Trees a	Total m	Total a
male	13	13	33	38	46	51
male	0	44	0	77	0	121
female	4	0	11	3	15	3
female	0	50	0	21	71	0
male	58	0	51	0	109	0
male	17	27	10	7	27	34
male	0	20	0	45	0	65
female	0	72	0	60	0	132
female	0	69	0	94	0	163
male	0	0	4	29	4	29
male	5	23	2	74	7	97
female	2	29	1	74	3	103
female	15	21	27	2	23	42
female	17	2	52	1	69	3
Totals	131	370	191	525	322	895

B. Resident minimus Matches.

Sex of Pair	Rock m	Rock a	Trees m	Trees a	Total m	Total a
male	13	0	97	1	110	1
male	65	0	15	0	80	0
female	46	0	37	1	83	1
male	10	44	2	76	12	120
male	1	19	1	74	2	93
female	[illegible]	38	14	42	19	80
male	[illegible]	19	4	35	11	54
female	[illegible]	0	56	0	77	0
male	[illegible]	10	108	15	151	25
male	30	0	41	0	71	0
female	0	26	0	34	0	60
male	3	48	25	90	28	138
Totals	244	204	400	368	644	572

APPENDIX IV

Number of agonistic encounters won by each individual in each simultaneous match between the two northern subspecies of _minimus_ (m) and _amoenus_ (a).

Sex of Pair	Rock m	Rock a	Trees m	Trees a	Total m	Total a
female	0	23	0	29	0	52
male	0	33	0	99	0	132
male	0	42	1	80	1	122
female	0	13	0	54	0	67
male	68	0	86	0	154	0
female	0	22	0	64	0	86
female	0	38	1	46	1	84
male	0	35	0	28	0	63
male	0	60	0	90	0	150
male	55	0	110	0	165	0
Totals	123	266	198	490	321	756