Page 11

THE BEHAVIOUR OF VANCOUVER ISLAND MARMOTS,
MARMOTA VANCOUVERENSIS

by

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required standard

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ABSTRACT

I studied the social behaviour of the Vancouver Island marmot, _Marmota vancouverensis_, during the summers of 1973 and 1974. Virtually nothing was known about the behaviour of this species at the outset of this study. Barash (1973b, 1974a) suggested that the social behaviour and social organization of marmot species was determined by the severity of the environment (the vegetative growing season) and its effect on the growth rate of marmots. He predicted that marmot species living in short growing season environments would be highly social but that social tolerance would decrease as the growing season increased. The objective of this study was to test this hypothesis by observing the social behaviour of Vancouver Island marmots and comparing this to the length of the vegetative growing season.

M. vancouverensis is endemic to Vancouver Island, British Columbia. The original colonizers of this species probably crossed to Vancouver Island via land connections that existed during the Illinoian glacial period, approximately 100,000 years ago, and survived subsequent glacial maxima on nunataks and coastal refugia or both. Vancouver Island marmots have been isolated from mainland forms for a length of time (10,000 to 100,000 years) sufficient to show specific evolutionary adaptations to their Vancouver Island environment.

Vancouver Island marmots live in small colonies in the subalpine parkland. Social groups consisted of one adult male, one adult female, and variable numbers of two-year-olds, yearlings, and infants. Social groups were highly integrated with a large amount of communication occurring among colony members. Alarm calls were given in response to potential predators and could be heard over the whole colony. Short whistles were given in response to aerial predators (e.g. eagles) and long whistles were given in response to terrestrial predators (e.g. black bears). Both calls are narrow bandwidth sounds, a characteristic that makes them difficult to locate. The most common social behaviour that occurred among colony members was a nose touching behaviour termed greeting. All age-sex classes of Vancouver Island marmots engaged in greetings as well as other social behaviour patterns in about the same proportions.

The vegetative growing season experienced by Vancouver Island marmots was approximately the same as that of _M. flaviventris_ but the social behaviour of Vancouver Island marmots most closely resembled _M. olympus_, a species living where the growing season is much shorter. On this basis I rejected Barash's hypothesis that the length of the vegetative growing season is sufficient to account for the variability that Barash observed among marmot species. I suggest that vegetative growing season not be used as an index of growth rate but that the time taken to reach adult size be measured directly. The degree of social tolerance is positively correlated with the length of time required to reach maturity.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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INTRODUCTION

SOCIOBIOLOGY AND BARASH'S HYPOTHESIS

Recently, there has been a marked increase in the number of investigators who are considering behaviour as a product of natural selection (Crook 1970, Barash 1974a & 1977, Alcock 1975, Brown 1975, Wilson 1975). Sociobiology (Wilson 1975) or socio-ecology (Crook 1970) is the systematic study of the evolution of social behaviour and social organization in relation to ecology, demography, and population genetics. This new approach to the study of animal behaviour has led to the formation of testable hypotheses concerning the adaptive significance (contribution to fitness), of social behaviour and social organization. This study was an attempt to test one such hypothesis.

Barash (1973b, 1974a) put forth a hypothesis to account for the evolution of marmot societies (*Marmota* spp). He showed that differences in social behaviour among marmot species were correlated with variations in the environment, specifically, the length of the vegetative growing season. Barash's measure of growing season was the number of frost-free days in the absence of snow cover (Barash 1973b). Woodchucks (*Marmota monax*) inhabit environments of low elevation with long (150 day) growing seasons. They are solitary and relatively aggressive animals (Bronson 1964) and the young disperse from their natal burrows when weaned (Vos and Gillespie 1960). Olympic marmots (*M. olympus*) inhabit high elevation alpine meadows that have a very short (40 to 70 day) growing season. They live in well integrated colonies and are socially tolerant, that is, their social behaviour is characterized by a high frequency of greetings (Barash 1973b, 1974a). Olympic marmots do not mature until their fourth summer and disperse during their third. Barash's hypothesis is that social tolerance, as measured by the rate with which greetings are performed, is inversely related to the length of the vegetative growing season. He reasoned that 1) shorter growing seasons result in lower growth rates in terms of the time required to reach adult size; 2) it is disadvantageous for subadult marmots to disperse when they are still "undersize", where size is measured as the weight of dispersing marmots relative to the weight of an adult of the same species; 3) in all marmot species, the minimum size for dispersers should be either the same proportion of the adult weight or dispersing marmots should be relatively more mature in species inhabiting increasingly severe environments; 4) aggression from adults causes the young to disperse; thus 5) the increase in social tolerance among marmots experiencing progressively shorter growing seasons may be due to the increasing necessity to inhibit the dispersal of undersized animals.

He also suggested that 1) it is important to have population size more closely regulated as environmental severity increases because under severe conditions the habitat would be easily overgrazed, and there would be strong competition for food; and 2) if marmot social behaviour regulates population size in a density dependent way; then 3) social tolerance should increase in severe environments because the operation of such a system of population regulation would require a closer physical proximity of colony members.

Barash's hypothesis is testable in that it predicts the degree of social tolerance for any marmot species when the length of the vegetative growing season under which that species evolved is known. Barash set out to test his own hypothesis by observing the social behaviour of the yellow-bellied marmot (M. flaviventris, Barash 1973a), the hoary marmot (M. caligata, Barash 1974b), and the European alpine marmot (M. marmota, Barash 1976b). His observations of hoary and yellow-bellied marmots were consistent with his hypothesis, but alpine marmots engaged in significantly fewer greetings than were expected on the basis of the short growing season of its alpine habitat. Barash did not reject his hypothesis on the basis of this one inconsistent result. He suggested that a blanket term such as sociality (social tolerance), may be inappropriate in that it obscures the differences between discrete parameters such as greeting and chasing, which may vary independently (Barash 1976b). Unfortunately, he does not go on to develop a revised hypothesis based on these discrete parameters. Armitage, Downhower, and Svendsen (1976) and Anderson, Armitage, and Hoffmann (1976) attempted to reject Barash's hypothesis because yellow-bellied marmots living at high elevations grew faster in terms of grams per day than did yellow-bellied marmots living at lower elevations. However, this does not constitute a test of

Barash's hypothesis since his hypothesis is based on the growth rate in terms of the time taken to reach adult size. The time taken to reach adult size is not related solely to the absolute weight gained per day, but it is also a function of the length of time each year during which marmots gain weight and the absolute weight of adult marmots of the species being considered.

At the outset of this investigation there still remained two marmot species in North America which had never been studied, _M. vancouverensis_ and _M. broweri_. The objective of this study was to document the life history and behaviour of Vancouver Island marmots and to provide another test of Barash's hypothesis of marmot sociality.

VANCOUVER ISLAND MARMOTS

The Vancouver Island marmot, _Marmota vancouverensis_ Swarth 1911, is endemic to Vancouver Island, British Columbia. Living in small colonies on steeply sloping subalpine meadows, Vancouver Island marmots are active for only a few months each summer. To avoid the rigors of the mountain winters, marmots hibernate for about eight months of the year. Even then it may be necessary for them to burrow out through many metres of snow in the spring. When I began this study, this was virtually all that was known about Vancouver Island marmots. This information was based on three very brief reports (Swarth 1912: 89-90, Carl 1944, Hardy 1955: B61) which indicated that the natural history of Vancouver Island marmots was similar to other species of alpine marmots (e.g. Barash 1973b) and amenable to study using similar methods.

Taxonomy and Evolutionary History

Swarth described the Vancouver Island marmot as a new species in 1911. The cranial and external characteristics of *M. vancouverensis* are quite different from any other marmot species (Swarth 1911, Howell 1915). The most obvious characteristics are: 1) the posterior border of the nasals which is deeply V-shaped and, 2) the pelage which is uniformly dark brown to black. However, the karyotype of *M. vancouverensis* is very similar to that of *M. caligata* (Rausch and Rausch 1971).

In 1915 Howell designated three groups of North American marmots based on morphological similarities. He included *M. vancouverensis* in the *M. caligata* group along with *M. caligata* and *M. olympus*. In 1965, Rausch and Rausch considered *M. broweri* to be a separate species within the *M. caligata* group. This group appears to be a natural association for biological reasons as well as the purely morphological ones used by Howell. Species in the *M. caligata* group fill similar ecological niches and have similar behaviour (see discusion). Their ectoparasites also reflect the close evolutionary relationships within this group. Fleas (Siphonaptera) collected from *M. vancouverensis* during this study were identified by Mr. G. P. Holland of Agriculture

Canada as *Thrassis* (*Thrassis*) *spenceri spenceri* Wagner. This subspecies of flea is found only on marmots in the *M. caligata* group (Stark 1970). I collected one tick (Acarina: Ixodidea) from *M. vancouverensis*. I am unaware of ticks having been collected from any other species in the *M. caligata* group. Since ticks, like fleas, tend to be host specific (Gregson 1956), it was not surprising to discover that the specimen from *M. vancouverensis* may represent a new species in the genus *Ixodes* (P. Zuk, Canadian Department of Agriculture, personal communication). Since only one subadult specimen is available the species probably cannot be described.

M. vancouverensis probably began to diverge from the ancestral *M. caligata* stock after crossing to Vancouver Island on temporary land connections and becoming isolated there. The fact that the following mammal species: musk ox *Symbos cavifrons*, mastodon *Mammut americanum*, mammoths *Mammut imperator* and *Mammut columbi*, horse *Equus* sp., and *Bison* sp. once lived on Vancouver Island suggests that land connections with the mainland existed during the late Pleistocene (Harington 1975). Harington (1975) believes that connections between Vancouver Island and the mainland existed on two occasions during the last (Fraser/Wisconsin) glaciation and at least once during the penultimate (Illinoian) glaciation. The most recent connection with the mainland probably existed just prior to the time of maximum development of continental ice during the Fraser glaciation about 20,000 years ago. At this time the sea level was depressed about 120 m below the present sea level and a narrow corridor would have joined Port Angeles and Victoria (Fig 1). During the Peak of the Illinoian glaciation (roughly 100,000 years ago, Wright and Frey 1965) sea levels were estimated to be 160 m below present levels and an even wider corridor would have joined Vancouver Island to the mainland. Marmots could also have crossed on the massive flood plain deposits that filled the whole Strait of Georgia region (Fig 1) during the Olympia Interglaciation about 30,000 years ago (date from Flint 1971).

Although little is known about the rate of animal speciation, Mayr (1963) has estimated that even a rapidly evolving island form would require a minimum of 100,000 years to achieve full specific status. If Mayr is correct, it is most likely that marmots colonized Vancouver Island during or before the Illinoian glaciation rather than at either opportunity during the Fraser glaciation.

The Vashon Stade of the Fraser glaciation covered most of Vancouver Island (Mathews, Fyles, and Nasmith 1970). Therefore, if marmots crossed to Vancouver Island before this period, there must have been either nunataks (high peaks and ridges emerging above the glaciers) or coastal refugia available on which the marmots could survive. Geological evidence indicates that both nunataks (Heusser 1960, Mathews <u>et al</u> 1970, Muller unpublished) and coastal refugia (W. H. Mathews personal communication) existed. There are existing nunataks in Alaska and the Yukon which are vegetated (Cooper 1942, Heusser 1954) and support arctic ground squirrel (*Spermophilus undulatus*) populations (Murray and Murray 1969). Foster (1965) concluded that some species of mammals survived the last glaciation on refugia on the Queen Charlotte Islands. Thus it is not difficult to imagine Vancouver Island marmots surviving the Vashon glaciacion on similar refugia. Other zoological evidence also supports the refugia concept. No species of mammal other than *M. vancouverensis* presently exists exclusively in the alpine-subalpine environment on Vancouver Island and no other mammal species on the island has diverged to the point of being recognized as a distinct species. In addition, white-tailed ptarmigan (*Lagopus leucurus*) are also found in alpine environments and a well differentiated race (*L. leucurus saxatalis*) of this relatively implastic species is confined to Vancouver Island (McCabe and Cowan 1945). Other arguments for and against the nunatak survival hypothesis are discussed by Ives (1974).

M. vancouverensis probably crossed to Vancouver Island via land connections that existed during the Illinoian glacial period and the species survived the glacial maxima of the Fraser glaciation on nunataks or coastal refugia or both. As the glaciers retreated free dispersal was probably made possible by the existence of alpine habitat at the edge of the retreating ice. As the forests closed in below them Vancouver Island marmots would have gradually become isolated on the mountain peaks that they now occupy. A similar example of post glacial colonization of mountain tops has been postulated for the mountain hare (*Lepus timidus*) in Europe (Hoffmann 1974).

METHODS

STUDY AREAS

I made most of my observations at two colonies situated about one kilometre apart on the southern end of Green Mountain, on Vancouver Island, British Columbia (numbers 1 and 2, Fig 1). The colony on the Haley Lake study area (colony number 1, Fig 1 and 2) has presumably been in continuous existence since its first discovery in 1932 by K. Racey and I. McT. Cowan, since its characteristics have not changed (I. McT. Cowan personal communication). I also made brief observations on the other Green Mountain colonies (numbers 3, 4, and 5, Fig 1) and on Mt Washington, Mt Heather, and Buttler Peak (Fig 1, Table I).

METHODS OF OBSERVATION

I recorded observations on the behaviour of Vancouver Island marmots from 13 June until 16 September 1973 and from 30 April until 21 September 1974. The animals were observed from selected vantage points, without the use of a blind, at distances of between 50 and 300 m. Observations were made through binoculars of 7x35 or 10x40 magnification, or spotting scopes of 15-60 or 20-45 power. Only observations occurring at least 15 minutes after my arrival were included in my results -- a time I judged to be sufficient for the marmots to habituate to my presence. Observations were recorded in notebooks, on preconstructed tally charts or with a tape recorder.

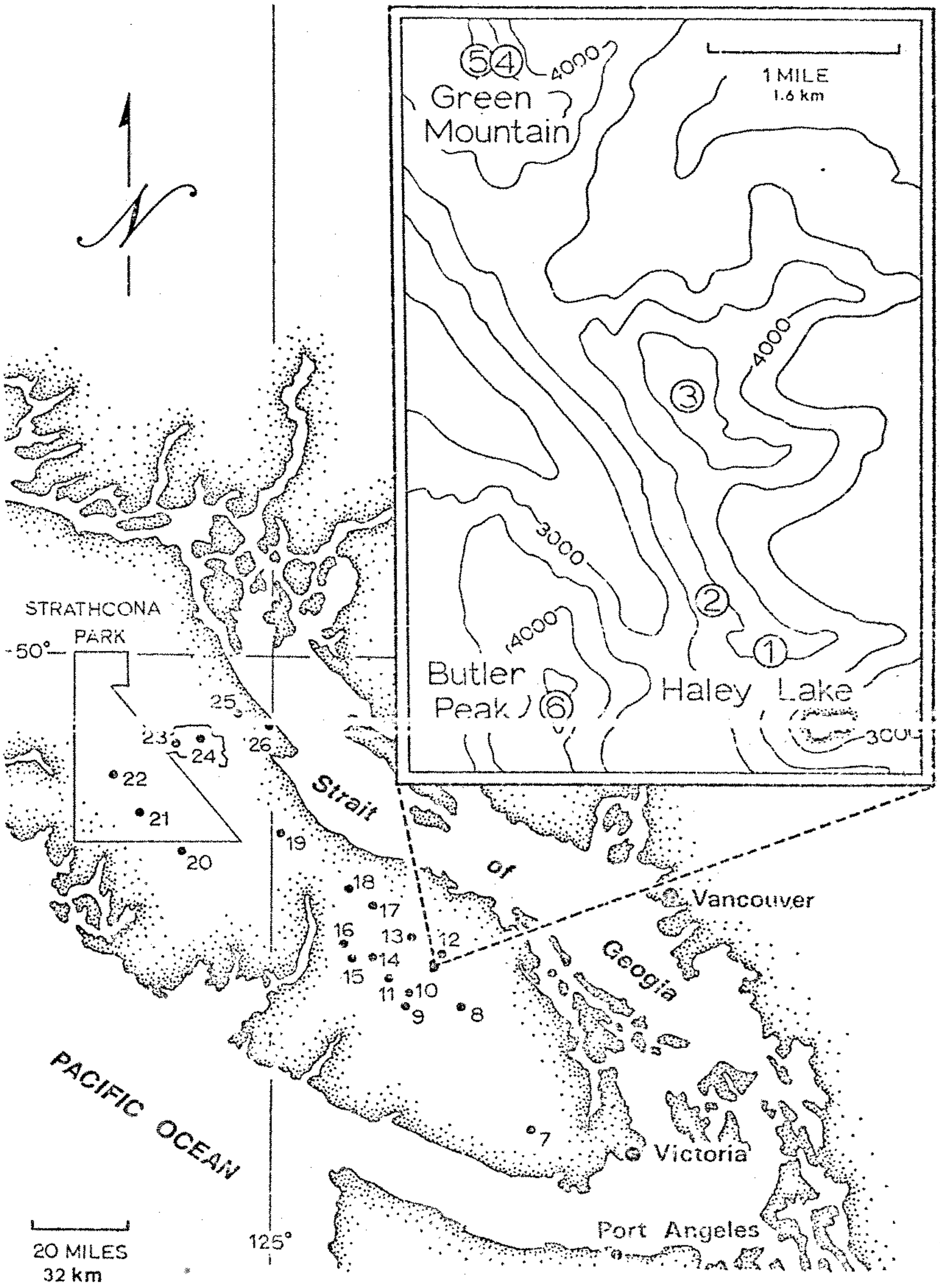
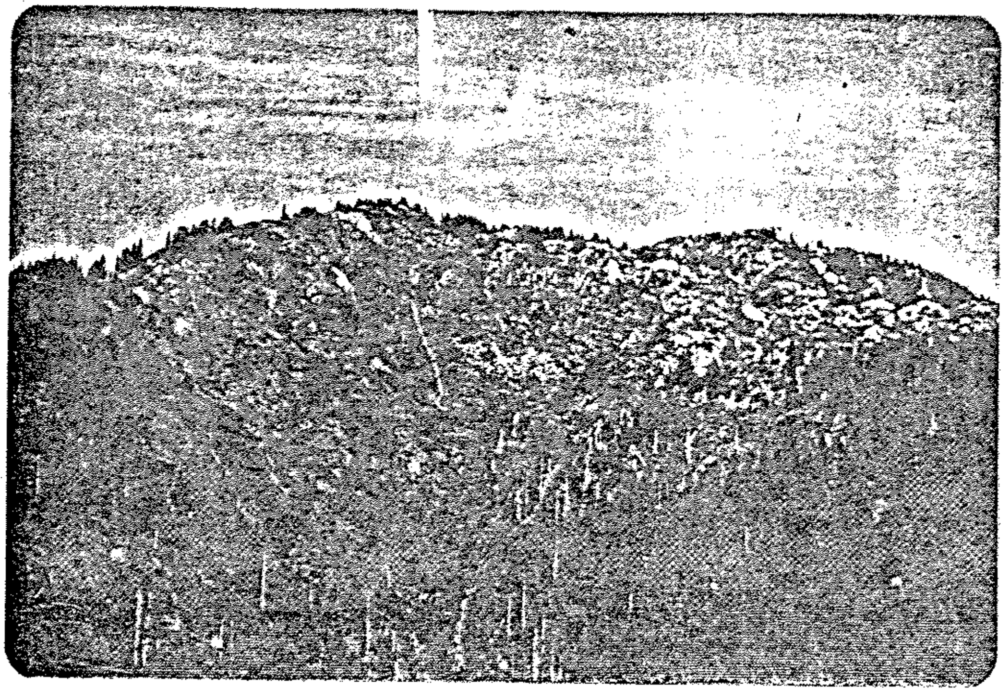

N
1 MILE
1.6 km
Green Mountain
4000
⑤
④
③
4000
3000
②
①
4000
Butler Peak
⑥
Haley Lake
3000
STRATHCONA
PARK
50°
25
23
24
26
22
21
20
19
Strait
of
Geogia
18
17
16
13
12
14
15
11
10
9
8
Vancouver
PACIFIC OCEAN
7
Victoria
Port Angeles
20 MILES
32 km
125°

Figure 2. Photographs of the Haley Lake study area

A. Photograph cf the whole Hale Lake colony
B. Close-up photograph of the part of the Haley Iake colony used most extensively by marmots (see also Fig 22, 23, and 24)



A

B

Table I. Habitat characteristics of Vancouver Island marmot colonies

Colony Name and Number	North Latitude	West Longitude	Slope (Degrees)	Aspect	Elevation (Meters)
1 Haley Lake	49° 01'	124° 19'	33-63(1)	SSE	1100-1400
2 Green Mt	49° 01'	124° 19'	35(1)	WSW	1150-1350
3 Green Mt	49° 02'	124° 20'	33-45(2)	SE	1500-1600
4 Ski Club	49° 03'	124° 20'	40(1)	E	1550-1600
5 Ski Club	49° 03'	124° 20'	35-56(1)	SSW	1550-1600
6 Buttler Peak	49° 00'	124° 20'	35-70(2)	S	1500-1550
7 Heather Mt	49° 53'	124° 30'	33(2)	S	1300-1400
8 Mt Washington	49° 40'	125° 14'	20(2)	WSW	1500-1600

(1) degree of slope measured with a clinometer
(2) degree of slope estimated

To obtain quantitative data on marmot behaviour I used a focal-animal sampling method (Altmann 1974). Focal-animal sampling consisted of selecting one individual and continuously recording its behaviour. Often more than one individual could be observed at one time, but it was never possible to observe all animals at all times (Ad libitum sampling, Altmann 1974). I was rarely faced with decisions on when to terminate observations on a focal individual because focal animals usually disappeared from view within a short time. Some observation periods were devoted to scan sampling: the recording of the behaviour and location of each animal every 10 minutes.

ANALYSIS OF SOCIAL BEHAVIOUR DATA

I considered a social "interaction" to be an uninterrupted series of social behaviour patterns or "acts" between two individuals. Interactions were considered to be distinct if they were separated by an interval of more than one minute. I counted a social behaviour pattern only once unless it was separated by some other act other than tail raising, since tail raising always occurred at the same time as some other act. Interactions among three animals (triadic interactions) were treated as a set of dyads (interactions between two animals).

I arbitrarily decided that a focal animal sampling period had to be greater than 15 minutes in duration before I would include it in estimating the rates of interaction. I felt that by only considering sampling periods that were longer than 15 minutes I would eliminate biasses inherent in short sampling periods.

I calculated the rate, R, that any group of animals, i, (i.e. adult males), performed any social behaviour, B, from the following formula:

$$Ri(B) = \frac{Si(B)}{SHi} \qquad (1)$$

where

Si(B) is the number of all of the B acts involving or performed by group i during sampling periods (S), when individuals in group i were the focal individuals, and

SHi is the total time in hours (animal-hours) of sampling periods where individuals in group i were the focal individuals.

The rate, Ri(B), is therefore an estimate of the number of B acts that animals in group i were involved in during each hour that they were active above ground and in plain view (i.e. not per hour that I sat observing the colony). The units of Ri(B) are interactions per animal-hour. The rates of behaviour for individual marmots were obtained by considering the group as being composed of only one animal.

The rate that group i performed act B with any specific group j, is:

$$IR(B)i:j = \frac{Si(B)i:j + Sj(B)i:j}{(2)\ (SHi + SHj)} \qquad (2)$$

where

Si(B)i:j is the sum of all B acts that occurred between i and j during sampling periods when the participant from group i was the focal individual, and

there is a 2 in the denominator to correct for the fact that by watching each group independently I effectively counted each interaction twice.

The units of IR(B)i:j are interactions per animal-hour, where animal-hours represents the number of hours that animals in groups i and j were active above ground and in plain view.

Some dyads never interacted during sampling periods, indicating Ri(B)i:j = 0, even though they may have interacted during observation periods which were of a shorter duration, thus indicating that Ri(B)i:j is greater than zero. A non-zero estimate of Ri(B)i:j can be calculated if Si(B)i:j is calculated rather than counted directly. The total number of B acts occurring between groups i and j over all observations regardless of their duration is T(B)i:j, and the total number of B acts occurring between group i and any other animal of known age and sex is T(B)i. If my observations of behavioural interactions were unbiassed then Si(B)i:j should be the same proportion of Si(B) as T(B)i:j is of T(B)i.

Thus,

$$\frac{Si(B)i:j}{Si(B)} = \frac{T(B)i:j}{T(B)i}$$

and

$$Si(B)i:j = \frac{Si(B) \times T(B)i:j}{T(B)i} \qquad (3)$$

Substituting equation (4) into equation (3) yields:

$$IR(B)i:j = \frac{\dfrac{Si(B) \times T(B)i:j}{T(B)i} + \dfrac{Sj(B) \times T(B)i:j}{T(B)j}}{(2)\ (SHi + SHj)} \qquad (4a)$$

Equation 4a is the formula I used to calculate interaction rates.

It was necessary to be more explicit in the calculation of interaction rates for some social behaviour patterns, since social behaviour patterns could be either reciprocal or non-reciprocal. I considered social behaviour patterns to be reciprocal if the act appeared to be a mutual exchange of signals between the interactants (e.g. greeting, see also section on Social Behaviour Patterns). Non-reciprocal behaviours were those in which the interactants acted very differently from each other (i.e. chasing). Only one interaction rate estimate per dyad was calculated for each reciprocal act since the rate that animal i greeted with animal j was the same as the rate that j greeted with i, i.e:

$Ri(G)i:j = Ri(G)j:i$

and

$IR(G)i:j = IR(G)j:i.$

However, in the case of non-reciprocal acts, the rate that animal i chased animal j is not necessarily equal to the rate at which j chased i, i.e:

$$Ri(C)i:j \neq Ri(C)j:i.$$

Thus for each non-reciprocal behaviour, two estimates of interaction rate were calculated for each dyad, IR(B)i:j and IR(B)j:i.

where

$$IR(B)i:j = \frac{\dfrac{Si(B) \times T(B)i:j}{T(B)i} + \dfrac{Sj(B) \times T(B)i:j}{T(B)j}}{(2)\ (SHi + SHj)}$$

and

$$IR(B)j:i = \frac{\dfrac{Si(B) \times T(B)j:i}{T(B)i} + \dfrac{Sj(B) \times T(B)j:i}{T(B)j}}{(2)\ (SHi + SHj)} \qquad (4b)$$

The interaction rates for a specific dyad can be added to get the total interaction rate or to get the rate for any group of behaviour patterns (i.e. all agonistic acts). There is no simple relationship between Ri(B) and IR(B)i:j, when IR(B)i:j is summed for all j's, because IR(B)i:j is a function of SHj whereas Ri(B) is not.

The formula that I have developed for calculating interaction rates yield the same results as those equations used by Armitage (1976a) for some dyads. However, Armitage calculates mean rates incorrectly by adding rates in "any combination desired" (Armitage 1976a).

Unless otherwise indicated, a significance level of 0.05 was used for all statistical tests.

TRAPPING AND MARKING

In 1974 marmots were captured in 25x30x80 cm or 22x22x63 cm live traps manufactured by Tomahawk Live Traps Co., Tomahawk, Wisconsin, U. S. A. Baits used were peanut butter, peanuts and the leaves and flowers of preferred species of food plants when these were available (Appendix I).

Marmots were transferred from the traps to a handling cone similar to the one illustrated by Taber and Cowan (1971). No tranquilization was necessary. Animals were measured using a flexible steel millimetre tape while being held as nearly as possible in an extended position. I recorded the sex, and weighed the marmot with a 12 Kg spring balance (Pesola Scales, Basle, Switzerland) that could be read to the nearest 100 g. The occurrence of ectoparasites and a description of the molt was also recorded. Each animal was marked by attaching a single numbered rabbit ear tag (style #4-1538) supplied by the National Band and Tag Co., Newport, Kentucky, U. S. A. With each tag one or two coloured plastic markers of Dymo embossing tape (Dymo of Canada Ltd., Missisauga, Ontario), approximately 1x2 cm, were applied. Ear tags were placed as far from the margin of the ear as possible before the thickness of the ear became limiting. Tags were occasionally lost by other animals biting the coloured markers and ripping the whole tag from the ear. Tags were most frequently lost in the traps or during handling. Most animals were tagged at least twice during this study.

In an attempt to permanently mark animals I tried the freeze branding techniques described by Farrell, Koger, and Winward (1966), Hadow (1972) and Churchill and Coburn (unpublished). The desired result of freeze branding is a regrowth of white hair in the shape of the brand which can be recognized at a distance. This result requires that the melanocytes be destroyed but not the hair follicle. In previous laboratory studies, the regrowth of white hair occurred in 3 to 6 weeks and was retained through subsequent molts (Farrell et al 1966, Taylor 1969, Hadow 1972, Churchill and Coburn unpublished, Lazarus and Rowe 1975). I used two brass branding "irons:" one a 1x5 cm rectangle, and the other a circle, 3 cm in outside diameter and 1.6 cm in inside diameter. Each brand therefore had a surface area of 5 cm^2. Each animal was marked with a unique combination of two brands by varying the brand orrientation and position on the body. Brands were applied to a shaved area on the body for exactly 30 seconds.

MEASUREMENT OF MICROCLIMATE

In 1973 daily maximum and minimum temperatures were recorded. In 1974 all of the following measurements were obtained. Daily rainfall was recorded with a Tru-Check Rain Gauge (Tru-Check Inc., Albert Lee Minnesota). A continuous record of temperature and humidity was obtained from 12 June until 3 November using a 31 day Casella thermohygrograph. The thermohygrograph was enclosed in a Stevenson Screen which was situated on a small eminence in the centre of colony number one. Additional weather information was obtained from instruments operated by the Secretariat for the Environment Land Use Committee of the Province of British Columbia. These instruments were located approximately 300 m below colonies 5 and 6.

VOCALIZATIONS

I recorded vocalizations of both trapped and free ranging marmots with a Uher 4000IC Report tape recorder. The microphone used was either an ElectroVoice 644 Sound Spot directional microphone or a Sony Dynamic M136 microphone. The recording speed was always 19.05 cm per s. Sonograms were made from these recordings on a Kay Co. Missilyzer model 675. Recordings of both trapped and free ranging marmots were used in the calculations of whistle length and frequency. All other data were from free ranging marmots only.

RESULTS

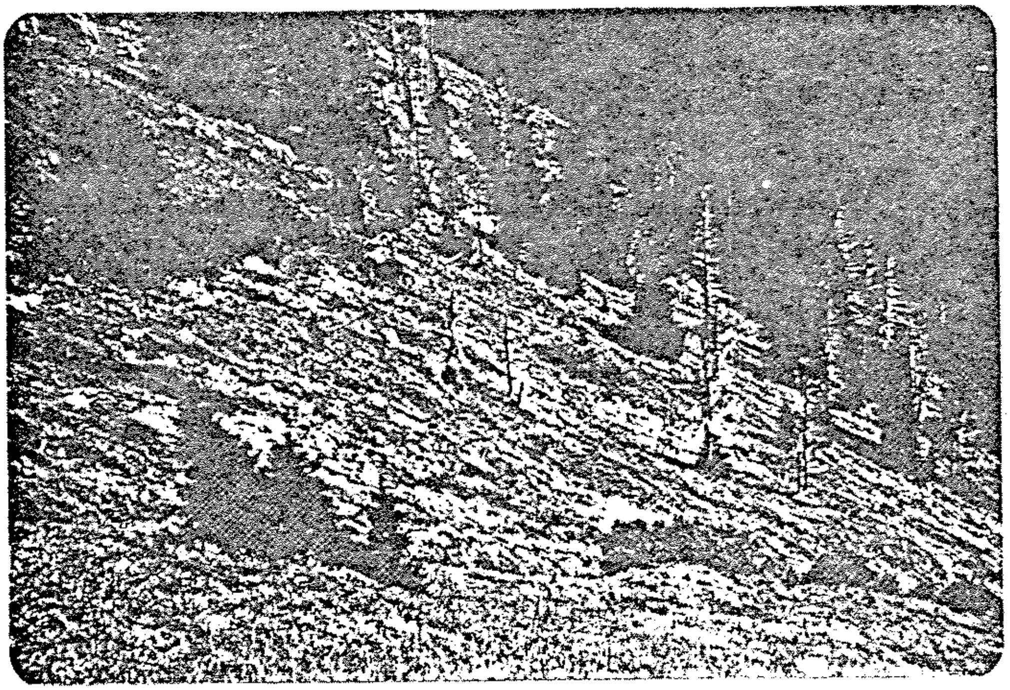
HABITAT CHARACTERISTICS

Vancouver Island marmots live in subalpine habitats that are characterized by steep cliffs, talus debris, and open meadows that are usually oriented south of the east-west line (Table I, Fig 2 and 3). Below the talus, the slope becomes less steep, the substrate becomes more stable, and herbaceous plant communities develop. Where the slope is steep enough, avalanches and snow creep inhibit the establishment of trees. Evidence of these forces can be seen in the form of uprooted saplings and the distinct basal crook in all established trees (Fig 3A).

All of the marmot colonies that I visited had plant communites that were characteristic of the Parkland Subzone of the Subalpine Mountain Hemlock Zone of British Columbia (Brooke, Peterson, and Krajina 1970). Within the Parkland Subzone Brooke _et al_ (1970) describe eight plant associations. Plants found on the Haley Lake study area such as mountain hemlock _Tsuga mertensiana_, yellow cedar _Chamaecyparis nootkatensis_, blue-leaf huckleberry _Vaccinium deliciosum_, partridgefoot _Leutkea pectinata_, and mountain daisy _Erigeron peregrinus_ (see also Appendix I) were characteristic of the Nano-tsucetum mertensianae association, subassociation nano-tsugetum mertensianae. Other plant associations were also present on the Haley Lake study area and on other colonies. Three colonies, Mt

Figure 3. Photographs of Vancouver Island marmot habitat

A. The Haley Lake colony illustrating a typical open meadow habitat
B. The Mt Washington colony illustrating the dense cover of white rhododendron and alpine fir



A

B

Washington, Heather Mt, and Central Green Mt (colony 3) differed from the others in that they were not below cliffs. Open meadows were characteristic of all marmot colonies except Mt Washington. Marmot burrows on Mt Washington were located in an area with numerous small, 1-5 m, trees, mainly alpine fir Abies lasiocarpa. The area was also covered by a dense growth of white rhododendron Rhododendron albiflorum, and Vaccinium sp. (Fig 3B).

The climate of the Subalpine Mountain Hemlock Zone is characterized by cool short summers and wet winters with considerable precipitation falling as snow (Table II). The length of the growing season is difficult to determine in subalpine areas since minimum air temperatures are often well above freezing while snow still persists on the site due to the great accumulations during the winter (Brooke et al 1970 and Table II). On the Haley Lake study area in 1974, the number of frost-free days was above average at 135 days (Table II), but the effective growing season was about two weeks less on much of the colony (Table II) as a result of a persistent snowpack. However, the snow pack was not evenly distributed. The cliffs above the colony were too steep to accumulate much snow and therefore became snow free much ealier than the rest of the colony. The cliffs on the other colonies were also the first areas to become snow free. A small part of colony 2 was free of snow very early in 1974, apparently having been kept relatively snow free by the prevailing wind. Marmots foraged on these early snow free areas until the snow melted from the main part

Table II. Climatic characteristics of the Haley Lake study area and a typical Parkland Subzone location in the Coast Mountains, after Brooke *et al* 1970

Climatic Characteristics	Haley Lake Study Area	Year	Brooke *et al* 1970
annual precipitation	-	-	285
in cm and percent snow	-	-	35%
rainfall from June through September (cm)	25	1974	50
mean temperature July through September (°C)	13.0	1973	12.0
	15.5	1974	
date of the last frost in the spring	13-20 June	1973	end of May
	3 June	1974	
number of frost-free days	115	1973	114
	135	1974	
maximum accumulation of snow (cm)	approximately 300	1974	370
last accumulation of snow in the spring	early June	1973	late June
	late June	1974	

of the colony. On the Haley Lake study area in 1974 marmots had to forage on the cliffs for 6 weeks after emergence in the spring.

Steep slopes are characteristic of Vancouver Island marmot habitat because they are susceptible to avalanches. Avalanches provide suitable habitat 1) by maintaining herbaceous communities through the inhibition of tree growth, and 2) by reducing the accumulation of snow, relative to flatter areas, which in turn results in the meadow becoming snow free earlier in the spring, thus increasing the effective growing season.

The average area of 8 marmot colonies was about two hectares (range 0.5 to 4.0).

PHYSICAL CHARACTERISTICS

I recognized the following age classes of Vancouver Island marmots: infants, yearlings, two-year-olds, and adults. Identification of age classes was based on weights (Fig 4). I did not trap any infants during this study, but infants were easily distinguished because of their small size (Fig 4). My sample size was too small to compare the differences between the weights of male and female yearlings, but yearlings as a group weighed less than two-year-olds ($F=123.13$; d.f.=1,16; $p<0.001$).

Some females had weights that were significantly greater than female yearlings ($F=65.6$; d.f.=1,13; $p<0.001$) but

Figure 4. Seasonal changes in the weights of Vancouver Island marmots

The growth rate equations are as follows:

Adults, sexes combined $y = 0.0245x + 2.466$

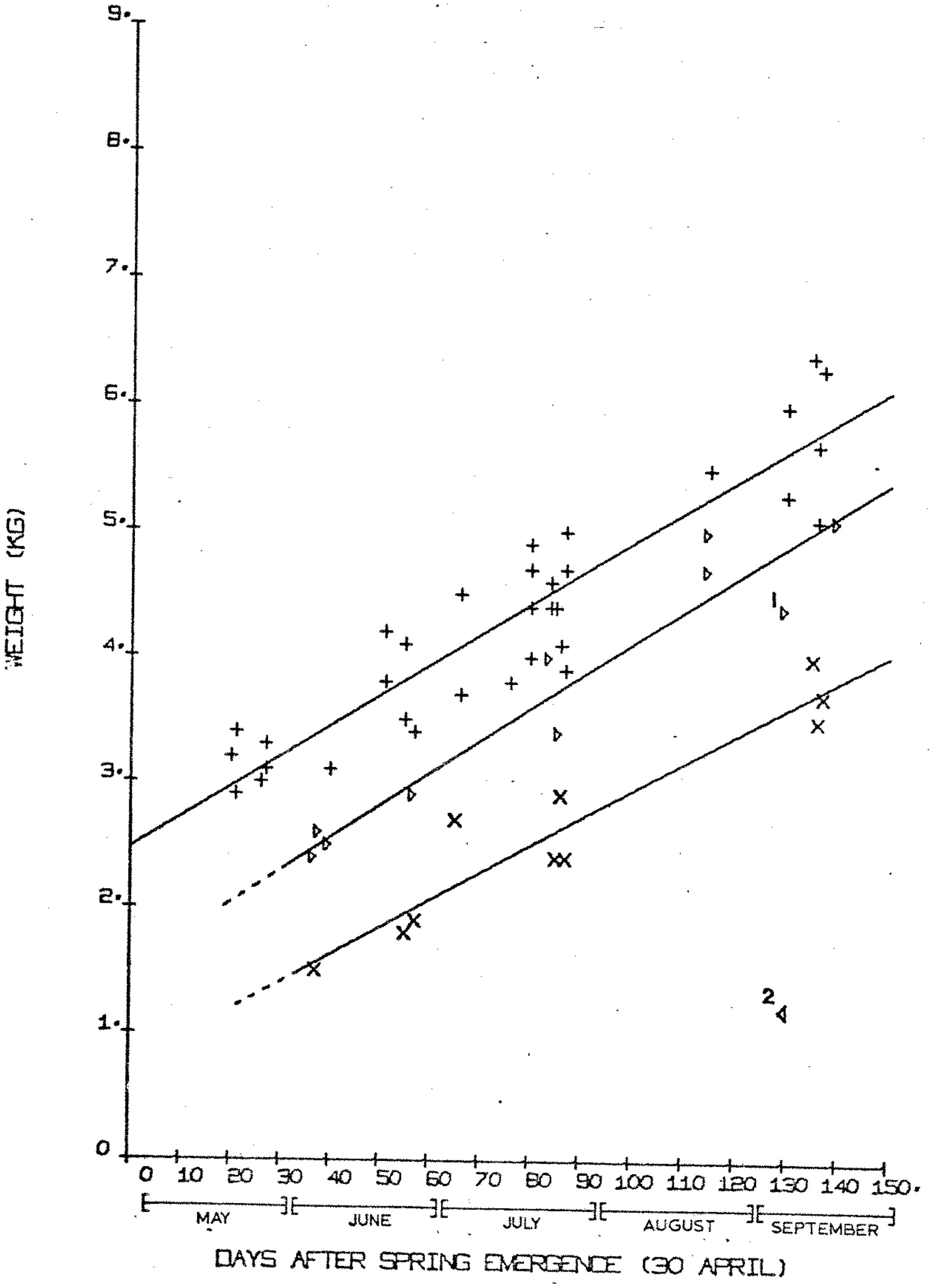
Two-year-old females $y = 0.0259x + 1.516$

Yearlings, sexes combined $y = 0.0230x + 0.584$

where y is the weight in kilograms
and x is the number of days since spring emergence (30 April).

[1] known aged two-year-old

[2] infant female; data from a specimen collected from Mt Washington in 1965, University of Alaska specimen #28754


WEIGHT (KG)
9
8
7
6
5
4
3
2
1
0
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
MAY
JUNE
JULY
AUGUST
SEPTEMBER
DAYS AFTER SPRING EMERGENCE (30 APRIL)
1
2

significantly less than the largest females (F=18.7; d.f.=1,22; P<0.001). I assumed that these animals were two-year-olds. In 1975, I captured one female known to be two years old. She weighed slightly less than the average two-year-weight predicted from the growth rate equation (Fig 4). This observation is consistent with the assumption that two-year-olds weigh less than adults. Two-year-olds can be recognized by weight in M. caligata (Barash 1974b) and M. olympus (Barash 1973b).

All males that were non-yearlings had similar weights. The absence of any males recognizable as two-year-olds could be the result of the absence of any two-year-old males on my study areas or the growth of males being such that they reach their adult (heaviest) weight as two-year-olds. In M. olympus, two-year-old males are still distinguishable from adult males on the basis of weight (Barash 1973b). I assumed that the same would be true for Vancouver Island marmots and that I had no two-year-old males on my study areas. The term adult, then, refers to animals that are considered to be at least three years old. Adult males weighed significantly more than adult females (Fig 5; F=6.87 d.f.=1,28 p=0.014).

Growth rate appears to be linear for all sex and age classes throughout the summer (Fig 4 and 5). Analysis of covariance indicated that the rate of weight gain did not differ significantly among sex and age classes.

Barash (1973b) used the change in M. olympus tooth colour

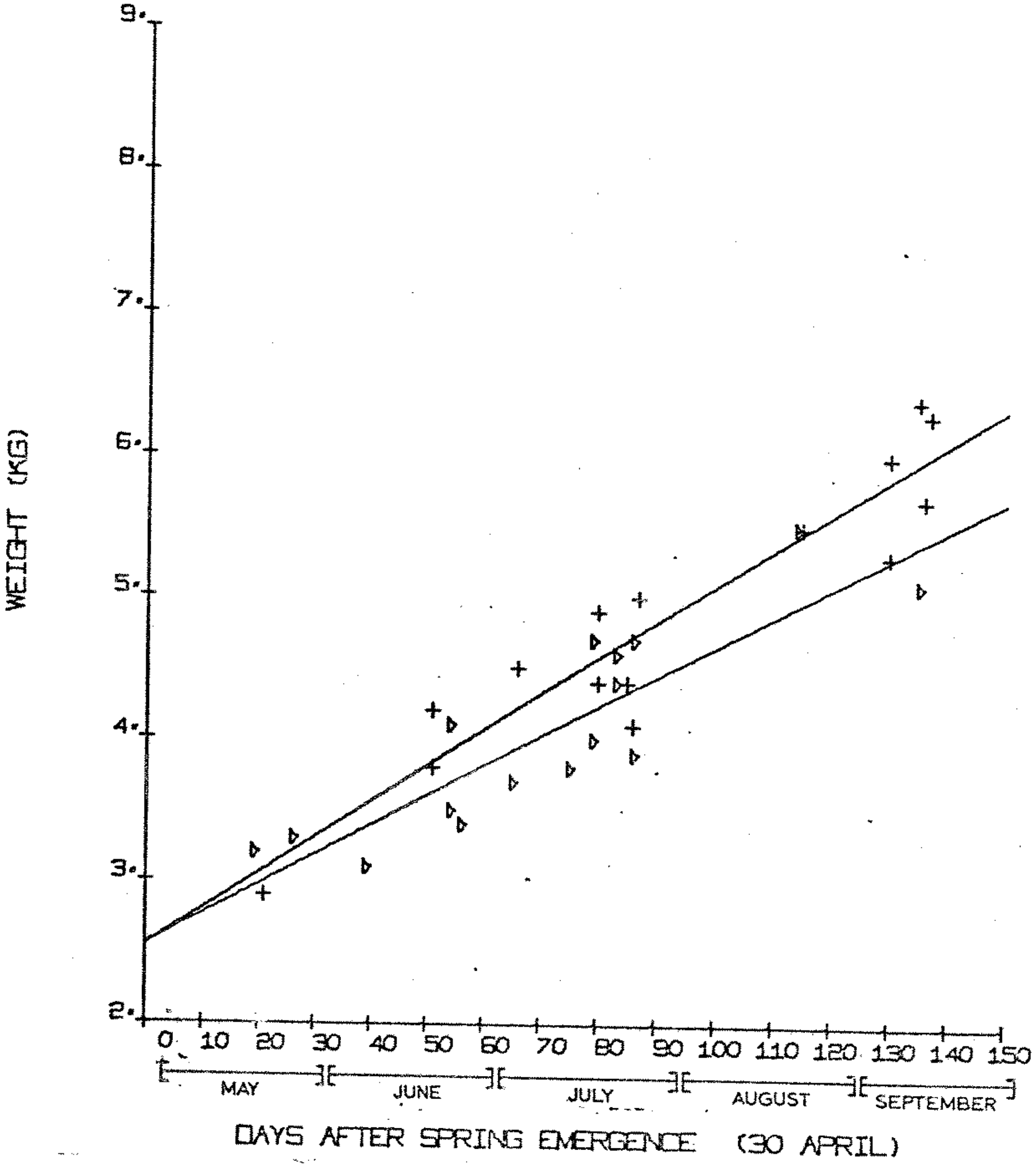
Figure 5. Seasonal changes in the weights of adult marmots

The growth rate equations are as follows:

Adult males $y = 0.0210x + 2.561$

Adult females $y = 0.0263x + 2.489$

where y is the weight in kilograms
and x is the number of days since spring emergence
(30 April).



WEIGHT (KG)
9.
8.
7.
6.
5.
4.
3.
2.
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
MAY
JUNE
JULY
AUGUST
SEPTEMBER
DAYS AFTER SPRING EMERGENCE (30 APRIL)

(from dull white to dark orange) as an aid in separating age classes. This was not possible in Vancouver Island marmots since the tooth colour of all Vancouver Island marmots was dull white.

The fresh pelage of M. vancouverensis is black or very dark brown. This colour is uniform over most of the body except for a conspicuous patch of white fur around the nose and mouth, a small white mark on the forehead, and some white streaking on the breast and abdomen. The colour of the fresh pelage gradually fades over the summer and following spring to a light cinnamon brown. Vancouver Island marmots molt only once per year.

The progression of the molt was easily observed in the field because the fresh pelage contrasted so sharply with the old faded fur. Animals first showed signs of molting in mid-July. The new fur emerged first on the rump, or on the forelegs and shoulders. The emergence of fresh pelage over the rest of the body was extremely variable. The last areas to molt were usually the back of the head, the tail, and the rump. Some animals did not appear to complete their molt by the time they hibernated in late September; nonetheless, molting finished at this time. Incompletely molted animals emerged from hibernatiom the next spring at the same stage of molt as they were at the previous fall, and no subsequent change occurred until the next July. If an individual had not completed its molt from the previous year, the molt began first in the areas having the oldest pelage. Young animals emerged from the burrows with black fur. They did not appear to molt during their first summer but molting would be difficult to detect because of the absence of any colour change. I could not detect any other differences in molting characteristics among different age and sex classes.

Davis (1966) noted that *M. monax* also had a variability in the progression of the molt, although it always began on the rump. He also observed that some animals did not complete their molt each year. One molt per year appears to be the rule among marmots, *M. monax* (Hamilton 1934, Davis 1966), *M. vancouverensis* (this study), *M. flaviventris* (Armitage 1974), and *M. olympus* (Walker 1964), although this was disputed by Barash (1973b) for *M. olympus*.

All freeze brands were applied on either the 23, 24, or 25 July 1974. This was the earliest date possible because a labour strike prevented the production of dry ice until this time. At the time of application, fresh pelage had already begun to grow over much of the body. Four weeks after branding no regrowth of fur had occurred. The branded areas were bare, the club hairs and a layer of skin having been sloughed off. Seven weeks after branding, the brands had still not grown in completely. The fur which was in the process of growing in was either black, the normal colour of fresh pelage, white, as expected, or rarely, black with white tips. No brands were visible at a distance as white fur in 1974. In June 1975 the brands had still not regrown on the one individual for which detailed observations were possible. No animals displayed white brand markings which were visible from a distance at this time. In August 1975, the brands on one individual had regrown with normal coloured pigmentation. However, three marmots had brands that were identifiable at a distance of about 100 m when viewed through a 15-60 power spotting scope. On close observation I found that these brands were only sparsely covered with white fur.

Since on Vancouver Island marmots the white fur did not become visible until the next molt after branding, over one year later, freeze branding was useless as a marking technique for this study. However, in the future the efficacy of freeze branding might be increased in two ways. One, branding could be done earlier in the summer to minimize the time between branding and the beginning of the molt. This could result in brands becoming visible in three to six weeks as in the laboratory studies (Hadow 1972, Churchill and Coburn unpublished, Lazarus and Rowe 1975). A second improvement that could be made is the length of time during which the brand was applied. The application time is very important to achieve good results (Farrell _et al_ 1966, Hadow 1972, Churchill and Coburn unpublished). Free ranging marmots may require a different branding time than was predicted from experiments with Abert's squirrels (_Sciurus aberti_) and fox squirrels (_Sciurus niger_) (Hadow 1973) and Columbian ground squirrels (_Spermophilus columbianus_, Churchill and Coburn unpublished). It is not clear from my results whether the branding time that I used was too short or too long (if either). Since the brands took a long time to regrow and normal pigmentation sometimes developed, the application time appeared to be too long (Hadow 1972). However, the resulting intermediate pigmentation in some animals indicated that the application time was too short (Churchill and Coburn unpublished).

Lazarus and Rowe (1975) used a commercially available pressurized refrigerant as a freeze branding agent. Their results are extremely encouraging and their technique appears to be much more efficient than using dry ice, especially under field conditions. A pressurized refrigerant available in Canada similar to the one used by Lazarus and Rowe (1975) is Can.O.Gas Refrigerant 12, Virginia Chemicals Inc., Portsmouth, Va. U.S.A.

COLONY COMPOSITION

I considered a colony to be a group of animals that was isolated both geographically and socially from other such localities. I knew the exact population size for two colonies, colonies one and two on Green Mountain (Fig 1). These results are presented in Table III. Since I did not trap animals in 1973, I was only able to recognize infants and older animals and was unable to determine their sex. However, I knew the status of most animals in 1974. The average colony size in June, before the infants emerged above ground, was 8.3 animals (n=4, Table III). All the other colonies that I observed appeared to be of a similar size. The average size of five litters was 3.0

±.32 (SE) infants (n=5).

Movement of marmots between colonies was very rare. There were only four occasions, that I knew of, when marmots moved between colonies on Green Mountain. I saw tracks of marmots in the snow between colonies one and two on 20 May 1974 and most of the way from colony one to colony three on 11 June 1974. One adult male was observed on colony one until 2 June 1974. On 12 June he was seen on colony two where he remained for the duration of the summer. An adult male immigrated to colony one from an unknown location on, or shortly before, 25 June 1974. He remained there for the duration of the summer. Colony one therefore was occupied by three different adult males in June 1974; however, there were only two present at any one time (Table III). I was unable to determine the sex of three marmots when I first captured them. They were rarely seen subsequently and were never recaptured; therefore, their sex was never determined.

ACTIVITY PATTERNS

The general pattern of Vancouver Island marmot activity is quite similar to that reported for other marmot species (Armitage 1962, Gray 1967, Barash 1973b, Hayes 1976). Vancouver Island marmots have an annual schedule made up of a summer activity period of 4 to 5 months and a winter hibernation period of 7 to 8 months. In 1974 marmots were active on 30 April, the first day that I visited the Haley Lake study area. Tracks in

Table III. Age and sex composition of marmot colonies one and two

			Number of Marmots of Each Age and Sex									
Colony	Year	Month	AM	AF	A?	2F	2?	YM	YF	Y?	I?	TOTAL
1	1973	June			11							11
		July			11						6	17
		Aug			8						4	12
		Sept			8						4	12
	1974	May	2	2	1	1	1	1	2	1		11
		June	2	2	1	1	1	1	2	1		11
		July	2	2	1	1		1	2	1		10
		Aug	2	2	1	1			2			8
		Sept	2	2		1			1			6
2	1973	June			6							6
		July			4						2	6
		Aug			4						2	6
	1974	May		1	1	1		1				4
		June	1	1	1	1		1				5
		July	1	1		1		1				4
		Aug	1	1		1		1				4

A = Adult　? = Sex unknown　I = Infant　F = Female
M = Male　2 = Two-year-old　Y = Yearling

the snow indicated that marmots had probably not been active for very long and all individuals had not necessarily ended their hibernation at this time. There was no sign that any animals had yet emerged when I visited the Haley Lake study area on 17 April 1975. I last saw marmots on 16 September 1973 and 21 September 1974. I observed various colonies for many hours, on several days after these dates. Naturalists recorded seeing marmots on the Haley Lake study area on 30 September and 1 October 1972 (Bob Morris and Ted Barsby personal communication). Thus I considered early May to be a reasonable estimate of spring emergence with most individuals in hibernation again by mid-September.

I did not notice differences among age-sex classes with respect to the time of spring emergence or fall hibernation but I have few observations from these periods. It would be quite unusual if Vancouver Island marmots did not have age specific emergence and hibernation times since this is characteristic of all other marmot and ground squirrel species that I know of (e.g. Vos and Gillespie 1960, Armitage 1962, Iverson and Turner 1972, Yeaton 1972, Barash 1973b). Both litters of infants that were born on the Haley Lake study area in 1973 emerged from their burrows for the first time on 11 July. Swarth (1912) noted that in the Mt Douglas area no litters had emerged by the third week in July 1911.

I compiled activity budgets for each individual in terms of the percent of the total observation time that a marmot spent resting (lying or sitting outside of the burrow), feeding, in the burrow, moving (without feeding), engaging in social behaviour, and grass collecting. Activity budgets for the months of May through September are presented in Figures 6 to 10. Only the data for resting, feeding, and in burrow time are presented since these three behaviours accounted for more than 93% of the time budgets of all animals in each month. The data were combined for all individuals since there were no significant differences among age-sex classes with respect to these three activity patterns.

The daily pattern of activity varied with the time of year. A midday activity lull was not apparent in May and September. In June, July, and August marmots were much more active in the mornings and evenings than at midday. The obvious decline in midday activity in July and August seemed to be the result of three factors; temperature, an inherent circadian rhythm, and a general decline in the amount of time spent feeding as the summer progressed.

I divided the day into three periods, morning, midday, and evening, based on the duration of a marmot day. These periods varied slightly between months but the midday period was usually between 1100 and 1600 hours. The maximum daily temperature occurred during the midday period except on a few unusually cool days. The percent of time spent feeding at midday dropped off dramatically when the maximum daily temperature exceeded 20°C.

Maximum Daily Temperature (°C)	Percent of Time Spent Feeding During the Midday Period
0 - 14.9	23
15 - 19.9	22
20 - 24.9	6
25 - 29.9	0

Also, the time spent in the burrow at midday was directly correlated with the maximum daily temperature ($r=0.69$, $p<0.01$). Temperatures over 20°C were much more common in July and August than in the other months.

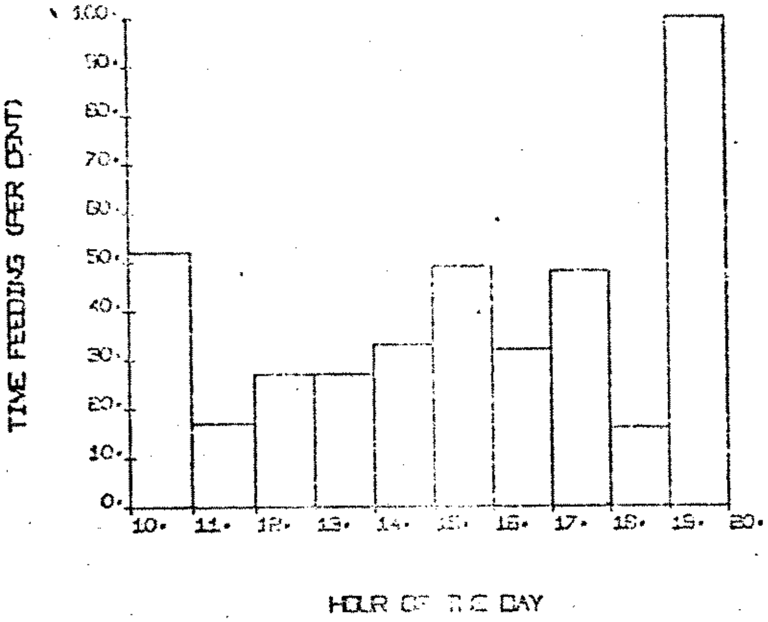
When the maximum temperature was less than 20°C marmots still fed sigificantly less during midday than they did during the morning and evening periods (data from morning and evening periods were lumped and tested against the midday period; $t=2.90$, $df=63$, $p<0.01$). Thus there was a bimodal pattern of daily feeding activity which was accentuated by high temperatures.

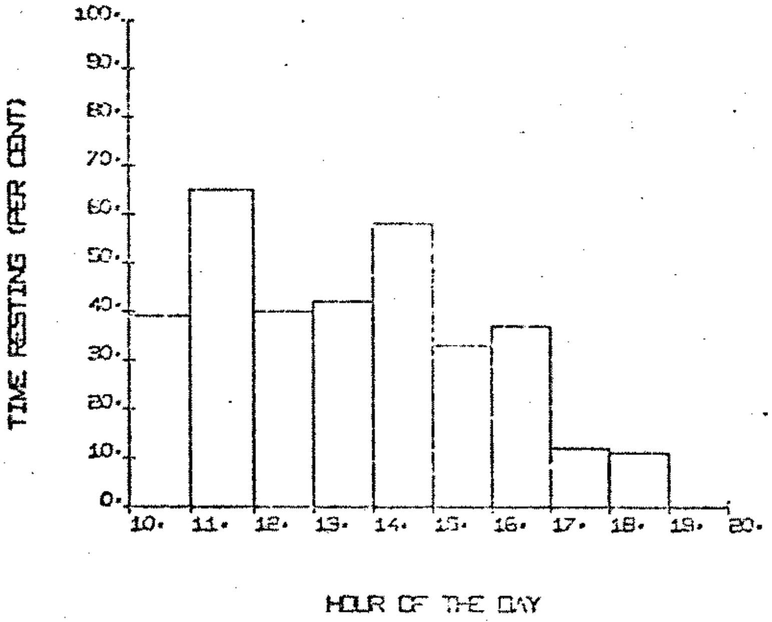
The total time spent feeding per day decreased throughout the summer. This trend was probably the result of an increase in both food quality and quantity over the summer. As the summer progressed vegetation quantity increased as the snow melted and vegetation quality increased as more species came into flower. Flowers are more nutritious than vegetative parts (Svoboda 1972) and are selected by marmots when available (Appendix I). As the time required to obtain sufficient food decreased, there would be less pressure to feed at midday, further accentuating the activity lulls in July and August. The

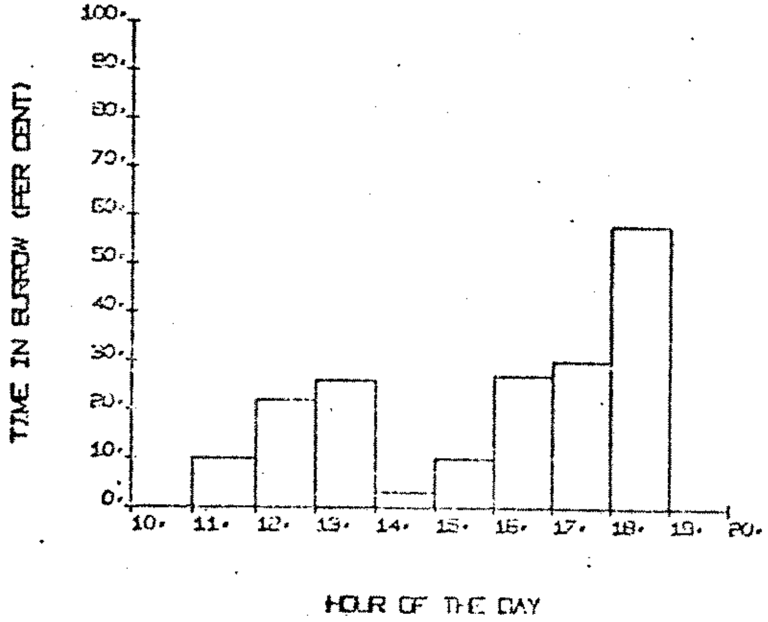
Figure 6. Activity budgets for May, all animals combined

65 animal-hours of observation

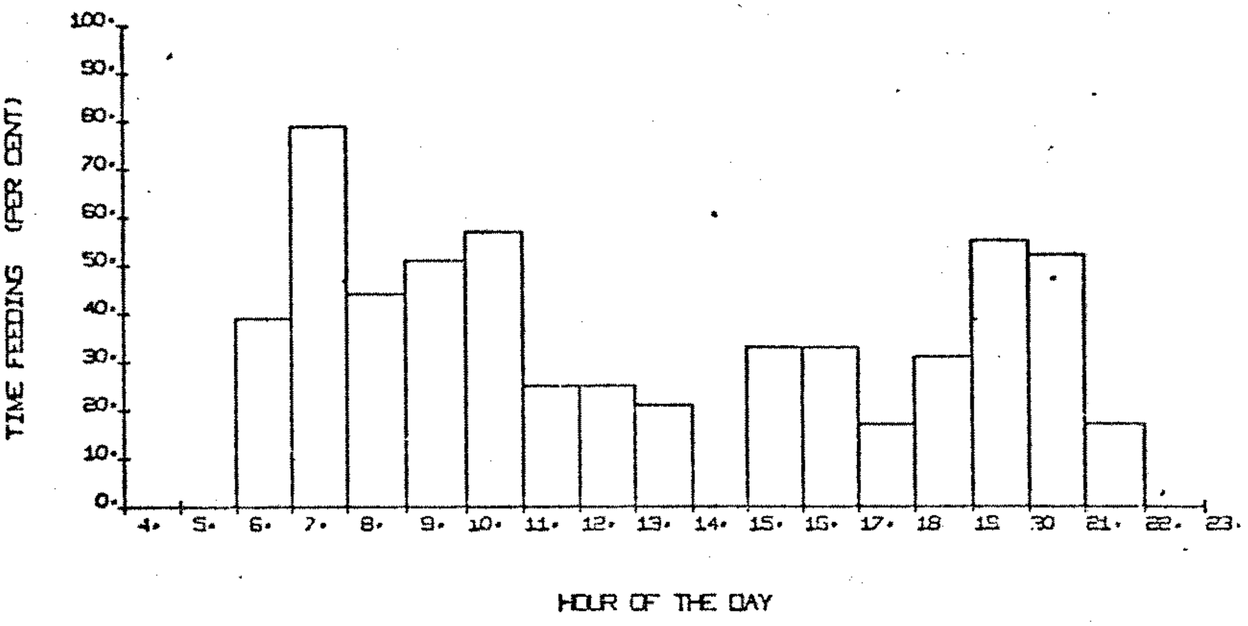
MAY ACTIVITY (ALL ANIMALS)

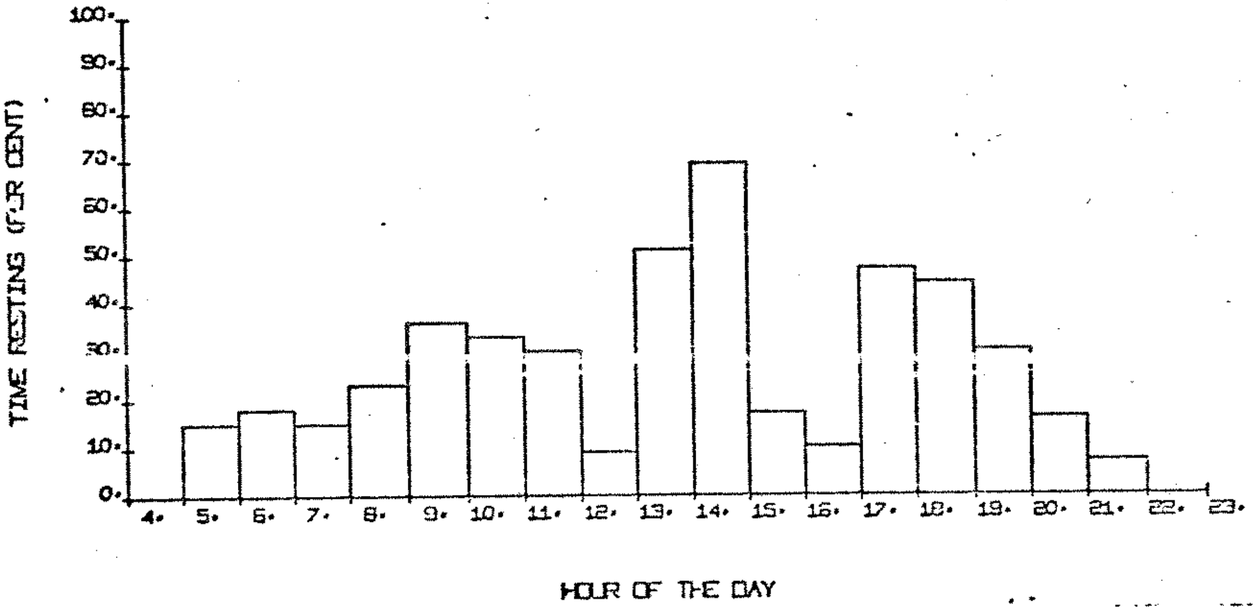


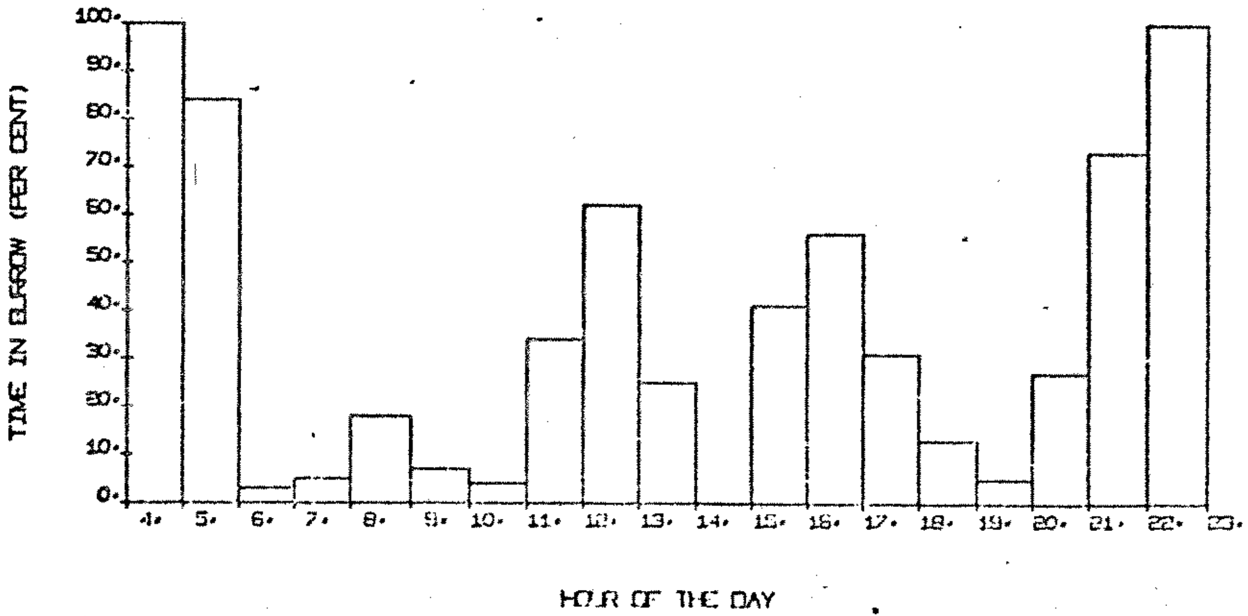




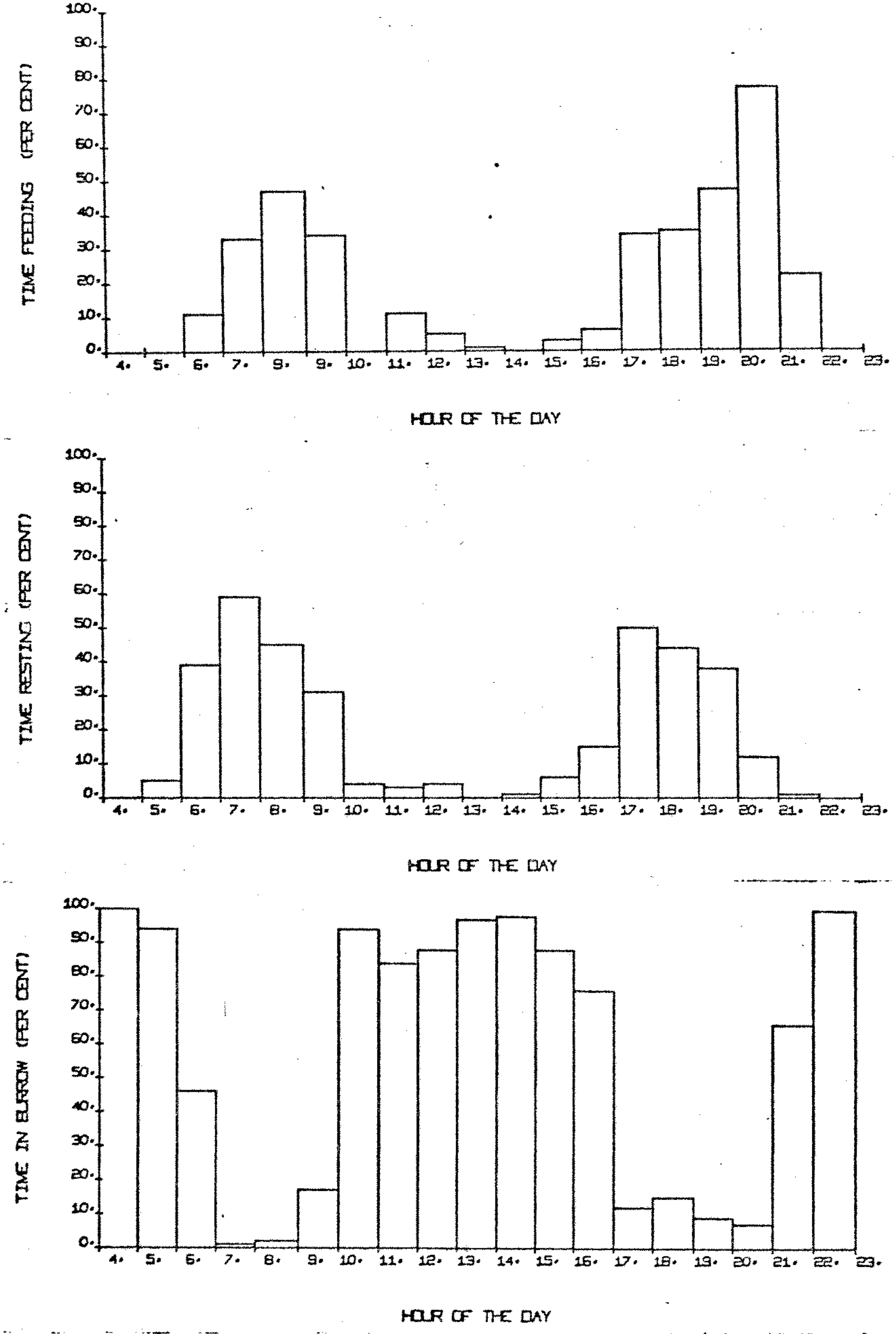
JUNE ACTIVITY (ALL ANIMALS)



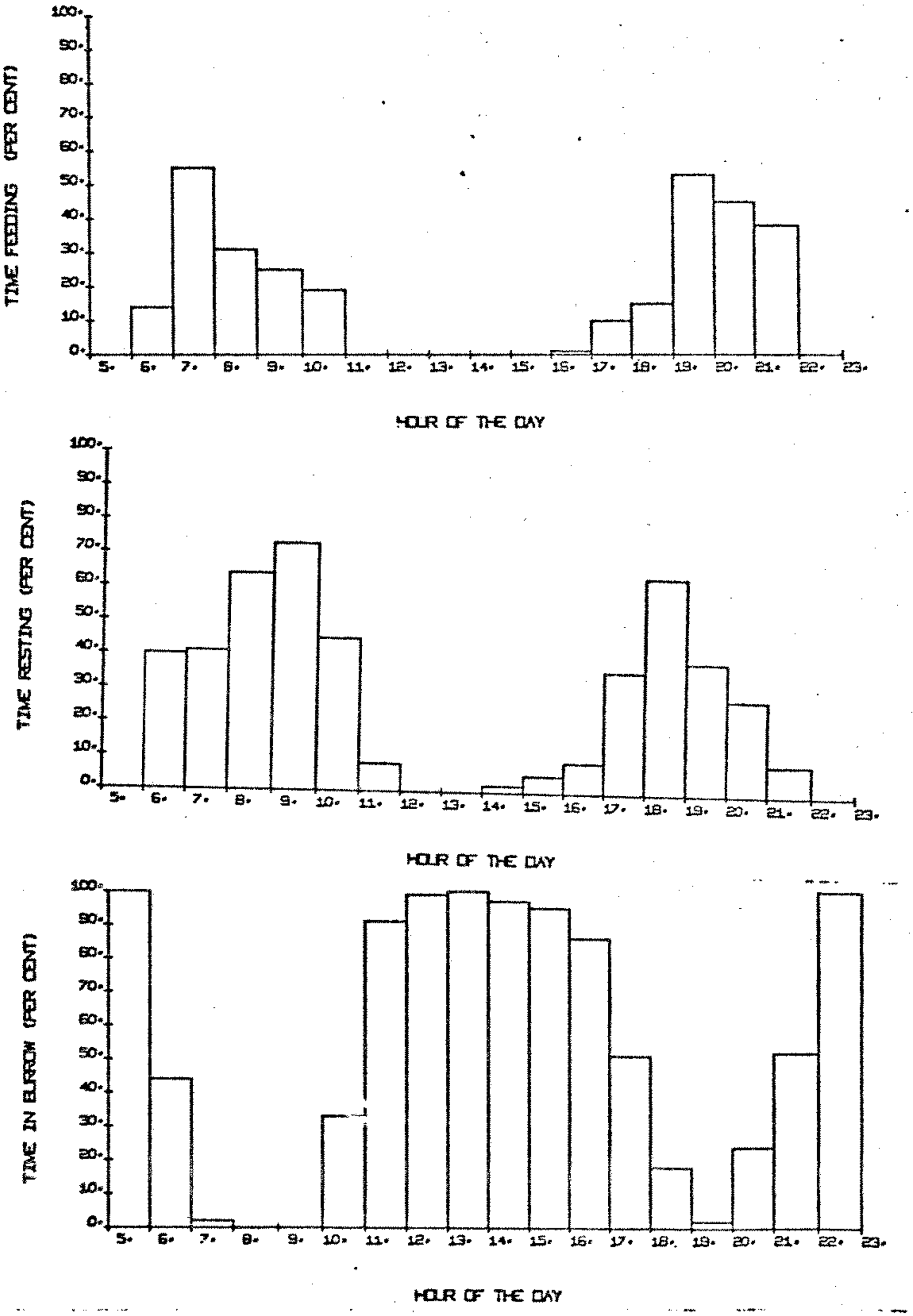




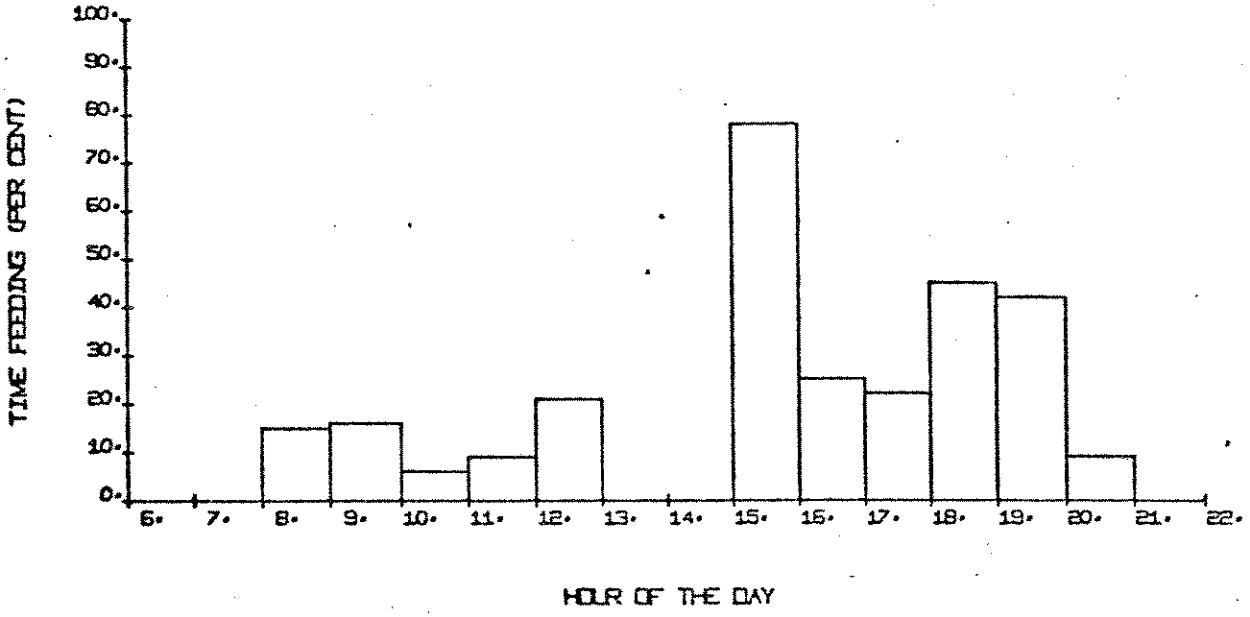
JULY ACTIVITY (ALL ANIMALS)

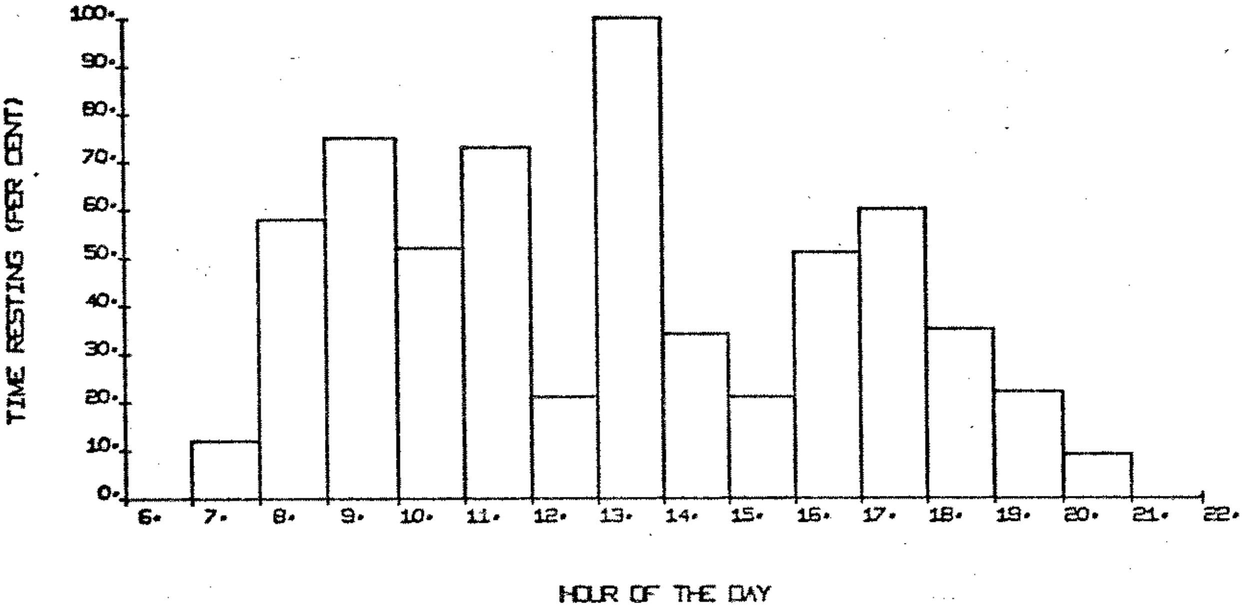


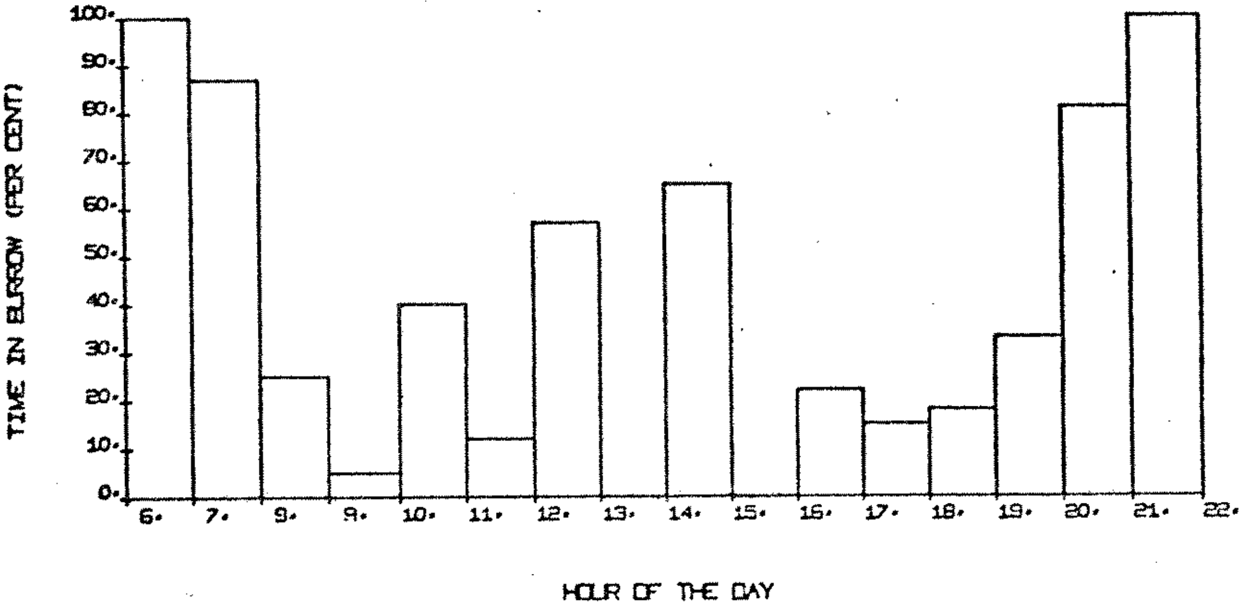
AUGUST ACTIVITY (ALL ANIMALS)



[illegible]


TIME FEEDING (PER CENT)
100.
90.
80.
70.
60.
50.
40.
30.
20.
10.
0.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
17.
18.
19.
20.
21.
22.
HOUR OF THE DAY


TIME RESTING (PER CENT)
100.
90.
80.
70.
60.
50.
40.
30.
20.
10.
0.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
17.
18.
19.
20.
21.
22.
HOUR OF THE DAY


TIME IN BURROW (PER CENT)
100.
90.
80.
70.
60.
50.
40.
30.
20.
10.
0.
6.
7.
8.
9.
10.
11.
12.
13.
14.
15.
16.
17.
18.
19.
20.
21.
22.
HOUR OF THE DAY

absence of a midday activity lull in September may be an effect of short day length or metabolic changes of upcoming hibernation on the basic circadian rhythm.

I saw marmots collecting the brown dead stems of grasses and sedges and taking them into their burrows on 152 occasions. I assumed that this material was used for bedding since I never saw marmots eating it above ground. The frequency of grass collecting decreased through the summer but there was a slight increase in September just prior to hibernation. Adult females collected more often than the other age-sex classes. I observed marmots collecting grass at all times of day, but it occurred most often at the very end of the day, just before they entered the burrow for the night.

VOCALIZATIONS

Whistles

The sound most frequently produced by Vancouver Island marmots is a loud piercing "whistle" which originates in the vocal chords. The dominant frequency of a whistle is the first harmonic or fundamental frequency. The first harmonic occurs at 2910 ±33 Hz (n=36). Whistles also possess a second harmonic at about 5700 Hz and a third harmonic at about 8400 Hz. Both of these harmonics contain much less energy than does the fundamental frequency (Fig 11 and 12). The intensity of the sound did not vary appreciably throughout the duration of the

Figure 11. Representative sonogram of a short whistle

Recording speed: 19.05 cm per s
Playback speed: 4.76 cm per s
Narrow bandwidth filter

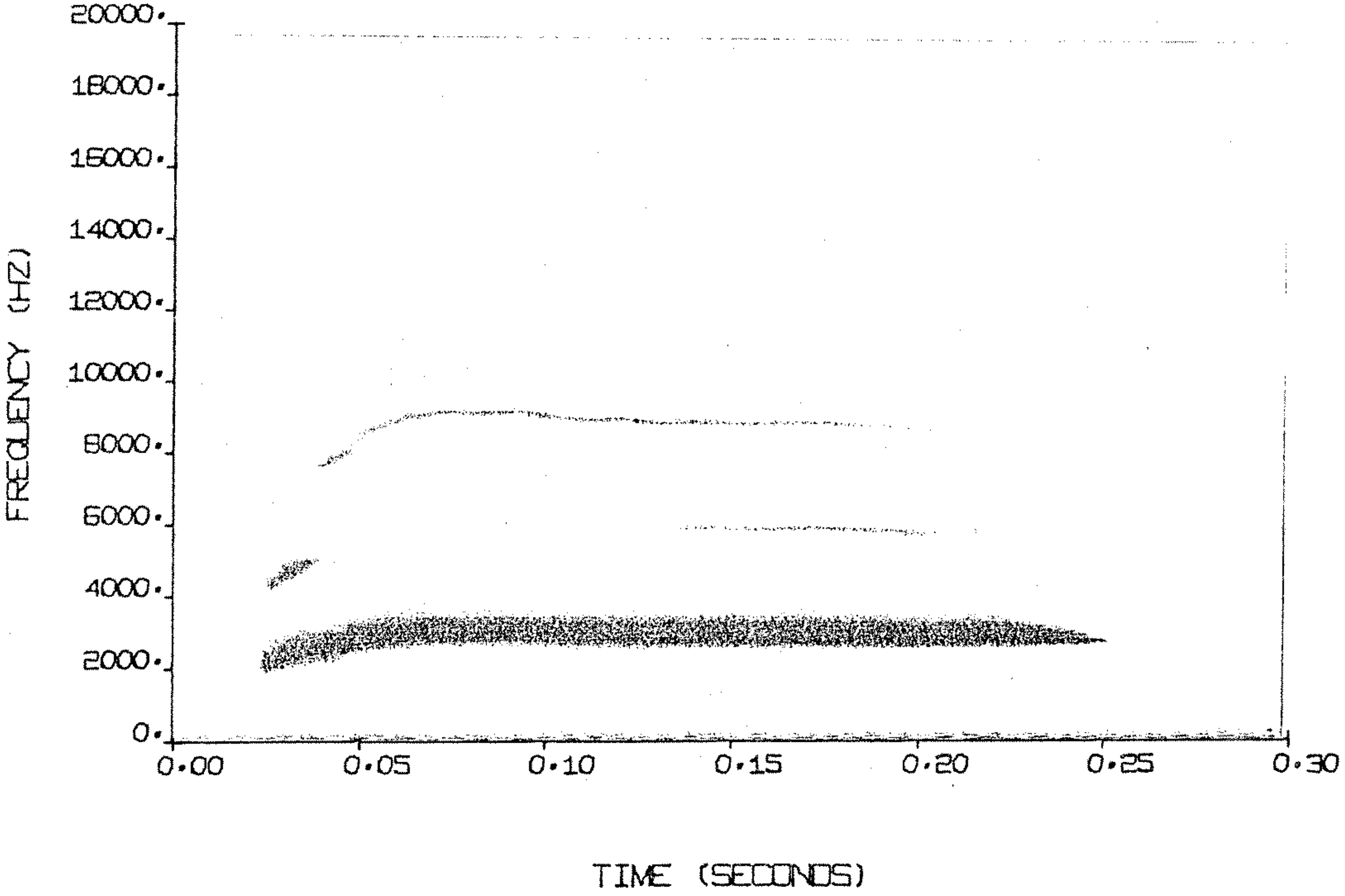
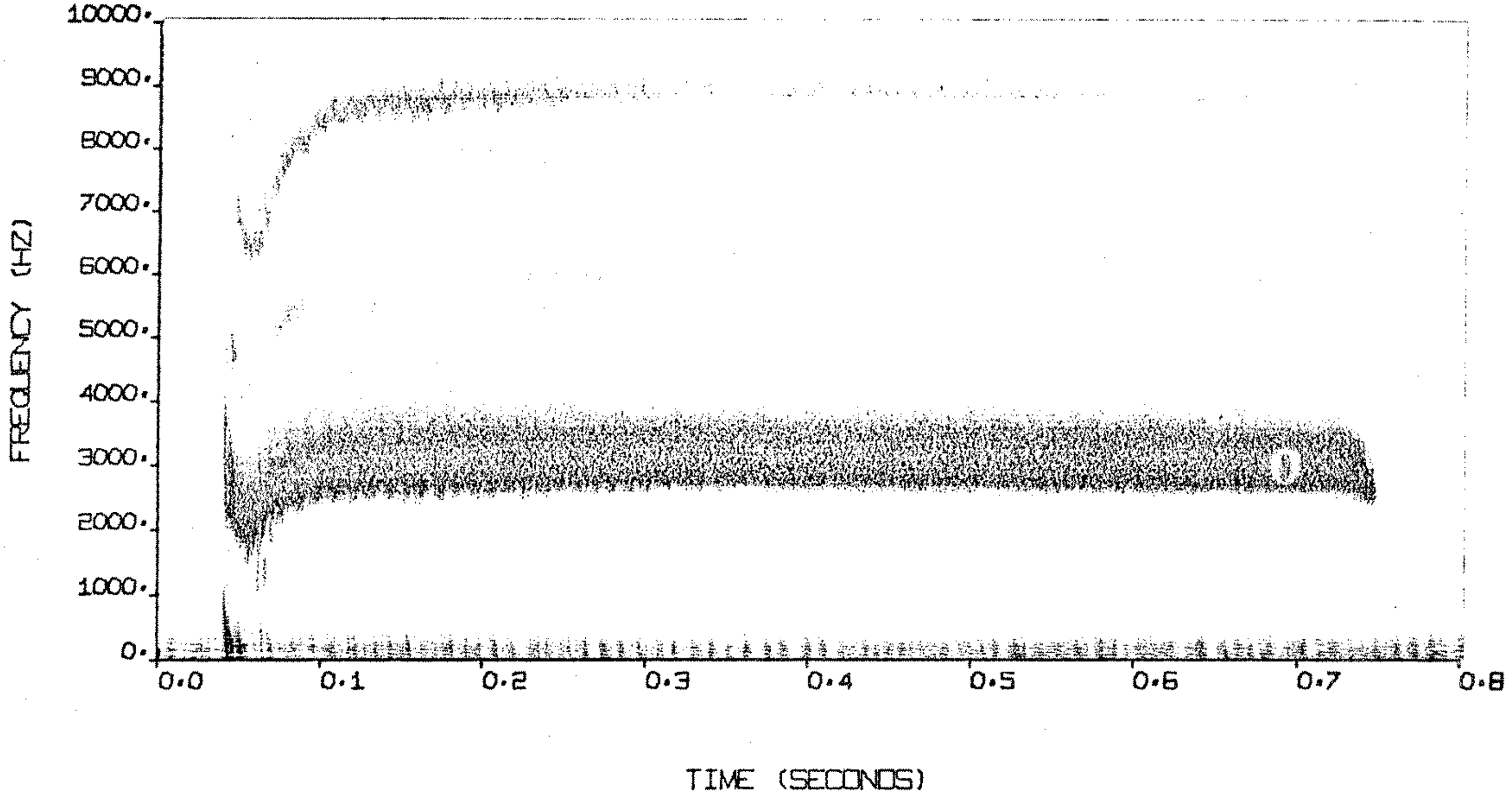

20000
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
FREQUENCY (HZ)
0·00
0·05
0·10
0·15
0·20
0·25
0·30
TIME (SECONDS)

Figure 12. Representative sonogram of a long whistle

Recording speed: 19.05 cm per s
Playback speed: 9.35 cm per s
Wide bandwidth filter


10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
FREQUENCY (HZ)
0·0
0·1
0·2
0·3
0·4
0·5
0·6
0·7
0·8
TIME (SECONDS)
0

whistle.

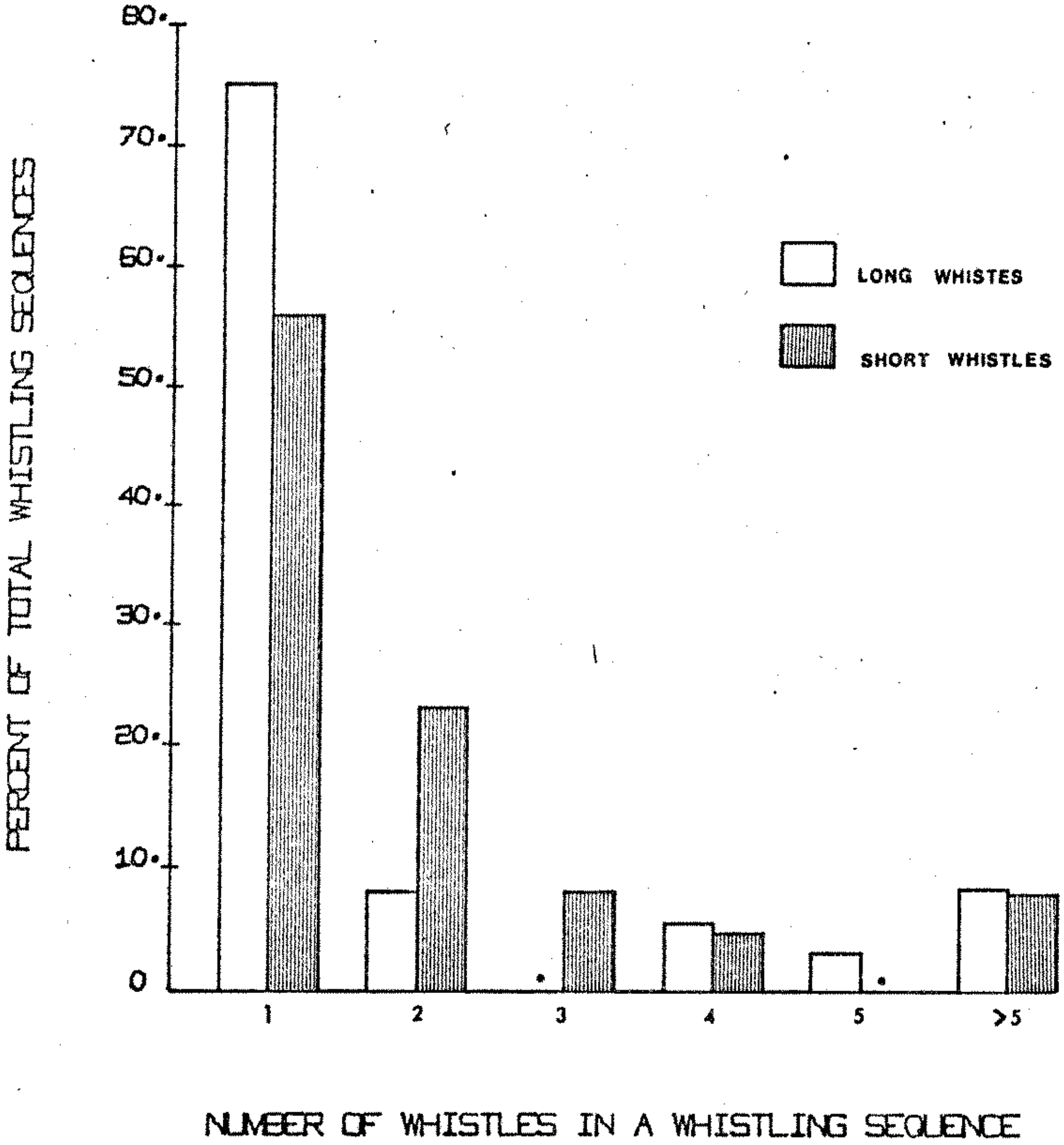
I subjectively classified most marmot whistles that I heard in the field as being either "long", "medium", or "short" in duration. I then used sonograms to determine the duration of each of these whistle types. The results were:

whistle classification	mean duration (s)	range (s)	SE	n
long	0.57	0.27 - 0.84	0.052	14
medium	0.26	0.23 - 0.29	0.009	7
short	0.20	0.12 - 0.26	0.009	17

The inability to distinguish medium whistles was not serious since most whistles that I heard in the field were clearly either long or short. Medium whistles were therefore omitted from subsequent analysis except where noted.

There was no significant difference between the whistles of trapped and free ranging marmots with respect to duration (t=1.50) or frequency (t=1.05).

A whistling sequence was considered to be any whistle or group of whistles that were less than one minute apart. Most whistling sequences consisted of a single whistle (Fig 13). The longest sequence of long whistles was 50 whistles in 9 minutes. One sequence of short whistles lasted 28 minutes and contained about 400 whistles. The interval between whistles varied with the length of the whistle. Long whistles had a mean inter-whistle interval of 17.9 ±1.59 s and short whistles averaged 2.9


PERCENT OF TOTAL WHISTLING SEQUENCES
80
70
60
50
40
30
20
10
0
LONG WHISTES
SHORT WHISTLES
1
2
3
4
5
>5
NUMBER OF WHISTLES IN A WHISTLING SEQUENCE

±0.08 s between whistles.

Marmot whistles serve primarily a warning function (Armitage 1962, Waring 1966, Barash 1973b, 1975). Vancouver Island marmots always whistled when cougars (*Felis concolor*), black bears (*Ursus americanus*), golden eagles (*Aquila chrysaetos*), bald eagles (*Haliaetus leucocephalus*), or red-tailed hawks (*Buteo jamaicensis*) were detected. These species are probably the major predators of Vancouver Island marmots. On one occasion I saw a golden eagle make an unsuccessful attack on a marmot. On another, I am quite sure that two cougars caught a marmot at a spot where trees partially obscured my view. All of these predators have been reported to prey on other marmot species (cougars, Barash 1973b, 1975; black bears, Banfield 1974; golden eagles, Olendorff 1976, Barash 1975, Armitage and Downhower 1974; bald eagles, Beebe 1974; red-tailed hawks, Bent 1937). Two important predators of other marmot species, coyotes (*Canis latrans*) and grizzly bear (*Ursus arctos*), are absent from Vancouver Island (Cowan and Guiguet 1965).

Whistles were given only 27 of 61 times (56%) that smaller raptors (Faloniformes) and ravens (*Corvus corax*) were present (Table IV). Whistles also occurred occasionally for other causes, but I could not associate any cause for 59% of the whistles (Table IV).

Since such a large proportion of whistling sequences was not associated with obvious predators, it is possible that

Table IV. Causes of whistling and keeaw sequences

Stimuli	Whistling Sequences Number	Whistling Sequences Percent	Keeaw Sequences Number	Keeaw Sequences Percent
Potential Predators				
black bears	13	6.1	1	2.6
cougars	3	1.4	1	2.6
bald eagles	4	1.9	5	13.2
golden eagles	5	2.4	5	13.2
unidentified eagles	6	2.8	1	2.6
red-tailed hawks	5	2.4	1	2.6
subtotal	36	17.0	14	36.8
Small Raptors and Ravens				
marsh hawks	10	4.7		
sharp-shinned hawks	4	1.9		
Cooper's hawks	3	1.4		
sparrow hawks	1	0.5		
unidentified small raptors	4	1.9		
ravens	5	2.4	2	5.3
subtotal	27	12.8	2	5.3
Miscellaneous Causes				
intraspecific chases	5	2.4		
aircraft	4	1.9		
black-tailed deer	4	1.9		
people	3	1.4	2	5.3
band-tailed pigeons?	1	0.5	1	2.6
common flickers?	2	0.9		
Canada jays?	1	0.5		
snow and rock slides	2	0.9		
sudden hail storm	1	0.5		
subtotal	23	10.8	3	7.9
Unknown Causes	126	59.4	19	50.0
Grand Total	212	100.1	38	100.0

whistles could have some other function in addition to being alarm calls. Bopp (1955) interpreted the whistles of Marmota marmota as territorial calls. However this function has been disputed by Armitage (1962) and Barash (1973b), both of whom emphasized the warning function of this call. The reaction of marmots was the same whether or not I was able to associate a cause for them. Therefore, I think that the "unknown" causes of many of the whistles I heard were due to either predators that I did not see or common disturbances such as sliding snow, rain, wind, hail, or moving fog patches that alarmed certain individuals (Table IV).

I rarely knew which marmot whistled but in each case when I did the individual was already at a burrow entrance. Upon hearing a whistle marmots usually ran to a burrow entrance or to the top of a rock that had a burrow underneath. Marmots rarely ran and entered a burrow directly; in fact, they frequently emerged from the burrow at the sound of a whistle. Once at a burrow entrance marmots looked about for the cause of the disturbance. Marmots do not immediately enter their burrows when disturbed presumably because it is adaptive to keep any predator in sight and avoid, if possible, the risk of having to subsequently emerge from a burrow when the above ground situation is unknown. Emerging from a burrow definitely involves some risk because predators may wait at a burrow entrance until the occupant emerges. Coyotes (Canis latrans) have been observed catching Spermophilus columbianus (Don Bowen personal communication) and M. caligata (I. McT. Cowan personal communication), and foxes (*Vulpes vulpes*) have been observed catching *S. undulatus* (Gordon Haber personal communication) using this technique. Spring hares, south African rodents in the genus *Pedetes*, are presumably subjected to the same hunting tactics. They apparently confound awaiting predators by emerging from their burrows with a great leap (Vaughan 1972). Marmots usually remained at their burrows only a few minutes after the predators had disappeared and whistling had stopped. No "all clear" call was apparent.

Occasionally some marmots did not appear to react to whistles at all, or they merely looked around from where they happened to be at the time. The intensity (loudness) of the whistle, and not the whistle duration or interval as suggested by Waring (1966), Barash (1973b), and Gray (1975), appeared to determine what action marmots would take. Although intensity was not measured in the field, it was obvious from listening to whistles that intensity varied greatly. More intense whistles resulted in more marmots running to burrows.

Long whistles were more often associated with terrestrial disturbances, and short whistles were more often associated with aerial disturbances.

	number of whistling sequences	
disturbance type	long	short
aerial	5	25
terrestrial	14	3

$X^2=16.81$ df=1 $p<0.001$ n=47

Two whistling sequences were dropped from the analysis because there were both long and short whistles in the sequence. However, both instances were consistent with the above results if only the first call of each sequence was considered. Four sequences were dropped from the analysis because the calls were of a medium length.

I did not record very detailed observations of the way Vancouver Island marmots reacted to alarm calls. Thus I could not detect any differences between responses to long and short whistles.

Keeaws

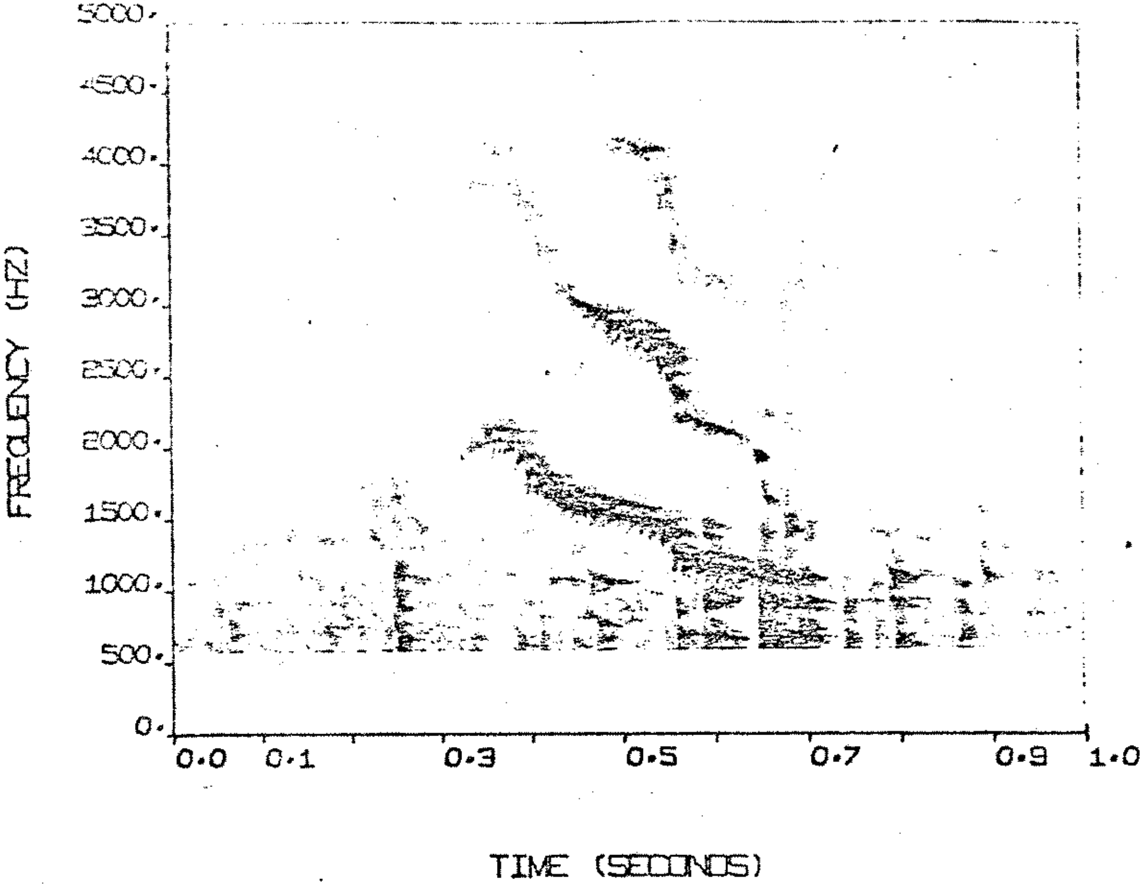
Vancouver Island marmots produced a sound that has not previously been recorded for other marmots. This vocalization was a faint two-syllable call which sounded like a "kee-aw". The fundamental frequency of a keeaw changed in two stages from 1912 ±39 Hz to 1109 ±57 Hz (Fig 14). There are at least two harmonics, both less intense than the fundamental frequency. The mean duration of a keeaw call was 0.29 ±0.016 s. Keeaws were usually given in a long series that varied considerably in length. On two occasions only single keeaws were given but the mean number of keeaws per sequence was 102 ±27. On one occasion about 900 keeaws were given in 60 minutes by one individual. The interval between keeaws averaged 3.8 ±0.15 s. In long calling sequences the interval between calls increased toward the end of the sequence.

Keeaws were frequently associated with disturbances and therefore also with whistles (Table IV and Fig 15). However, keeaws were usually given after whistling had stopped and the predators had left the area. Keeaws therefore seemed to represent a state of "uneasiness" or low intensity alarm.

Upon hearing keeaw calls some marmots did not appear to react at all, but many marmots ran to a rock or burrow and rested there. Marmots gradually resumed their previous activities within a few minutes after the calling started, even when keeaws continued. In all but one instance only one animal

Figure 14. Representative sonograms of keeaws

Recording speed: 19.05 cm per s
Playback speed: 19.05 cm per s
narrow bandwidth filter


5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
FREQUENCY (HZ)
0.0
0.1
0.3
0.5
0.7
0.9
1.0
TIME (SECONDS)

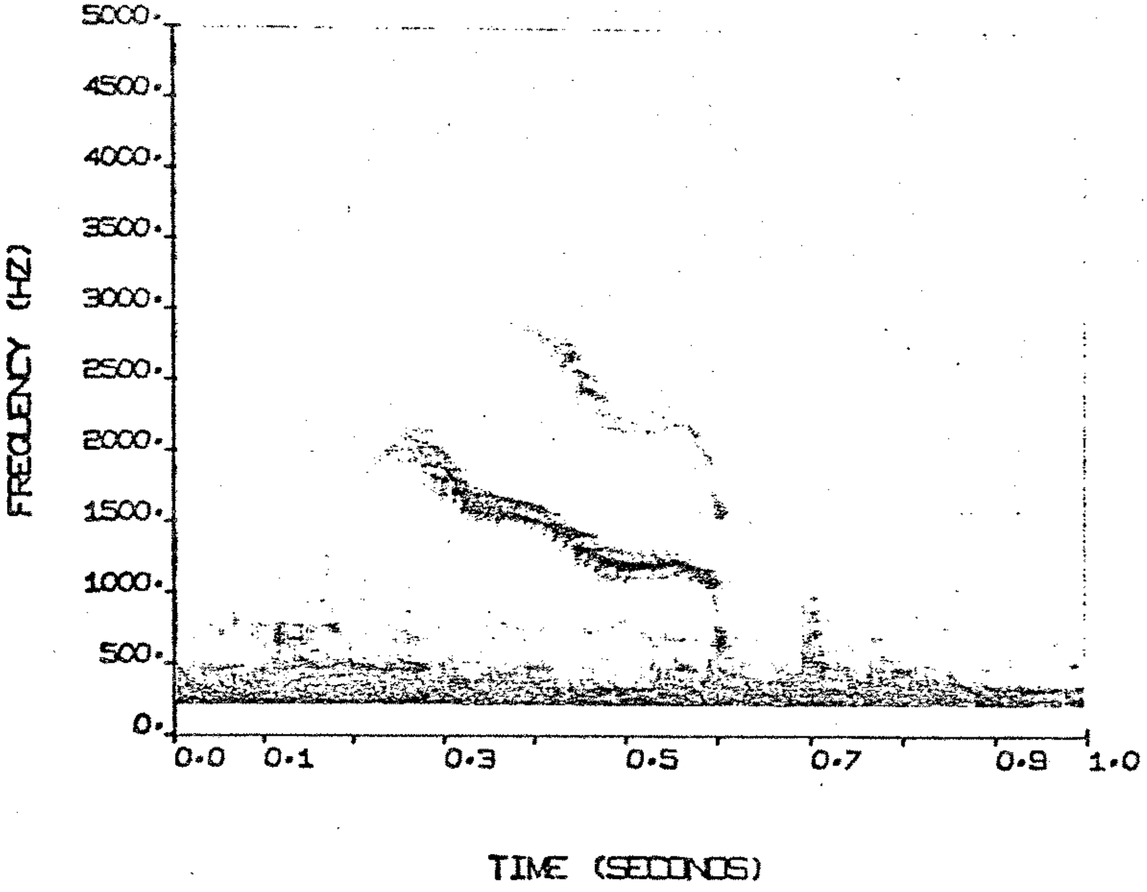
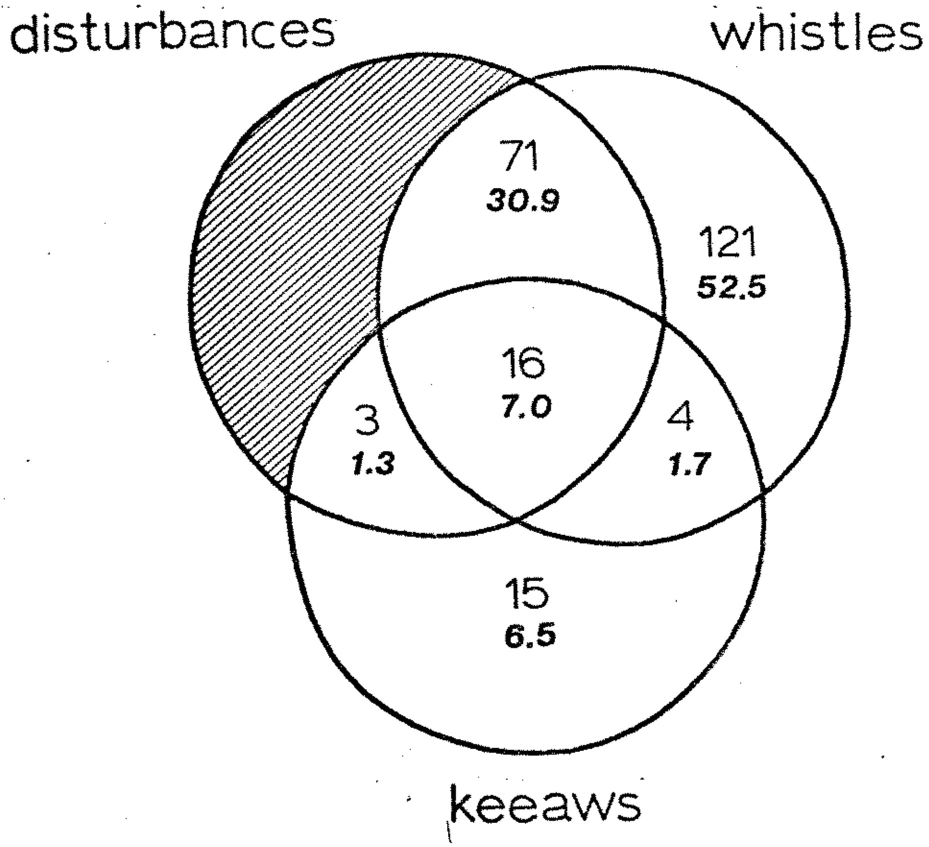

5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
FREQUENCY (HZ)
0.0
0.1
0.3
0.5
0.7
0.9
1.0
TIME (SECONDS)

Figure 15. Frequency with which whistles and keeaws occurred together and separately with and without a known disturbance as a stimulus

Light numbers indicate the number of observations dark numbers indicate the percent of the total vocalization sequences


disturbances
whistles
keeaws
71
30.9
121
52.5
16
7.0
3
1.3
4
1.7
15
6.5

gave keeaws at any one time.

Rapid Chirps

On one occasion when I approached a marmot colony I heard a rapid series of equally spaced, very short whistles or chirps. I did not record this call, nor did I ever hear it again.

Hisses

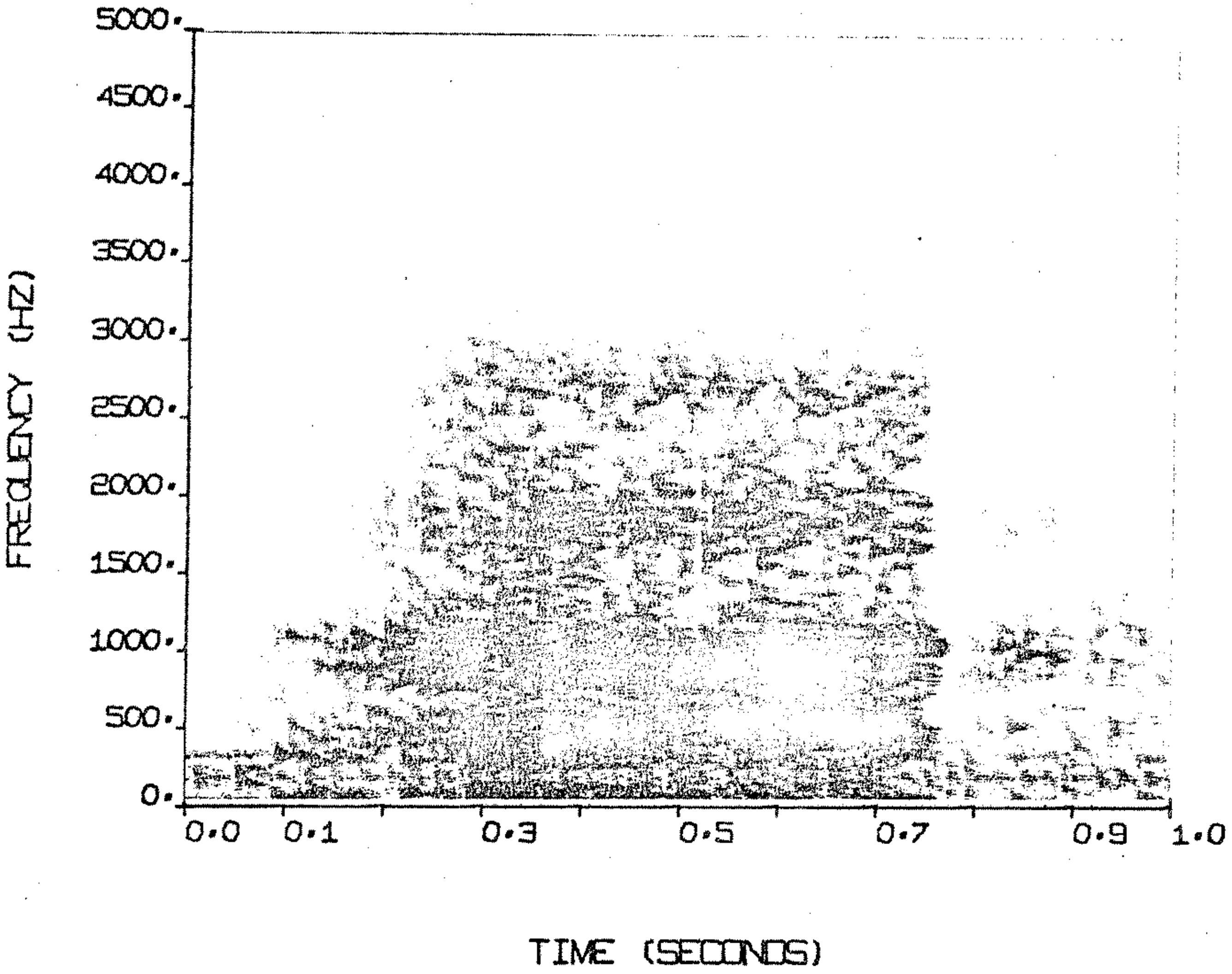
Individuals in live traps occasionally "hissed" when I approached the trap. When a hiss was given the marmot faced me with its mouth open, crouched, and sometimes lunged in an attempt to bite. The hiss spans a wide range of frequencies between 70 and 3000 Hz (Fig 16). Harmonic structure, if any, is very weak.

Tooth Chatters

A tooth chatter denotes threat in many rodents (Balph and Balph 1966; Waring 1966,1970; Ewer 1968; Barash 1973b; Brooks and Banks 1973). I heard a Vancouver Island marmot tooth chatter on only one occasion. This occurred when I was handling the animal, an adult male, for tagging. I did not hear either a hiss or a tooth chatter from free ranging marmots.

Figure 16. Representative sonogram of a hiss

Recording speed: 19.05 cm per s
Playback speed: 19.05 cm per s
Narrow bandwidth filter


5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
FREQUENCY (HZ)
0.0
0.1
0.3
0.5
0.7
0.9
1.0
TIME (SECONDS)

Screams and Growls

"Screams" and "growls" were occasionally heard during play-fights and chases but were not recorded. A growl is a brief low frequency sound probably with a wide range of frequencies. Screams sounded like long high frequency growls.

SOCIAL BEHAVIOUR

Social Behaviour Patterns

I recognized 13 social behaviour patterns in Vancouver Island marmots. Greeting, anal sniffing, and play-fighting were considered to be reciprocal acts because both interactants behaved in a similar manner when performing these behaviours. Chasing, mounting, alert, avoidance, tail raising, lunging, suckling, social grooming, play-fight invitation, and play-chasing were considered to be non-reciprocal acts because the behaviour only describes the action of one of the interactants. The description of scent marking is included in this section both for convienience and because of its social significance.

Greeting (G). Greeting consists of two or more marmots touching their noses together, or one animal sniffing the cheek, ear, or (rarely) side of another individual. This behaviour pattern has been described for at least five other species of *Marmota* (*M. flaviventris*, Armitage 1962; *M. monax*, Bronson 1964; *M. olympus*, Barash 1973b; *M. caligata*, Barash 1974b; *M. marmota*, Barash 1976b) and was the most common social behaviour pattern that I observed (Table VI).

Anal sniffing (AS). Anal sniffing consists of two animals standing together with their bodies parallel while nuzzling the anal region of the other marmot.

Mounting (Mo). Mounting involved one animal straddling the other from behind with its forelegs and placing its ventral surface in contact with the dorsal surface of another. I never observed the dorsal animal thrusting or biting the back of the other marmot as was seen in the sexual behaviour of *M. flaviventris* (Armitage 1965) and *M. olympus* (Barash 1973b).

Suckling (S) and Social Grooming (SG). Both of these acts were observed occurring only between adult females and their infants.

Avoidance (Av). I recorded avoidance behaviour only when I was sure that an animal's departure was in response to another individual. This occurred when a marmot either ran away during an interaction or moved away from an approaching marmot once the latter was within 3 m. Avoidance does not include animals that were fleeing during a chase.

Alert (Al). Alert behaviour was performed by marmots that appeared to be uneasy about the approach of another individual. The alerted animal watched the approaching marmot from a rigid crouched stance.

Lunging (L). Lunging consists of thrusting the front paws foreward toward another marmot, occasionally making contact.

Tail Raising (TR). Tail raising is a graded display which consists of a marmot erecting the hair on the tail and raising the tail up, noticeably arched. The tail may be raised further until the fluffed tail lies flat along the back of the animal. When this display is given the tail is usually moved very slowly or held motionless at any point within this range of positions. All tail raising displays were performed at the same time as one of four behaviour patterns: either greeting, anal sniffing, alert, or play-fighting. However, not all of the occurrences of these behaviours were accompanied by tail raising. Thus, one could consider tail raising to be an optional component of each of these behaviours rather than as a separate behaviour pattern.

Very similar tail raising behaviour was also observed by Barash (1973b:184,198, and Fig 23) in _M. olympus_, by Gray (1967:44 and 50) in _M. caligata_, and by Armitage (1962:325 and Fig 5) and Waring (1966:181) in _M. flaviventris_. This behaviour is very different from the the rapid pumping and swirling that is characteristic of tail movements in _M. marmota_ (Koeing 1957) and from the "tail flagging" of _M. flaviventris_ in which the arched tail is raised up and waved from side to side (Armitage 1974:243). Tail raising in _M. monax_ also involves rapid tail movement (Bronson 1964:471).

Chasing (C) and *Play-chasing* (PC). Chasing was an agonistic encounter that differed from what I termed play-chasing in the following ways:

1. Play chases were slower and shorter, usually less than 7-10 metres.

2. Play-chases were always silent whereas agonistic chases were occasionally accompanied by whistles, squeals, or growls.

3. Play-chases always ended with the interactants resting or feeding close together or interacting in a non-agonistic way. Agonistic chases were rarely followed by other acts since the interactants were usually separate after the chase (Fig 17). Chasing and play-chasing always caused the other marmot to flee, thus it was not necessary to distinguish "fleeing" as a separate behaviour pattern.

Play-fighting (PF). Play-fighting consists of two marmots rising up on their hind legs and pushing with their forelimbs against the other marmot's chest or shoulders. This behaviour has also been described for *M. olympus* (Barash 1973b), *M. flaviventris* (Armitage 1973, 1974, Barash 1973a), *M. caligata* (Barash 1974b), and *M. marmota* (Barash 1976b).

Play-fight Invitation (PI). A play-fight invitation was a visual signal that appeared to indicate that the marmot performing this behaviour was prepared to play-fight. This posture ranged from simply raising the shoulders to raising the whole body into a vertical position on the back legs.

Scent Marking (SM). Vancouver Island marmots frequently made long sweeping motions with their cheeks against rocks that were at the entrances to burrows. This behaviour presumably deposits scent in the form of secretions of their face glands. Marmots sometimes scent marked after social interaction, but scent marking was usually performed as an individual behaviour. All North American and some, if not all, Eurasian marmot species have face glands (Rausch and Rausch 1971:90) and use them for scent marking (*M. caligata*, Gray 1967:48; *M. marmota*, Koeing 1957:519; Asian marmots, Bibikov 1967 cited in Rausch and Rausch 1971:90; *M. monax* and *M. broweri*, Rausch and Rausch 1971:90-91; *M. olympus*, Barash 1973b:184; *M. flaviventris*, Armitage 1976b).

Dominance Relationships

Three behaviour patterns, chasing, avoidance, and lunging, clearly indicated the dominant marmot of an interaction. The dominant marmot in a chase was the animal doing the chasing. Lunging was also characteristic of dominant animals since it usually caused other marmots to move away. Flight and avoidance therefore, characterized the subordinate individuals of an interaction. A dominance matrix based on chasing, lunging, and avoidance was constructed as described by Brown(1975) and is presented in Table Va. It is apparent from these data that a dominance hierarchy existed in the form, adult males > adult females > two-year-old females > yearling males > yearling females.

Table V. Dominance matrices of age and sex classes of Vancouver Island marmots

(a). Dominance Matrix Based on the Frequency of Occurrence of Chases, Avoidance, and Lunges Between Age:sex Classes

Dominant	Subordinate							Row Totals	Column Totals
	AM*	AF	2F	2?	YM	YF	Y?		
AM		3				2	2	7	1
AF	1	2	7	2		10	2	24	4
2F					1	1	2	4	7
2?								0	2
YM		1				1		2	1
YF								0	14
Y?								0	6

(b). Dominance Matrix Based on the Frequency of Occurrence of Eight Behaviour Patterns (C, Av, Al, L, PI, TR, M, SG) Between Age:sex Classes

dominant	subordinate									row Totals	column totals
	AM	AF	A?	2F	2?	YM	YF	Y?	I?		
AM		23	1	8	4	2	7	3		48	6
AF	2	2	1	13	2		10	3	3	36	29
A?									3	3	3
2F	3	3	1			2	2	3		14	21
2?	1									1	6
YM		1					3			4	4
YF										0	22
Y?										0	9
I?										0	6

* KEY AS IN TABLE III

When the other ten behaviour patterns were analyzed with respect to the dominance relationships indicated in Table Va, it was apparent that tail raising, play-fight invitations, mounting, social grooming, and alert, were also status indicating behaviours. Dominant marmots performed play-fight invitations, social grooming, and mounting, and subordinate marmots performed alert and tail raising behaviour. The dominance matrix based on all 8 of these behaviours is presented in Table Vb. Of the 11 exceptions (reversals), five (possibly six) of these occurred between age and sex classes that were adjacent in the dominance hierarchy, where variation would be most likely to occur.

No dominance relationships were apparent among the other 5 behaviour patterns. There were no significant differences between the number of dominant and subordinate marmots that initiated greetings ($X^2=0.78$, n=33), play-fights ($X^2=0.06$, n=17), or anal sniffs ($X^2=2.00$, n=18). Subordinates did not terminate any more greetings ($X^2=1.00$, n=25) or play-fights ($X^2=0.60$, n=15) than did dominant marmots.

The Frequency of Social Behaviour Patterns

I observed a total of 785 behavioural acts occurring in 587 social interactions over the two summers that I observed Vancouver Island marmots. The frequency that each act was observed between age-sex classes is presented in Table VI and the relative frequencies that each behaviour occurred within age-sex classes is presented in Table VII. The data in Table VI do not indicate the actor or recipient in non-reciprocal interactions, the table just shows how frequently each dyad was observed in a specific social behaviour pattern (see section on Dominance Relationships).

The most striking feature of the data in Table VII is that all age-sex classes used the same behaviour patterns in approximately the same proportions. Greeting and play-fighting were the most common social behaviour patterns used by Vancouver Island marmots. They accounted for 65% of all behaviour patterns that I observed over the whole study and were characteristic of the behaviour of all six age-sex classes that I recognized. Tail raising was usually the next most commonly used behaviour pattern. The frequency of the other 10 acts varied among different age-sex classes but they were all relatively rare. The degree of similarity among age-sex classes (Table VII) can not be compared statistically because the data are not independent i.e. greetings occurring between adult males and adult females increase the greeting frequency of both of these groups.

Table VI. The frequency of occurrence of each social behaviour pattern between age-sex classes

DYAD	G	AS	C	Av	Al	TR	PF	PC	PI	L	Mo	SG	S	TOTAL
AM:AF	33	4	2	2	1	18	16				2			78
AM:2F	7	1			3	5	8		1		1			26
AM:YF	6	2	2			4	9		1					24
AM:YM	4					2	5							11
AM:?	21	5	6	5	2	9	7		1	1				57
AF:AF			2											2
AF:2F	41		3	4	1	6	11		3					69
AF:YF	7	2	6	1			5			3				24
AF:YM	8		1				4							13
AF:I	11											3	5	19
AF:?	18	4	9	4	2	7	3	1		2	2			52
2F:YF	6	1		1		1	1							10
2F:YM	3			1	1		4							9
2F:?	8			2		1	4							15
YF:YF	1					1	4							6
YF:YM	1			1					1					3
YF:?	4		1				1	1						7
YM:?	1													1
I:I	16	1					13	2						32
I:?	24	1		1		3	4	2						35
?:?	70	6	28	6		31	118	30		1	2			292
TOTAL	290	27	60	28	10	88	217	36	7	7	7	3	5	785

M = Male
F = Female
? = Sex and age unknown
A = Adult
PI = Play-fight Invitation

2 = Two-year-old
Y = Yearling
I = Infant
G = Greeting
S = Suckling

C = Chasing
Av = Avoidance
PF = Play-fighting
TR = Tail Raising
Al = Alert

PC = Play-chasing
L = Lunging
Mo = Mounting
SC = Social Grooming
AS = Anal Sniffing

Table VII. Percentages of social behaviour patterns per age-sex class

AGE-SEX CLASS	G	AS	C	Av	Al	TR	PF	PC	PI	L	Mo	SG	S	ROW TOTAL	TOTAL ACTS
AM	36	6	5	4	3	19	23		2	1	2			101	196
AF	46	4	10	4	2	12	15	<1	1	2	2	1	2	101	259
2F	50	2	2	6	4	10	22		3		1			100	129
YF	33	6	11	4		9	30	1	3	4				101	80
YM	46		3	5	3	5	35		3					100	37
I	57	3		1		3	25	5				3	4	101	118
?	29	3	10	3	1	11	34	9	<1	1	1			102	751
AVERAGE	37	3	8	4	1	11	28	5	1	1	1	<1	1	101	1570

M = Male
F = Female
? = Sex and age unknown
A = Adult
PI = Play-fight Invitation

2 = Two-year-old
Y = Yearling
I = Infant
G = Greeting
S = Suckling

C = Chasing
Av = Avoidance
PF = Play-fighting
TR = Tail Raising
Al = Alert

PC = Play-chasing
L = Lunging
Mo = Mounting
SG = Social Grooming
AS = Anal Sniffing

The similarity in the behaviour of age-sex classes on the whole does not reveal anything about the nature of interactions occurring between specific dyads. It was not possible to compare the absolute frequencies with which different behaviour patterns occurred between dyads because the observation times differed among individuals (see section on Rates of Social Behaviour). However, what can be compared are the frequencies of occurrence of any given act as a proportion of the total number of acts.

In order to test for similarity between dyads I compared the relative frequency with which acts occurred between different dyads (Table VI) using a Chi-square test for independence. When it was necessary to lump the frequencies of certain behaviours to avoid expected values less than one, I lumped: 1) chasing, alert, avoidance, and lunging, because of the agonistic nature of these acts (see also Armitage 1962, 1973, 1976a), and 2) greeting and anal sniffing, because of the cohesive nature of these acts. If the total number of acts was less than twenty I used the Fisher Exact Probability test. Thirteen of 15 comparisons were not significant (Table VIII), thus indicating that the behaviour patterns were independent of the interactants. That is, the behaviour patterns used in infant : infant interactions were not different from the behaviours used between infants and non-infants nor were the behaviour patterns used in adult male : yearling male interactions different from those used in adult male : adult

Table VIII. Comparisons of the relative frequency with which social behaviour patterns occurred between different age-sex classes

COMPARISON	n	X^2	df	p
AM:AF - AM:2F	104	2.76	4	.60
AM:AF - AM:YF	102	3.75	4	.44
AM:YF - AM:YM	35	.49	2	.78
AM:YF - AM:2F	50	.35	4	.98
AM:YF - AF:YF	48	11.55	4	.02*
AM:YM - AF:YM	24	1.62	2	.45
AM:2F - AF:2F	95	5.49	3	.14
AF:2F - AF:YF	93	25.96	3	<.01*
AF:YF - AF:YM	37	4.68	2	.09
AF:2F - AF:YM	82	.17	3	.91
AF:YF - YF:YF	30	4.80	2	.09
2F:YF - YF:YF	16[1]			.96
2F:YM - 2F:YF	19[1]			.42
YF:YF - YF:YM	9[1]			.21
I:I - I:NI	67	2.59	2	.27

* = $P<0.05$
[1] = Fisher Exact Probability Test, N<20
M = Male 2 = Two-year-old
F = Female I = Infant
A = Adult NI = Non-infant

female or adult male : yearling female interactions. Chi-square for the comparisons between adult females and yearling females and other dyads were significant at the 5% level (* in Table VIII, AF:2F and AM:YF) or the 10% level (YF:YF and AF:YM, Table VIII). There was more aggression between adult females and yearling females than there was between other dyads. For example, greetings made up a much higher proportion of the interactions between adult females and two-year-old females than between adult females and yearling females (59% vs 29%), while the opposite trend was evident with chases (4% vs 25%).

A few dyads were sufficiently different from the general pattern of behaviour that I observed between age-sex classes as a whole, that statistical tests were not required. Adult males were never seen to interact with other adult males even though there were two individuals present on the Haley Lake study area throughout the whole of 1974. Adult females interacted on only two occasions, both of which were chases. Infants experienced significantly less agonistic behaviour (C, Al, Av, L) than did non-infants ($X^2=13.59$, $p<0.01$, df=1).

Interaction Sequences

Most of the 587 social interactions that I observed during this study consisted of only one behaviour pattern. However, 21% (124 of 587) of all interactions consisted of a sequence of two or more acts. The average length of an interaction sequence was 2.6 acts (SE=0.12, range= 2-7). There were no significant differences among age-sex classes or specific dyads in the average number of acts per interaction.

Greeting was usually the initial behaviour of an interaction sequence. Greetings began 53% of all interaction sequences, play-fighting began 30%, and seven other acts initiated the remaining 17% of the sequences.

The relative frequencies with which two-act sequences occurred is illustrated in Figure 17. Since tail raising always occurred at the same time as some other act, rather than before or after it, it was omitted from calculations relating to Figure 17. Most interactions proceeded from a greeting to a play-fight.

Some behaviour patterns occurred in interaction sequences much more often than they occurred as single acts. Twenty-five of 27 anal sniffs, 26 of 36 play-chases, and all seven play-fight intentions occurred in sequences.

Figure 17. Temporal context with which two-act sequences occurred

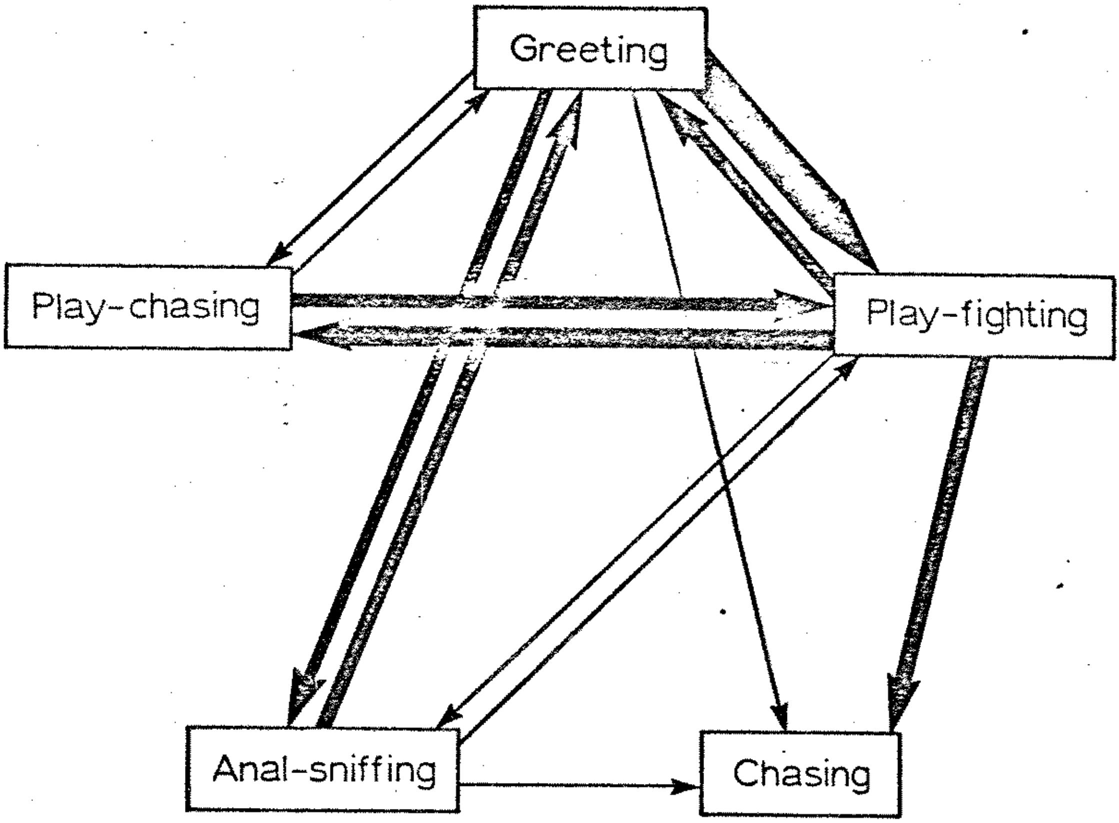
The width of the line is proportional to the the frequency with which the behaviour sequence occurred The narrowest line represents 2% of all sequences 26% of all sequences proceeded from a greeting to a play-fight

Rates of Social Behaviour

Field observations of behaviour rarely allow the investigator to observe each animal or each group of animals for an equal amount of time. The rate that a behaviour pattern is performed is therefore a more useful parameter for describing behaviour than is frequency. Rates can be used to compare the absolute differences in the behaviour between individuals and species, whereas counts can only be used to compare the relative frequency with which behaviour patterns occurred within the behaviour of individuals.

The rates of all behaviour patterns varied somewhat between colonies one and two (Fig 18). All marmots in colony two had higher greeting rates than did the corresponding age-sex class in colony one. I averaged the results of the two colonies for each behaviour of each age-sex class, to obtain the final estimate of interaction rates of Vancouver Island marmots. There was more variation in the rates of behaviour patterns among age:sex classes (Table IX) than there was in frequencies (Table VI). Rates of greeting and play-fighting were high in all age-sex class, with adult and two-year-old females having the highest greeting rates. Yearlings had the highest play-fighting rates and yearling females were most often involved in chases and lunges. Data on infant behaviour was omitted from the analysis

The rates of behaviour patterns per dyad are presented in


Greeting
Play-chasing
Play-fighting
Anal-sniffing
Chasing

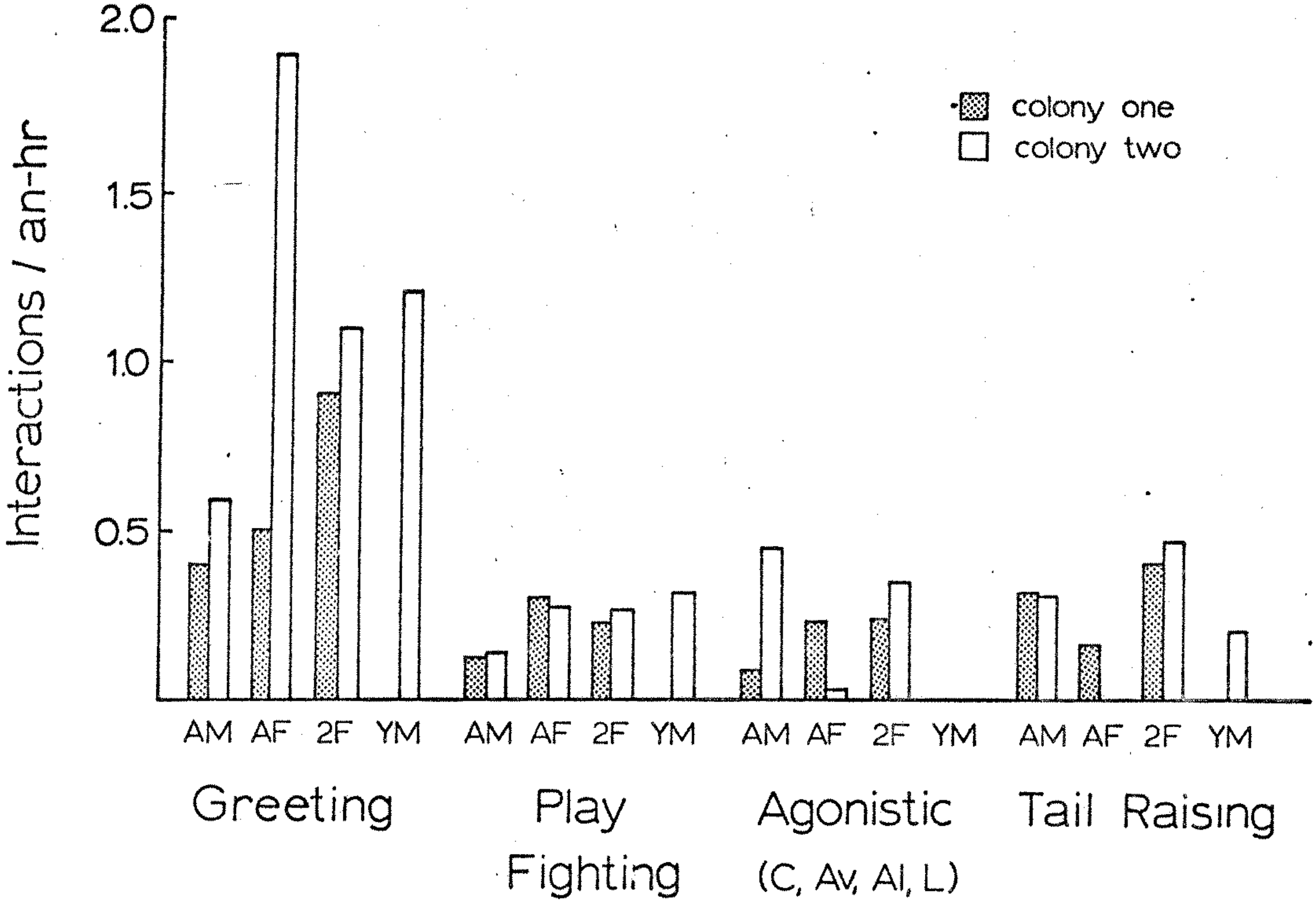

2.0
1.5
1.0
0.5
Interactions / an-hr
▨ colony one
☐ colony two
AM
AF
2F
YM
AM
AF
2F
YM
AM
AF
2F
YM
AM
AF
2F
YM
Greeting
Play Fighting
Agonistic (C, Av, Al, L)
Tail Raising

Table X. Interaction rate per dyad per behaviour per thousand hours

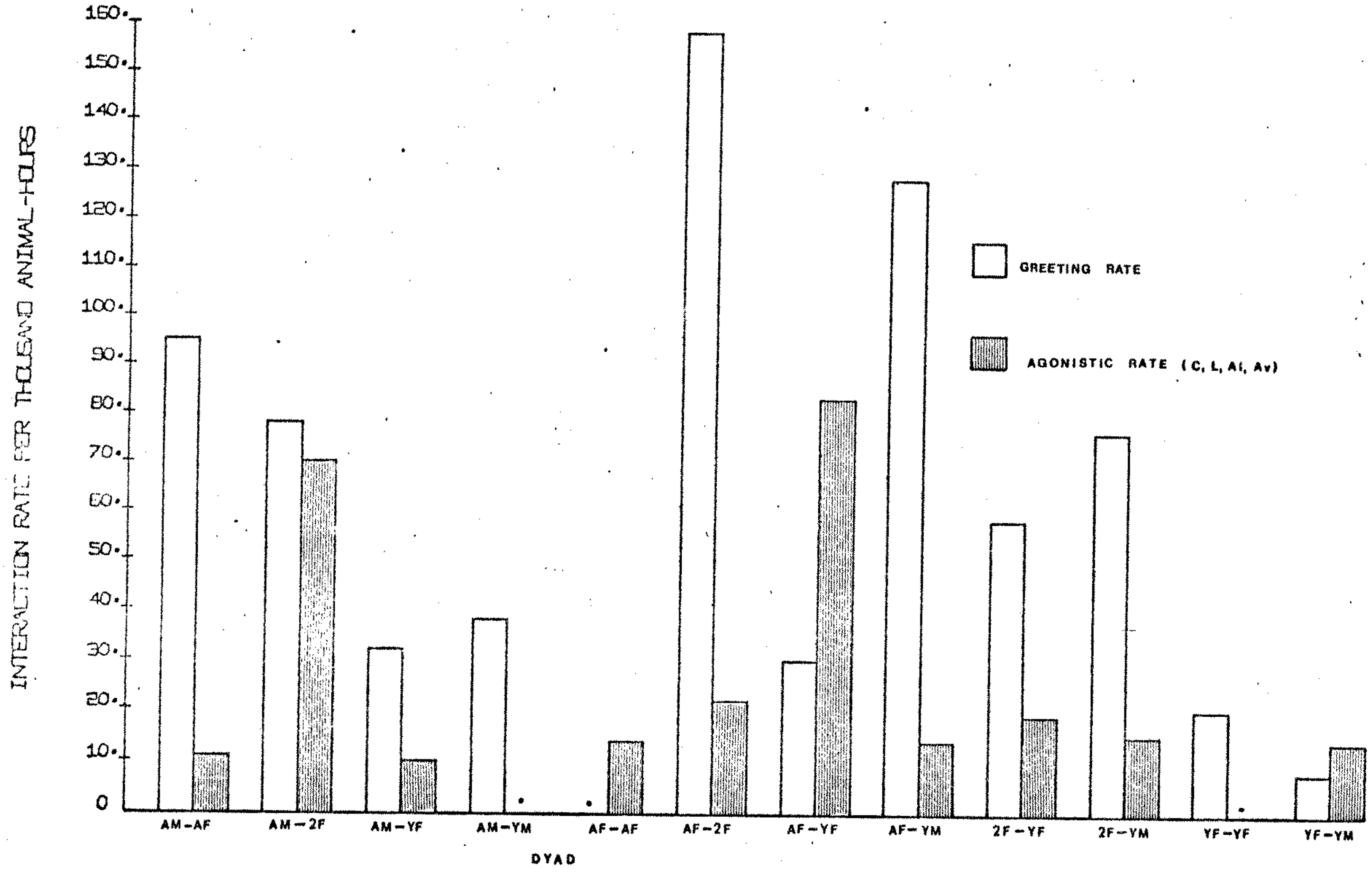
DYAD	G*	AS	C	Av	Al	TR	FF	PI	L	Mo
AM:AF	95	12	2	4	1	49	28			7
AM:2F	78	4			70	76	26			38
AM:YF	32	12	10			20	42			
AM:YM	38					35	30			
AF:AM	-	-		4		2	-			
AF:AF			14							
AF:2F	258		7	12		37	27	6		
AF:YF	30	9	41	6			30		36	
AF:YM	228						61			
2F:AM	-	-					-	38		
2F:AF	-	-			3	9	-			
2F:YF	58	8		11		15	9			
2F:YM	76				15		62			
YF:YF	20						73			
YF:YM	8									
YM:AF	-	-		14			-			
YM:YF	-	-	2				-			

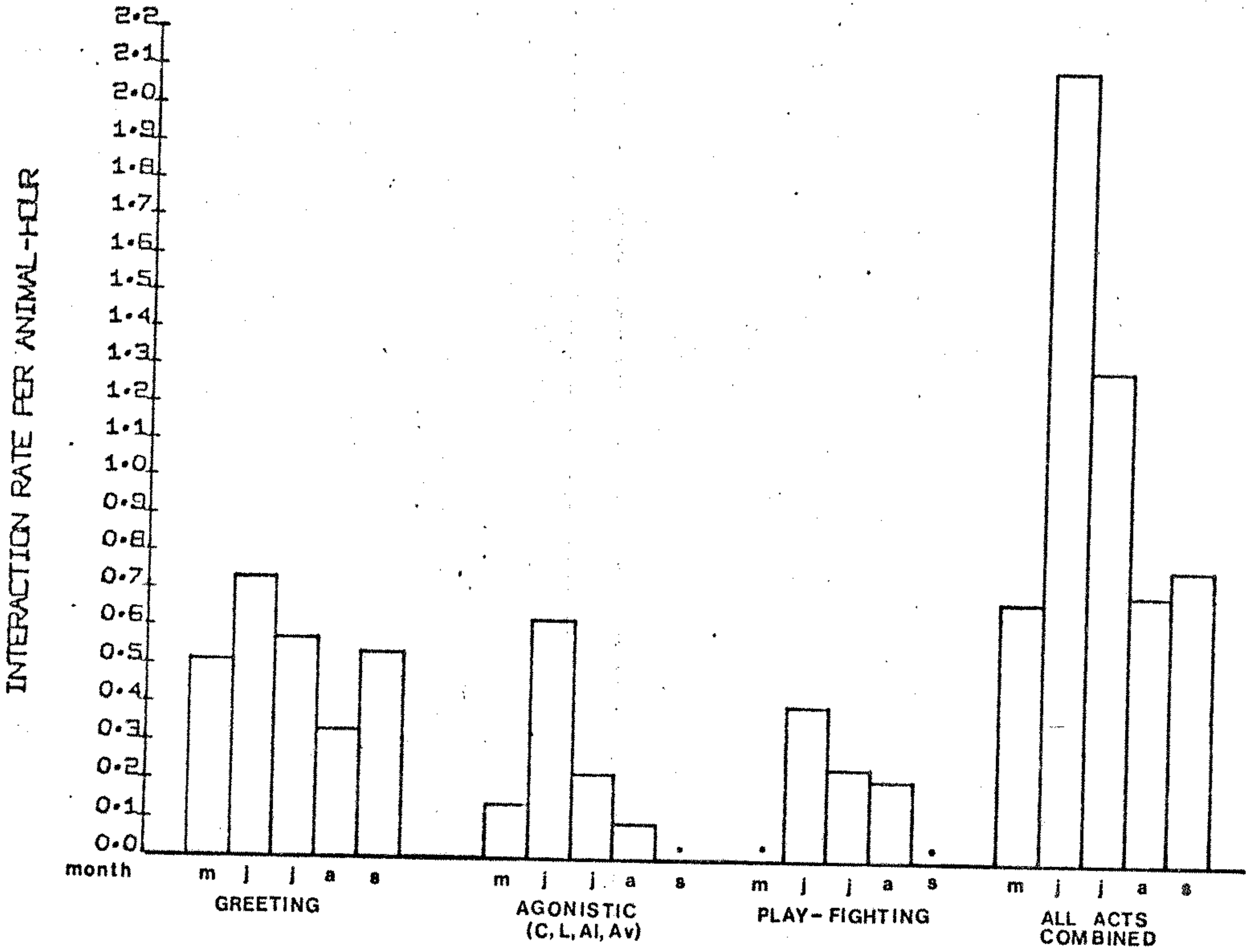
* KEY AS IN TABLE VI

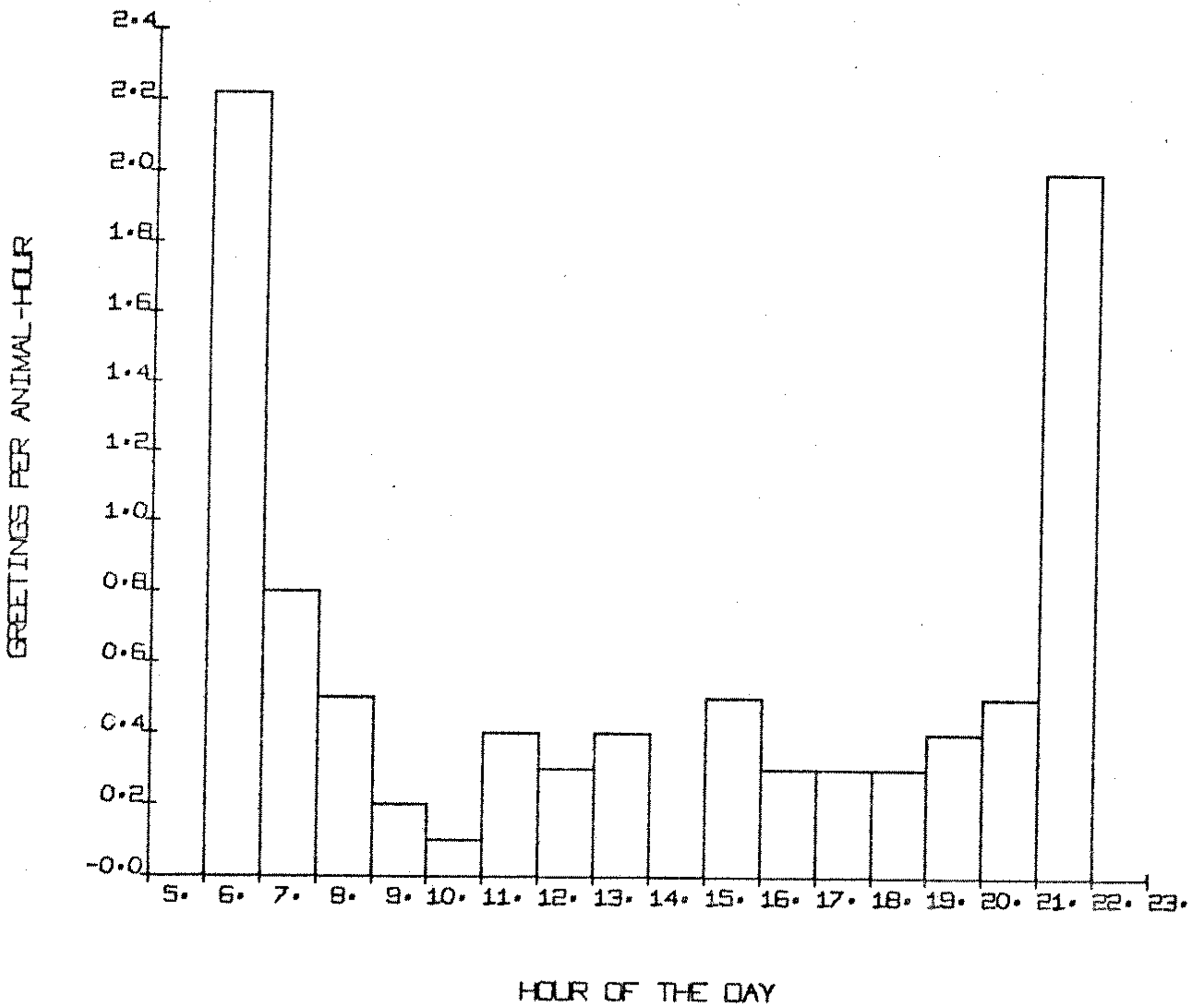
Table X. Two values are presented where appropriate, for non-reciprocal behaviour patterns, but as was noted in the discussion of Dominance Relationships, there were only a few reversals i.e. yearling males chasing adult females. Rates were highest for greeting and play-fighting in most dyads. The highest greeting rates occurred between adult and two-year-old females and adult females and yearling males. The dyad with the highest rate of agonistic behaviour was adult to yearling females. For most dyads (9 of 12) the greeting rates exceeded the rates of all agonistic acts combined (Fig 19).

The rates of all behaviour patterns were highest in June and generally declined through July, August, and September (Fig 20). Greeting rates varied less than other behaviour patterns while the rate of agonistic acts varied the most, being much higher in June than in all other months.

Greeting rate was relatively constant throughout the day, with increases just after emergence from the burrow in the morning, and just before marmots entered the burrow for the night (Fig 21).


160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
INTERACTION RATE PER THOUSAND ANIMAL-HOURS
GREETING RATE
AGONISTIC RATE (C, L, AI, Av)
AM-AF
AM-2F
AM-YF
AM-YM
AF-AF
AF-2F
AF-YF
AF-YM
2F-YF
2F-YM
YF-YF
YF-YM
DYAD


INTERACTION RATE PER ANIMAL-HOUR
2·2
2·1
2·0
1·9
1·8
1·7
1·6
1·5
1·4
1·3
1·2
1·1
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
0·1
0·0
month
m j j a s
GREETING
m j j a s
AGONISTIC
(C, L, Al, Av)
m j j a s
PLAY-FIGHTING
m j j a s
ALL ACTS
COMBINED



GREETINGS PER ANIMAL-HOUR
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1·0
0·8
0·6
0·4
0·2
-0·0
5·
6·
7·
8·
9·
10·
11·
12·
13·
14·
15·
16·
17·
18·
19·
20·
21·
22·
23·
HOUR OF THE DAY

Dispersion, Territoriality, and Scent Marking

On colony two, all four marmots had the same home range. The size of this area was approximately 3 Ha. On colony one, the dispersion of marmots was more complex. In May 1974 there was a large amount of home range overlap among all animals. Most of this overlap occurred in the area with steep cliffs (Fig 22). Until mid-June this was the only area free of snow, thus it was the only area where food was available.

By the middle of June, most of the snow had melted from the colony and marmots fed on plants that were growing on the cliffs much less frequently. At this time the amount of overlap between the home ranges of the two adult females gradually decreased. By July their ranges were completely separate and they remained that way for the duration of the summer. Adult female #15 occupied the lower half of the colony and adult female #12 occupied the upper half (Fig 23).

One adult male, #4, emigrated from colony one to colony two in early June and the remaining adult male, #13, moved over the whole colony, an area of about 4.5 Ha (Fig 22). However, a third adult male, #17, immigrated to colony one at the end of June and occupied a similar area to adult female #12 on the upper 2.2 Ha of the colony. Shortly after the arrival of adult male #17, adult male #13 drastically reduced his home range until it did not overlap at all with that of #17 (Fig 24). From July through until the animals hibernated in September there

Figure 22. Home ranges of the two adult females (#12 and #15) in May 1974, and the two adult males (#13 and #17) in June 1974, on the Haley Lake study area

The dots indicate the locations of scent markings made by adult male #13 before the arrival of adult male #17 (n=3).
This figure illustrates the same area shown in Fig 2B.

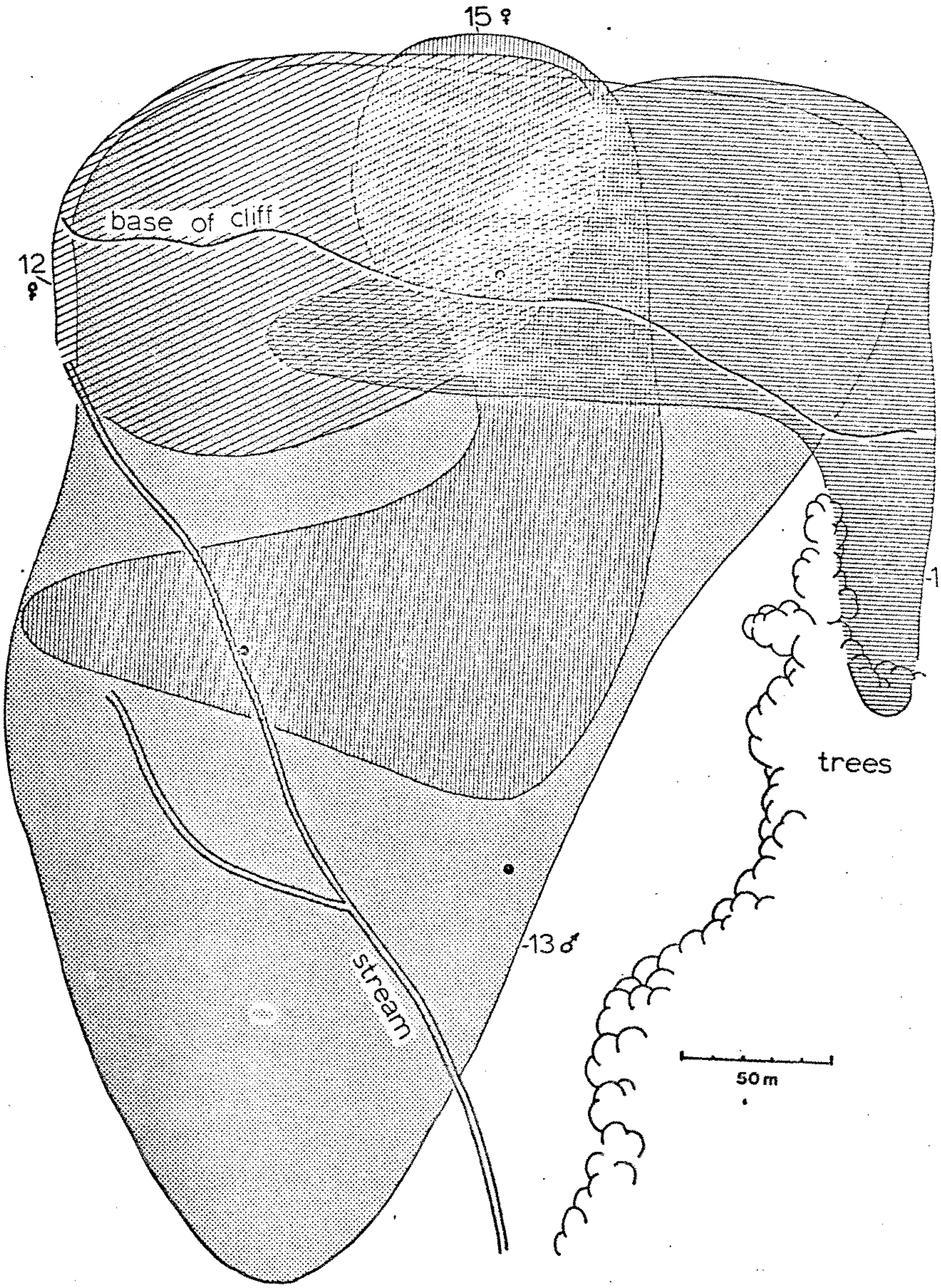

15 ♀
base of cliff
12 ♀
-17 ♂
trees
-13 ♂
stream
50 m

Figure 23. Home ranges of four female marmots on the Haley Lake study area in July 1974

Dots indicate the locations of all scent marks made by adult female #12 (n=4).
Circles indicate the locations of all scent marks made by two-year-old female #9 (n=5).
Triangles indicate the locations of all scent marks made by adult female #15 (n=5).
Arrows indicate the locations of chases.
#14 is a yearling female.
#17 is an adult male.

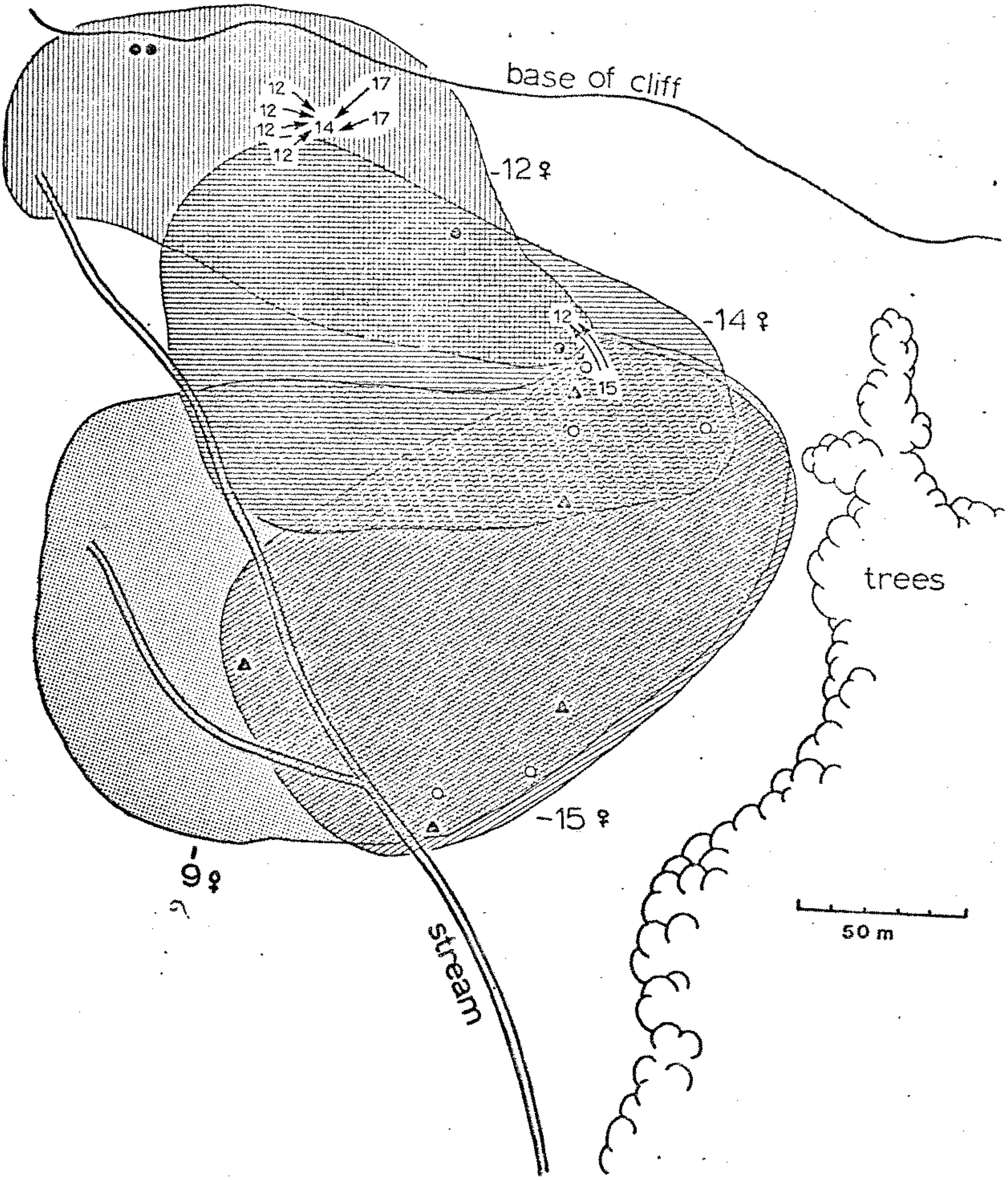
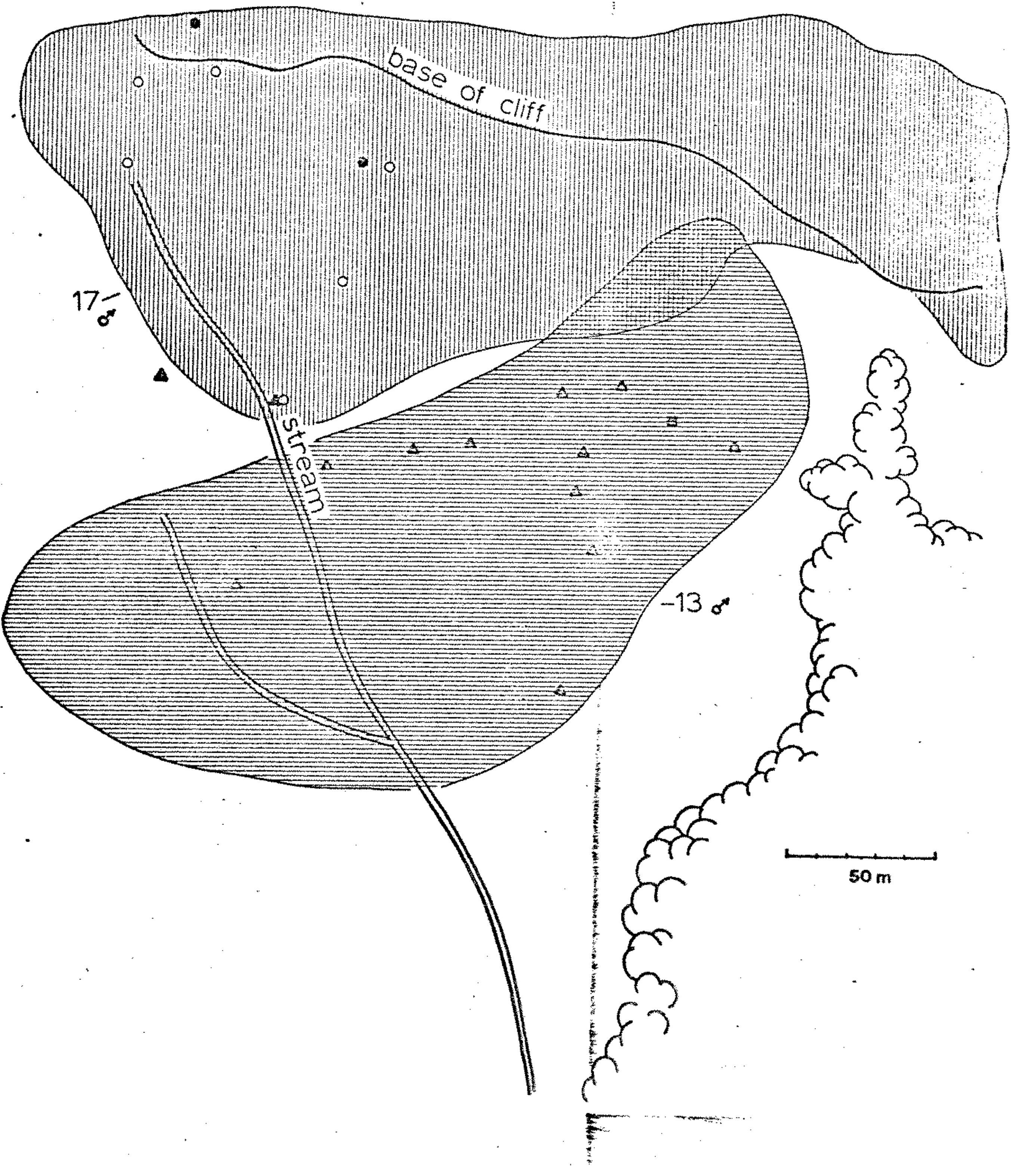

base of cliff
12
12
12
12
14
17
17
-12 ♀
-14 ♀
12
15
-15 ♀
-9 ♀
stream
trees
50 m

Figure 24. Home ranges of the two adult males on the Haley Lake study area in August 1974

Dots indicate the locations of all scent marks made by adult male #13 in June, after the arrival of adult male #17 (n=2).
Triangles indicate the locations (n=13) of all scent marks (n=17) made by adult male #13 in July.
Squares indicate the location of all scent marks made by adult male #13 in August (n=1).
Circles indicate the locations (n=6) of all scent marks (n=12) made by adult male #17.


base of cliff
stream
17
13
50 m

were clearly two main areas on the colony. The upper area was occupied by marmots #12 and #17 and the lower area was occupied by animals #13, #15, two two-year-olds, and three yearlings. Yearling female #14 was the only marmot that consistently used part of both areas (Fig 23). One adult animal occupied peripheral areas and was rarely seen.

I analysed the behavioural interactions between occupants of the upper and lower areas of colony one to determine the proximal causes of this pattern of dispersion. Adult females #12 and #15 interacted only on two occasions. Both of these interactions involved #15 chasing #12 from the area normally used only by the occupants of the lower area (Fig 23). Both adult females occasionally scent marked within their areas of exclusive use (Fig 23). Brown and Orians (1970) accept the concept of a territory being a defended area and explicitly define defense as being either 1. actual defense such as chasing away an intruder, or 2. performing identifying acts such as scent markings. Thus my data suggest that adult Vancouver Island marmot females are territorial with respect to other adult females, but that their territories are smaller than their home range.

I did not see any interactions at all between adult males #17 and #13 in spite of the dramatic change in the home range of #13 that appeared to be directly related to #17's arrival. There could have been some rare and significant interactions between these two marmots that I missed seeing but usually these two animals just avoided one another. Avoidance was probably enhanced by the deposition of scent marks. Adult males scent marked much more than adult females. The two-year-old female was the only other age-sex class of marmot observed to scent mark.

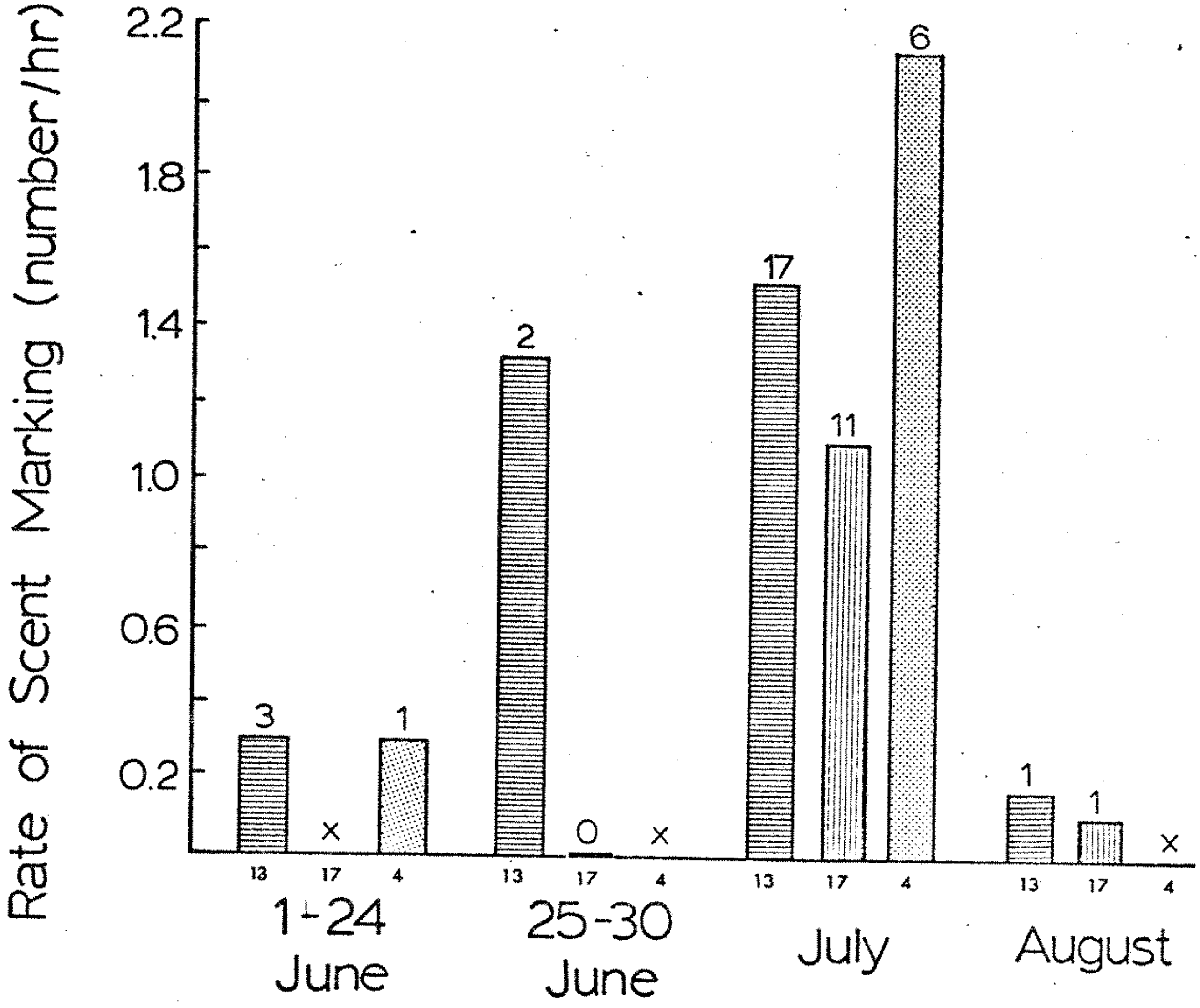
age-sex class	frequency of scent marking
adult males	42
adult females	9
two-year-old female	5

The distribution of #13's scent marks before and after the arrival of #17 is shown in Figures 22 and 24. Most of the scent marking that I observed was done by #13 just after the arrival of #17 (Fig 25). Adult male #4, on colony two, also increased his rate of scent marking in July (Fig 25). This increase may also have been due to the presence of the scent of another adult male since #4 had just immigrated to this locality. Even though the ranges of #13 and #17 still overlapped somewhat in July they each avoided the area enclosed by each others scent marks. The area enclosed by scent marks was also the area of maximum use of each marmot.

I analyzed the amount of time that marmots spent moving but not feeding. Adult males moved significantly more than other age-sex classes and adult male #13 moved significantly more than adult males #4 and #17. The relatively large amount of time spent moving by adult male #13 occurred as he patrolled his home range. Patrolling involved moving around the perimeter of the

Figure 25. Rates of scent marking by adult males #4, #13, and #17

Numbers above bars indicate the number of scent marking bouts observed
X indicates no data



Rate of Scent Marking (number/hr)
2.2
1.8
1.4
1.0
0.6
0.2
3
x
1
2
0
x
17
11
6
1
1
x
13
17
4
13
17
4
13
17
4
13
17
4
1-24
June
25-30
June
July
August

home range greeting other marmots and occasionally scent marking. Adult male #4 did not patrol his home range as often, probably because he never came into contact with other adult males. I think that adult male #17 patrolled less often than #13 because the physical characteristics of the habitat allowed him to see most of his home range from the tops of the rocks that he frequently rested on. Moving marmots made themselves more conspicuous than feeding marmots by preceeding more of their movements with tail flicks (67% vs 28%, $X^2=18.3$, $p<0.01$).

These observations indicate that adult Vancouver Island marmot males are also territorial with respect to other adult males. They occupied fixed areas of exclusive use that could be considered to be defended by scent marks.

Interactions occurred between adult female #12 and adult male #13 before the arrival of adult male #17. These interactions were similar to those occurring between adult female #15 and #13, and between #12 and #17 ($X^2 = 2.28$, $p>.25$). Thus adult female #12 did not try to defend the upper of the Haley Lake colony against #13, nor did she react aggressively to #17 when he first arrived. As I mentioned earlier, yearling female #14 consistently moved between the upper and lower areas. However, this individual was treated quite aggressively by both #12 and #17, 6 chases (Fig 23) and 3 lunges out of a total of 20 interactions. In the lower area none of the 12 interactions between #14 and #13, or #14 and #15, were chases or lunges. Some aggression did occur among marmots in the lower area but it did not appear to be related to specific locations and it appeared as if all occupants could move about freely anywhere within this area.

DISCUSSION

VOCALIZATIONS

Interspecific Comparisons of Marmot Vocalizations

The vocalizations of Vancouver Island marmots are very similar to those of M. caligata and M. olympus (Table XI). However, there are some important differences. Barash (1973b) never heard whistles from M. olympus that were as long as those commonly given by M. vancouverensis. Rapid chirps were often given by M. olympus (Barash 1973b) but I heard them from M. vancouverensis only once.

The keeaw of M. vancouverensis corresponds in M. caligata to a "queeuck" call (Gray 1967) and the "low frequency call" described by Taulman (1975). The medium call of M. olympus (Barash 1973b) although different in sound structure appears to be the homologous call in this species. In the one Olympic marmot calling sequence that I heard, the first few calls sounded exactly like a keeaw. Subsequent calls were pure toned whistles of a medium length as described by Barash (1973b). The duration and interval of medium M. olympus calls is quite similar to that of keeaws (Table XI). Keeaw, queeuck, low frequency and medium whistle calls were all given in prolonged sequences and all three calls seemed to indicate a state of uneasiness.

Table XI. A comparison of vocalizations within the *Marmota caligata* Group

Call Characteristics	*M. vancouverensis*	*M. caligata*	*M. olympus*(5)
Call Name	long whistle*	long call*(1)	-
Duration (s)	0.57	.56-.75(123)	
Interval (s)	17.9	13.6-16(14)	
Frequency (Hz)	2910	2800-3200(123)	
Call Name	medium whistle*	descending and ascending call*(1)	long call
Duration (s)	0.31	0.3(to 0.5)(1)	0.39
Interval (s)	6.5	3(1)	>5
Frequency (Hz)	2910	3500(1)	2700
Call Name	short whistle*	alarm chirp*(13)	medium call*
Duration (s)	0.22	0.1(1)	0.2
Interval (s)	2.9	1.3(1)	1-3
Frequency (Hz)	2910	2500-3200(13)	2700
Call Name	rapid chirps	accelerating chirp(13)	short call*
Duration (s)	<<< 0.22	0.1-variable(1)	0.095
Interval (s)	<<< 2.9	.05-variable(1)	0.36
Frequency (Hz)	?	2500-3200(1)	2700
Call Name	keeaw*	queeuck whistle(4)	-
Duration (s)	0.29	0.3(1)	
Interval (s)	3.8	1(4)	
Frequency (Hz)	1900-1100	2000-1500(1)	

* - calls used in correlation analysis on page 93
(1) Taulman 1975
(2) Waring 1966
(3) Pattie 1967
(4) Gray 1967
(5) Barash 1973b

Table IX. Interaction rate per age-sex class of behavioural acts per thousand hours

Age:Sex Class	Behaviour Pattern									
	G*	AS	C	Av	Al	TR	PF	PI	L	Mo
AM	488	513	0	99	160	301	138	74	0	24
AF	1225	32	56	32	0	80	265	8	32	74
2F	1005	23	22	45	203	440	271	102	0	79
YF	388	0	388	97	0	0	583	0	291	0
YM	606	0	0	0	0	101	303	0	0	0

* KEY AS IN TABLE VI

Altruism and Marmot Alarm Calling

Altruistic behaviour can be defined as behaviour that benefits another organism, not closely related, while being detrimental to the organism performing the behaviour. Benefit and detriment are defined in terms of the contribution to an animal's fitness where fitness is measured by the proportion of an animal's genes left in the the population gene pool (Pianka 1974). Since a marmot giving an alarm call may attract the attention of a predator and thereby subject itself to a greater risk of predation than if it had remained silent, marmot alarm calling appears to be altruistic. However, true altruism is virtually unknown (Pianka 1974) and if present would be very difficult to account for by natural selection.

There are three ways to account for the evolution of marmot alarm calling. The first explanation is kin selection. Kin selection is the evolution of characteristics within an individual that favour the survival of its close relatives but that are not necessarily beneficial to that individual. Kin selection could account for the evolution of alarm calling even if it involved some risk to the caller and if it incidentally benefitted some unrelated individuals. Kin selection has been considered an important selective force in the evolution of alarm calling in birds (Hamilton 1964, Maynard Smith 1965, Emlen 1973). The social organization of Vancouver Island marmots is such that the individuals receiving the alarm are likely to be closely related to the caller. Thus, kin selection could account for the existence of alarm calling in Vancouver Island marmots.

Secondly, alarm calling may be selected for because there is a direct benefit to the caller associated with calling. The individual could benefit from calling if it confused the predator (Maynard Smith 1965) or if it "manipulated" other marmots so as to make the caller less vulnerable than the other individuals (Charnov and Krebs 1975). Marmot calls could be manipulating other marmots by stimulating them to run to a burrow. The reacting marmots thus become more conspicuous (to me and presumably to predators as well) than the caller, who has already moved to a burrow entrance. As Charnov and Krebs (1975) argue, the individuals reacting to the call "use the information to their own benefit, but by doing so make it possible for the caller to benefit even more."

Trivers (1971) presented other arguments which would account for the evolution of alarm calling by direct selection for the individual caller. He argues that it is disadvantageous for an individual to have a predator kill a nearby conspecific because the predator may then be more likely to kill him in the near future. This could occur if the predator was more likely to

(1) develop a search image (Emlen 1973) for that prey species,

(2) learn the habits of the prey species and perfect its hunting techniques on it, and

(3) frequent the habitat of the prey species.

Giving alarm calls thus tends to prevent a predator from specializing on the caller's species and locality, thereby favouring the individual caller even though callers are incidentally altruistic to their non-calling neighbours (Trivers 1971, Charnov and Krebs 1975).

There may be another direct advantage to marmot alarm calling. It may be advantageous for an animal to have conspecifics around regardless of how closely related they are. The presence of conspecifics may be advantageous with respect to finding a mate or increasing winter survival due to the reduction of heat loss when animals hibernate in a group. Thus, there would be selection for alarm calling if the benefit derived from having other animals around exceeds the cost of calling.

Lastly, alarm calling could be brought about by group selection, which is selection favouring the survival of the group as a whole rather than the individual (Wynne-Edwards 1962). Group selection could account for a truly altruistic trait to evolve; however, if group selection exists at all it is rare (Lewontin 1970), less efficient than individual selection (Sterns 1976), and it should not be invoked if a simpler solution (direct or kin selection in the case of marmot alarm calling) exists (Williams 1966).

The above arguments were presented to account for the apparent cost (loss of fitness) associated with alarm calling. However, no information exists for any species that there is any net cost involved with alarm calling (Brown 1975). Observations of _Marmota_ species do not support the sugestion that the alarm caller is incurring any risk. Vancouver Island marmots appear to protect themselves before whistling. In all cases I observed, the caller was already at a burrow entrance. Barash (1975) saw eight instances of predation on various _Marmota_ species. Not one of these occasions was preceded by alarm calls from the victim.

From the above arguments I conclude that there is no true altruism associated with marmot alarm calling. If there is any cost at all associated with calling, benefits from direct or kin selection would be strong enough to select for alarm calling.

The Evolution of Whistle Structure

Marler (1955, 1957) was the first to point out how the physical properties of avian alarm calls could be related to their function. He observed that some bird species have convergently evolved alarm calls that have characteristics that appear to make them difficult to locate. Konishi (1973) tested the locatability properties of different sound characteristics using barn owls (_Tyto alba_), a species that is adapted for locating its prey by sound. His results indicated that barn owls locate sound by comparing the intensity of sound between ears. Binaural differences in intensity result from a shadow being cast by the head. Wide bandwidth noises are easier to locate than pure tones because they consist of many frequencies, each of which can be used for binaural intensity comparisons. Locatability by this method is also directly related to frequency (at least between 3 and 9 kHz). Thus, barn owls located narrow bandwidth pure tones of 3 kHz less accurately than any of the other sound characteristics tested with bandwidth being the primary characteristic determining the locatability of a sound.

Vancouver Island marmot alarm whistles have the precise characteristics of the most difficult-to-locate sound tested by Konishi (1973). Narrow bandwidth alarm calls are also found in many other (but by no means all) species of medium size, diurnal mammals (Table XII). A difficult-to-locate alarm call would presumably reduce the risk of predation to the caller. Thus predation pressure could select for the evolution of such alarm call charateristics in all of the species listed. The alarm calls of the birds recorded by Marler (1955, 1957) all had narrow bandwidths. It appears therefore that there has been remarkably strong convergence for the same alarm call characteristics in both birds and mammals. Selection for difficult-to-locate alarm calls does not indicate anything about the fitness of individuals giving difficult or easy to locate calls relative to no call. Thus, selection for specific call characteristics does not enter into the discussion of the altruistic nature of marmot alarm calling (non-callers vs callers).

The Evolution of Whistle Function

M. vancouverensis alarm calls not only indicate that there is a predator around but also what type of predator is present. The presence of situation specific alarm calls has not been shown for any other marmot species. Such alarm calls are relatively common among ecologically related species. Avian and terrestrial predators evoke specific alarm calls in at least four species of ground squirrels (*S. beecheyi*, Owings *et al* 1977, Fitch 1948; *S. armatus*, Balph and Balph 1966; *S. undulatus*, Melchior 1971; *S. beldingi*, Turner 1973), mountain viscachas (*Lagidium peruanum*, Pearson 1948), and perhaps black-tailed prairie dogs (*Cynomys ludovicianus*; King 1955, Waring 1970, Smith *et al* 1977). *M. olympus* (Barash 1973b), *M. flaviventris* (Armitage 1962 and personal communication, Waring 1966), and *M. caligata* (Gray 1967) do not appear to have situation specific calls.

If situation specific alarm calls are communicating specific information then the receivers of this information should exhibit a biologically appropriate response. Of the eight species that have situation specific alarm calls, only two, Belding's ground squirrel (Turner 1973) and black-tailed prairie dogs (King 1955) were observed to react differently to each call. I think that the lack of observations of specific responces in the other six species is probably due to the difficulty in detecting small differences between responses. For example, *M. vancouverensis* responds to both long and short whistles by running to a burrow and looking about for the cause of the disturbance. It would be advantageous in this situation if whistle length could provide information on where to begin looking for a predator, either in the air or on the ground. If this was the only variation in the response,it would be very difficult to detect or to test for.

Aerial predators probably exert the greatest selection for difficult-to-locate alarm calls. In all five species that have both situation specific and difficult-to-locate alarm calls (Table XII), avian predators evoked alarm calls that were less locatable than the corresponding call evoked by terrestrial predators. Avian predators may select more strongly for difficult-to-locate alarm call characteristics because their range and speed of attack is greater than that of terrestrial predators.

The presence or absence of difficult-to-locate and situation specific alarm calls is probably a function of the predation pressures and the variety of possible escape responses that a prey species possesses. As avian predation pressure increases there is increased selection for difficult-to-locate alarm calls. Situation specific alarm calls will only be selected for when there is selective pressure from both terrestrial and avian predators and individual prey can increase their chances of survival by responding differently to these different predators.

Table XII. A list of mammalian species that have narrow bandwidth alarm calls

Species	Reference
M. vancouverensis(2)	this study
M. olympus	Barash 1973b
M. caligata	Waring 1966
M. monax	Lloyd 1972(1)
Spermophilus armatus(2)	Balph and Balph 1966
S. richardsonii	Banfield 1974(1)
S. franklinii	Banfield 1974(1)
S. undulatus(2)	Melchior 1971
S. beecheyi(2)	Owings *et al* 1977
rock hyraxes: Hyracoidea	Mathews 1971(1)
Lagidium peruanum(2)	Pearson 1948 and Eisenberg 1974
Lagidium boxi	Rowlands 1974(1)
Octodon degus	Eisenberg 1974(1)
Chinchilla laniger	Eisenberg 1974(1)
Capromys pilorides	Eisenberg 1974(1)
Dolichotis patagonum	Eisenberg 1974(1)
Pediolagus salinicola	Eisenberg 1974(1)
Pectinator sp.	George 1974(1)
Microcavia spp.	Rood 1972:16(1)
Cavia spp.	Rood 1972:17(1)

(1) - No sonograms were presented but the verbal description appears to be appropriate, and a narrow bandwidth sound is relatively easy to describe.

(2) - Alarm calls are also predator-specific.

In addition to warning other marmots to seek cover, whistles may reduce predation by inhibiting attacks. If the predator is aware that it has been detected it may abandon an otherwise auspicious attack because of the overall low probability of capturing alerted prey. Alcock (1975) and Brown (1975) noted that alarm calls or signals may inhibit predator attacks. Warning calls may also function as mobbing calls in birds by discouraging a predator from remaining in the vicinity (Wilson 1975).

INTERSPECIFIC COMPARISONS OF MARMOT SOCIAL BEHAVIOUR

A Test of Barash's Hypothesis

In order to test the data obtained in this study against Barash's hypothesis of marmot sociality, it was first necessary to obtain explicit predictions pertaining to Vancouver Island marmots. The parameter necessary to make such predictions is an estimate of the length of the vegetative growing season, as measured by the number of frost-free days in the absence of snow cover (Barash 1973b). On the Haley Lake study area the number of frost-free days was 115 days in 1973 and 135 days in 1974 (Table II). The average number of frost-free days in typical subalpine parkland habitat is 114 days (Brooke <u>et al</u> 1970). The number of frost-free days was equivalent to the vegetative growing season in 1973 but in 1974 large amounts of snow persisted for two weeks after the last frost. This reduced the vegetative growing season to about 121 days. Snow typically persists for about 3 weeks after the last frost in subalpine environments (Brooke _et al_ 1970), thus average growing season in subalpine environments is about 93 days. The 93 to 121 day growing season is relatively long compared to that experienced by other marmot species. _M. olympus_ experiences a short growing season of 40 to 70 days, _M. flaviventris_ experiences an intermediate growing season of 70 to 100 days, and _M. monax_ in central Pennsylvania experiences a very long growing season of about 150 days (Barash 1974a). Barash's hypothesis would therefore predict that the social behaviour and social organization of _M. vancouverensis_ should be very similar to that of _M. flaviventris_. That is, Vancouver Island marmots should 1) be socially intolerant as indexed by having a very low greeting rate, 2) be moderately aggressive, 3) have individual territories or relatively distinct home ranges, and 4) grow quickly and disperse at an early age, probably as yearlings.

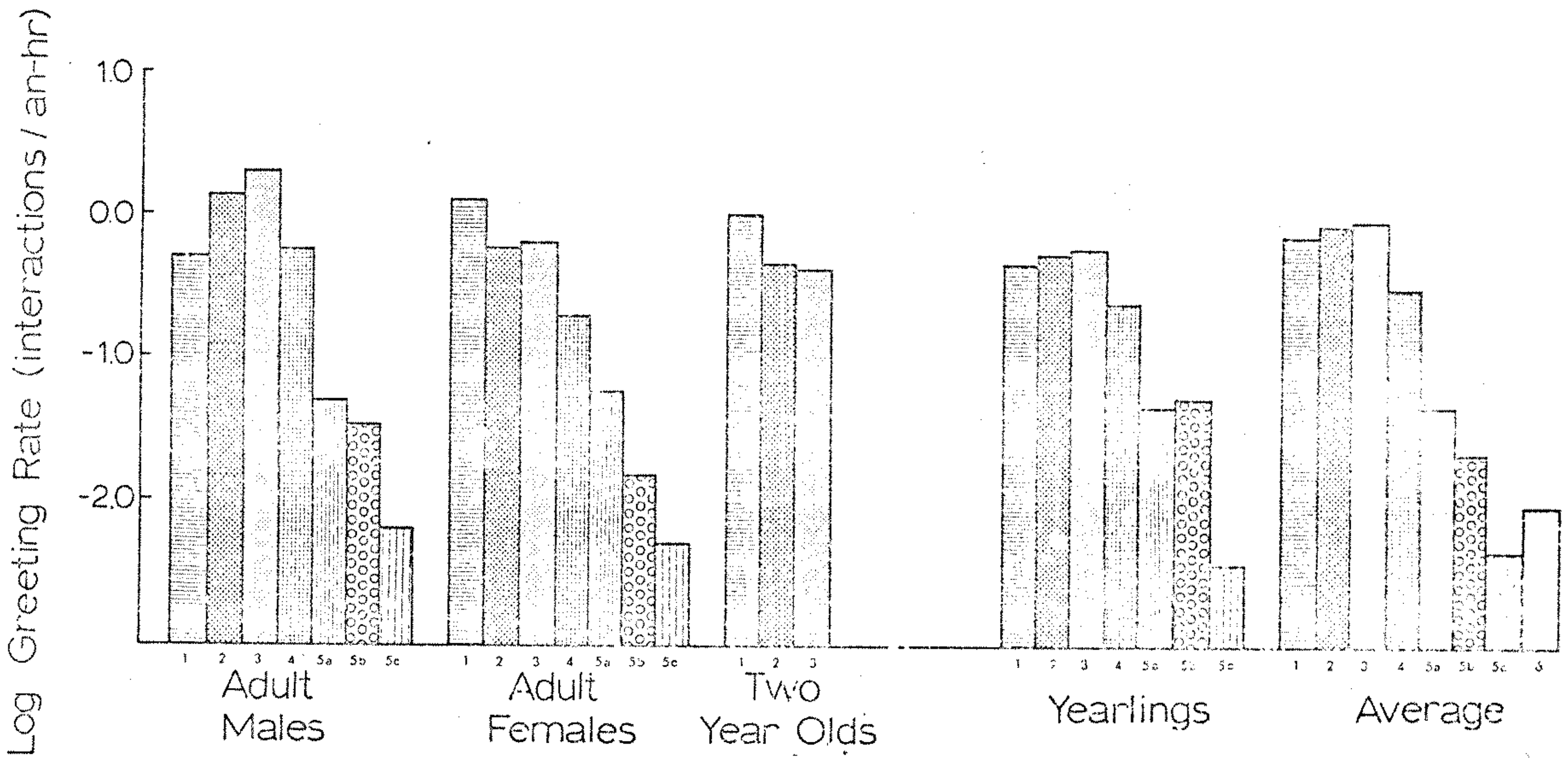
Individuals belonging to a highly integrated and stable social group would be likely to greet more often than individuals belonging to a less cohesive society because greeting presumably reinforces individual recognition and perhaps also functions as a method of scent sharing (King 1955; Barash 1973a, 1973b, 1974b; Steiner 1975). Individual recognition on the basis of scent has been demonstrated in many mammalian species (Halpin 1974, Shorey 1976). Scent sharing has been postulated for marmots, ground squirrels (_Spermophilus_ spp.), and prairie dogs (_Cynomys_ spp., Steiner 1975) and for mountain sheep (_Ovis_ spp., Geist 1971).

A comparison of Vancouver Island marmot greeting rates with those of other marmots reveals that Vancouver Island marmots are among the most social of all marmot species (Fig 26). The greeting rate of *M. vancouverensis* is much higher than all three estimates of the rate at which *M. flaviventris* greets. This result is inconsistent with the prediction based on Barash's hypothesis . The greeting rate of *M. marmota* (Barash 1976b, Tables II & IV) appears to be much higher than that of yellow-bellied marmots (Barash 1973a, Fig3); however, Barash (1976b) states that the greeting rates of *M. marmota* are significantly lower. Thus the rates of both greetings and chases in *M. marmota* are somewhat suspect, at least the way I am interpreting them.

The only behaviour pattern that Barash quantified was chasing (Barash 1973a, 1974b, 1976b) and he did not even present that data for *M. olympus* (Barash 1973b). I assumed the same chasing rate for *M. olympus* as *M. marmota* since Barash (1976b) states that the frequency of chasing did not differ significantly between these two species. Thus the only agonistic behaviour that I could compare among most marmot species was the chasing rate. Species with less social tolerance would likely participate in chases more frequently than socially tolerant species. Chasing rate varied less among marmot species than did greeting rates, with *M. vancouverensis* having a relatively low rate of chasing (Fig 27). However, the ratio of greetings to chases is probably the most meaningful

Figure 26. A comparison of greeting rates among marmot species

1 - *Marmota vancouverensis* (this study)
2 - *M. olympus* (Barash 1973b)
3 - *M. caligata* (Barash 1976b)
4 - *M. marmota* (Barash 1974b)
5a - *M. flaviventris* (Armitage 1974, 1976a)
5b - *M. flaviventris* (high elevation, Barash 1973a)
5c - *M. flaviventris* (medium elevation, Barash 1973a)
6 - *M. monax* (Bronson 1964)


Log Greeting Rate (interactions / an-hr)
1.0
0.0
-1.0
-2.0
1 2 3 4 5a 5b 5c
Adult Males
1 2 3 4 5a 5b 5c
Adult Females
1 2 3
Two Year Olds
1 2 3 4 5a 5b 5c
Yearlings
1 2 3 4 5a 5b 5c 6
Average

paramater to compare among marmot species. There are three reasons for this. First, socially intolerant species would be expected to have agonistic acts making up a higher proportion of their social interactions. Second, a comparison of the rate ratios should overcome the differences among authors in the methods used to calculate interaction rates. Third, a comparison of rate ratios is independent of any effects of colony size. When the rates of greeting to chases were compared, Vancouver Island marmots appeared to be the most social marmot species (Fig 28), a result quite out of line with Barash's hypothesis .

The third prediction of Barash's hypothesis is that Vancouver Island marmots should have individual territories or relatively distinct home ranges. This was clearly not the case. Vancouver Island marmots have completely overlapping home ranges within a colony or, in the case of colony one, within a section of a colony. Complete home range overlap among colony members was also found in _M. olympus_ (Barash 1973b) and _M. caligata_ (Barash 1974b). Yellow-bellied marmots are grouped into harems but may utilize individually distinct feeding areas (Armitage 1962, 1974), while woodchucks are essentially solitary (Bronson 1964).

The final prediction of Barash's hypothesis is that Vancouver Island marmots should grow and mature quickly, and disperse at an early age, presumably as yearlings. Growth was relatively slow, as yearlings of both sexes, two-year-old

Figure 27. A comparison of chasing rates among marmot species

1 - *Marmota vancouverensis* (this study)
2 - *M. olympus* (see text)
3 - *M. caligata* (Barash 1976b)
4 - *M. marmota* (Barash 1974b)
5a - *M. flaviventris* (Armitage 1974, Barash 1976a)
5b - *M. flaviventris* (high elevation, Barash 1973a)
5c - *M. flaviventris* (medium elevation, Barash 1973a)
6 - *M. monax* (Bronson 1964)

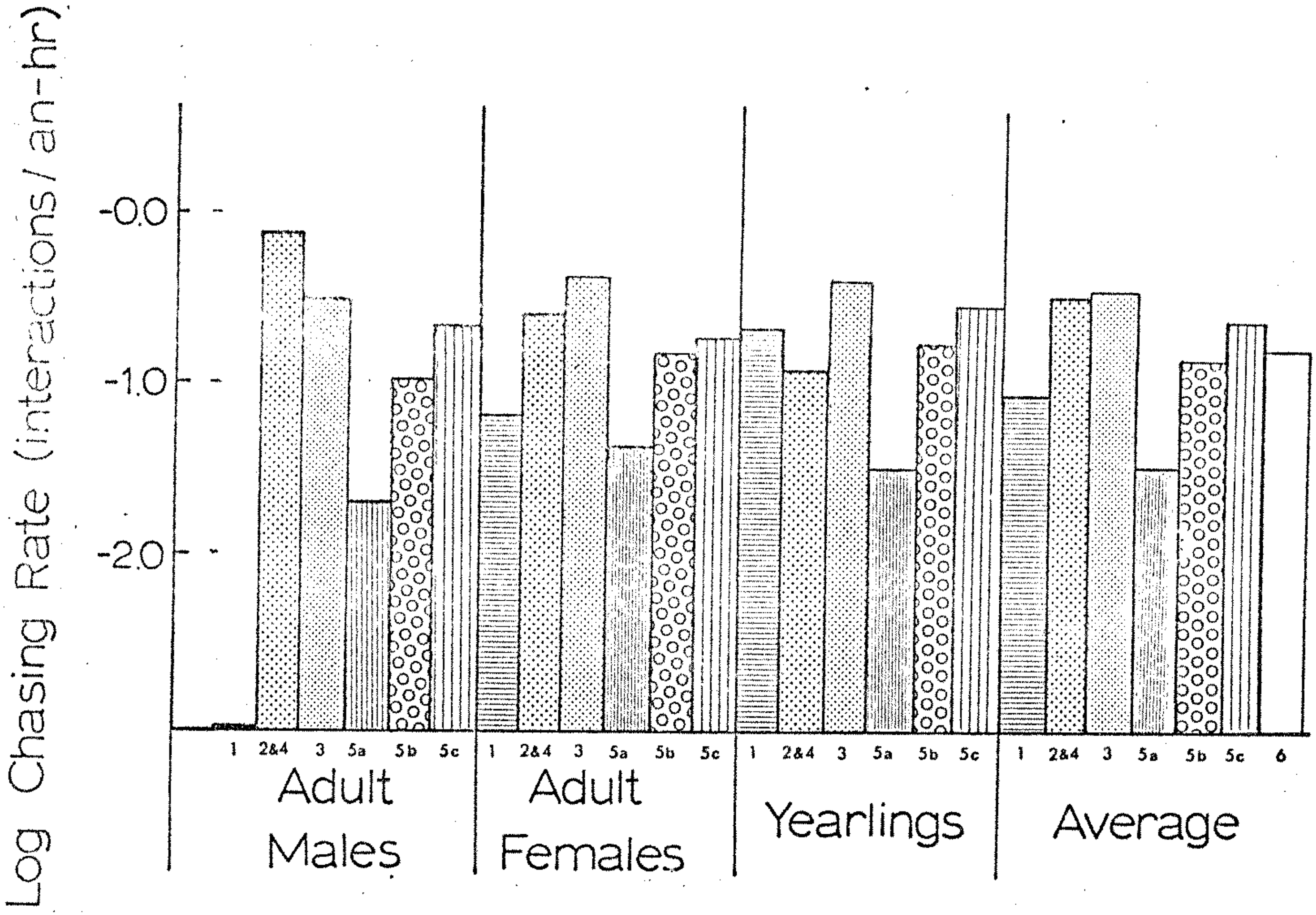
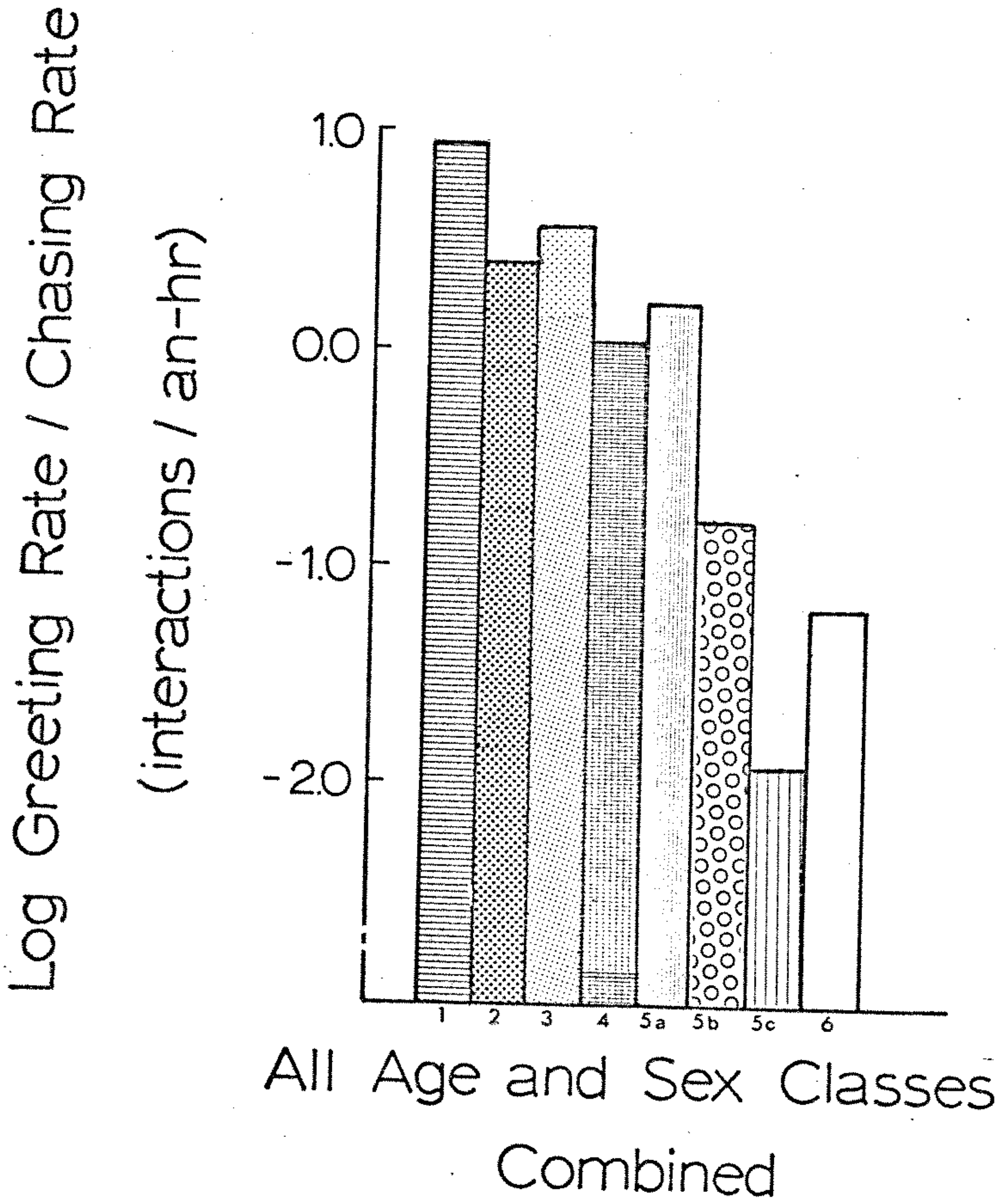

Log Chasing Rate (interactions / an-hr)
-0.0
-1.0
-2.0
1
2&4
3
5a
5b
5c
Adult Males
1
2&4
3
5a
5b
5c
Adult Females
1
2&4
3
5a
5b
5c
Yearlings
1
2&4
3
5a
5b
5c
6
Average

Figure 28. A comparison of the ratio of greetings to chases among marmot species

1 - *Marmota vancouverensis* (this study)
2 - *M. olympus* (Barash 1973b)
3 - *M. caligata* (Barash 1976b)
4 - *M. marmota* (Barash 1974b)
5a - *M. flaviventris* (Armitage 1974, 1976a)
5b - *M. flaviventris* (high elevation, Barash 1973a)
5c - *M. flaviventris* (medium elevation, Barash 1973a)
6 - *M. monax* (Bronson 1964)


Log Greeting Rate / Chasing Rate
(interactions / an-hr)
1.0
0.0
-1.0
-2.0
1
2
3
4
5a
5b
5c
6
All Age and Sex Classes
Combined

females, and perhaps also two-year-old males, were distinguishable from adults by weight (Fig 4). An index of growth rate can be obtained by comparing marmots after emergence from their first hibernation (yearlings) with the weight of adults at that time of year (Table XIII). Vancouver Island marmots grew slower than both _M_. _flaviventris_ and _M_. _monax_ (Table XIII).

Vancouver Island marmots appear to have delayed maturity equivalent to that of _M_. _olympus_. Two Vancouver Island marmots that I was sure had dispersed (males #4 and #17) were two years old or older, while neither of the two two-year-old females on my study areas produced litters. However, none of the adult females on colonies one or two had litters in 1974 either. If either my presence on the colony, my disturbance through trapping or the late spring in 1974 were responsible for the adult females not breeding then the same factors would be acting on both two-year-old and adult females. If any of these three reasons were responsible for adult females not breeding then I would have no basis for postulating that two-year-old females do not breed because they are immature. However, these three factors can be discounted: 1) Three females produced litters in 1973 when I observed but did not trap. Therefore my presence on the colony was not sufficient to inhibit breeding. 2) I trapped one adult female on the Ski Club colony (colony 5) in 1974 and she still produced a litter, thus trapping does not appear to be sufficient to inhibit breeding. 3) The persistence of snow late into the spring of 1974 was not sufficient to inhibit breeding

Table XIII. A comparison of the relative growth rates of yearling marmots

Species	Yearling/Adult Weight in the Spring (%)	Reference
M. caligata	18	Barash 1976a
M. vancouverensis	44	this study
M. olympus	30	Barash 1973b
M. flaviventris	50	J. Donaldson in prep
M. flaviventris	56	Armitage *et al* 1976
M. flaviventris[1]	75	Barash 1973a
M. flaviventris[2]	70	Barash 1973a
M. monax	65	Snyder *et al* 1961

[1] high elevation colony

[2] medium elevation colony

since breeding occurred on other colonies (e.g. Ski Club and Buttler Peak) even though the snow conditions were very similar in all areas. The most likely explanation for the failure of adult females on colonies one and two to breed in 1974, is that Vancouver Island marmot females may only breed in alternate years, a reproductive strategy similar to M. olympus. Biennial breeding could account for the absence of litters in 1974 because three litters had been born the previous year. Since marmots were not tagged in 1973, I cannot be sure that all three that produced litters in 1973 were the same ones present in 1974 but one distinctively marked individual was present in both years.

None of the four predictions of Barash's hypothesis were consistent with the observed data on M. vancouverensis. Vancouver Island marmots in all instances most closely resembled M. olympus, the species with the shortest growing season. Inconsistent results such as these lead one to either try to construct a new hypothesis, having rejected the old one, or to modify one or more of the assumptions of the existing one. The most obvious assumption to reject is, that vegetative growing season is a useful parameter for indicating the degree of social tolerance a marmot species should exhibit. The fundamental question that Barash was trying to answer when considering growing season was why some marmot species take longer than others to reach adult size. He found that among M. flaviventris, M. monax, and M. olympus the length of the growing season correlated with the length of time marmots took to mature. However, the results of this study and those of Anderson et al (1974) are inconsistent with this trend. Vancouver Island marmots do not appear to mature (breed) until their fourth summer with a 93-121 day growing season while yellow-bellied marmots mature one year earlier when the growing season is only 60-100 days (Barash 1974a, Anderson et al 1974). Thus when more data are considered, vegetative growing season does not appear to be a meaningful parameter affecting how quickly marmots reach maturity. Anderson et al (1974) suggest that the length of time that marmots grow throughout the summer (the marmot growing season), would be a more appropriate measure of environmental severity. However, the length of the marmot growing season does not correlate any better with the time taken to reach maturity than does the vegetative growing season. Olympic marmots gain weight for up to 120 days (Barash 1973b) while yellow-bellied marmots at high elevations grow for only 96 days (Anderson et al 1974) and mature one year earlier. Neither the marmot growing season nor the vegetative growing season are correlated with the age of maturity because the time taken to reach adult size is determined by the combination of three independent factors; 1) the rate that marmots put on weight in terms of grams per day, 2) the number of days that marmots continue to gain weight (the marmot growing season), and 3) the absolute weight of an adult marmot of the species being considered. These three factors varied among species but I could not determine any consistent unifying trends among them.

The most obvious way to determine how long it takes a marmot to reach adult size is to measure the growth rate directly. There is a significant negative correlation between the logarithm of the greeting rate and the weight of immature marmots 1) at the end of their second summer, expressed as a percent of the fall weight of an adult (r=0.86, n=6, p=0.03) and 2) the logarithm of the weight of yearlings after spring emergence from their first hibernation relative to the weight of adults at that time of year (r=0.95, n=7, p=0.001, and Table XIII). Thus, by measuring the growth rate directly rather than estimating it from the length of the vegetative growing season, relative social tolerance can be predicted for all marmot species.

The reason that Vancouver Island marmots take a long time to mature is not that they grow slowly in terms of grams per day or because they only gain weight for a short period each summer, for they are intermediate among marmot species with respect to both of these parameters. Vancouver Island marmots take a long time to mature because they have a relatively large adult body size. A large body size may be selected for because it increases the chance of successful dispersal. Vancouver Island marmots live in islands of subalpine habitat and the probability of successful dispersal to new habitats is probably low. However, the probability of successful dispersal probably increases with body size. This would occur if larger animals could travel further and faster, and survive for a longer period of time without food and shelter than could smaller animals. If aggression from adults causes dispersal (Barash 1974a), then social tolerance must increase along with any increase in the optimum body size of emigrants, so that undersized animals are not forced to disperse.

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Mammals of Washington

Appendix I. A List of Plant Species Found on the Haley Lake Study Area Indicating Those Species Known to be Eaten by Vancouver Island Marmots

Family and Scientific Name	Common Name	Plants Eaten
Selaginellaceae		
Selaginella wallacei	selaginella	
Polypodiaceae		
Adiantum pedatum	maidenhair fern	
Cryptogramma crispa	parsley fern	
Polystichum munitum	sword fern	
Pteridium aquilinum	bracken fern	fronds[0]
Cupressaceae		
Chamaecyparis nootkatensis	yellow cedar	bark[0]
Juniperis communis	dwarf juniper	
Pinaceae		
Abies amabilis	amabilis fir	
Abies lasiocarpa	alpine fir	
Pinus contorta	lodgepole pine	
Pinus monticola	western white pine	
Tsuga heterophylla	western hemlock	
Tsuga mertensiana	mountain hemlock	
Pseudotsuga menziesii	Douglas fir	
Betulaceae		
Alnus sinuata	Sitka alder	
Aristolochiaceae		
Asarum caudatum	wild ginger	
Portulacaceae		
Claytonia lanceolata	western springbeauty	
Caryophylaceae		
Arenaria macrophylla	bigleaf sandwort	
Silene menziesii	catchfly	
Ranunculaceae		
Actaea rubra	baneberry	
Aquilegia formosa	columbine	lvs[1], flws[2]
Delphinium sp.	larkspur	
Thalictrum occidentale	meadow rue	lvs, flws, fr[3]

Scrophulariaceae		
Castilleja miniata	Indian painthrush	ns*, flws*
Castilleja parviflora	Indian paintbrush	ns, flws
Mimulus guttatus	yellow monkey flower	
Pedicularis bracteosa	lousewort	
Penstemon davidsonii	penstemon	
Veronica wormskjoldii	speedwell	
Rubiaceae		
Galium boreale	northern bedstraw	
Caprifoliaceae		
Sambucus racemosa	red elderberry	bark
Valerianaceae		
Valeriana sitchensis	mountain valerian	lvs
Campanulaceae		
Campanula rotundifolia	bluebell	flws
Compositae		
Achillea millefolium	yarrow	
Agoseris aurantiaca	agoseris	
Anaphalis margaritacea	pearly everlasting	
Arnica latifolia	broad-leaf arnica	
Cirsium edule	Indian thistle	lvs°
Erigeron peregrinus	mountain daisy	
Eriophyllum lanatum	woolly sunflower	lvs°
Senicio triangularis	giant ragwort	
Taraxacum officinale	common dandelion	
Juncaceae		
Juncus drummondii	rush	
Cyperaceae		
Carex mertensii	sedge	
Carex nigricans	sedge	
Carex spectabilis	sedge	
Carex spp.	sedge	leaf tips, ns
Graminae		lvs, ns,
Agrostis diegoensis	bentgrass	
Bromus sitchensis	brome grass	
Elymus glaucus	blue wild-rye	
Melica subulata	Alaska oniongrass	
Phleum alpinum	mountain timothy	
Trisetum spicatum	spike trisetum	
Lilaceae		
Alium crenulatum	wild onion	
Erithronium grandiflorum	avalanche lily	lvs, ns, flws
Lilium columbianum	tiger lily	lvs, flws*
Smilacina racemosa	false Solomon's seal	
Stenanthium occidentale	western stenanthium	
Trillium ovatum	western trillium	
Veratrum viride	false hellebore	lvs

Orchidaceae		
Habenaria sp.	bog orchid	
Lichens		
Cladonia sp.		
Peltigera apthosa		
Solorina crocea		
Stereocaulon sp.		
Thanolia sp.		
Umbilicaria sp.	rock tripe	thalli

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[1] leaves
[2] flowers
[3] fruit
[4] new shoots
* preferred food
° rarely eaten