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THE UNIVERSITY OF ALBERTA

BEHAVIOR OF THE PIKA (OCHOTONA PRINCEPS) IN THE KANANASKIS REGION OF ALBERTA

by

Peggy Lynn Sharp

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING, 1973

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Behavior of the Pika (*Ochotona princeps*) in the Kananaskis Region of Alberta submitted by Peggy Lynn Sharp in partial fulfilment of the requirements for the degree of Master of Science.

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Date November 21, 1972.

ABSTRACT

The behavior of the pika (Ochotona princeps) was studied in spring and summer of 1969 and 1970 in the Kananaskis region of Alberta. Pikas were individually marked with ear tags. General activity, individual oriented behavior (including comfort and maintenance behavior and food getting behavior), and territorial and social behavior (including spatial and temporal use of home range, vocalization, agonistic and related behavior, reproductive and maternal behavior, and scent marking) were studied. Particular emphasis was placed on territorial and social behavior.

In summer, pikas avoided the hottest weather, and in early spring, they avoided the coldest weather.

Pikas reingest cecal feces as they issue from the cloaca. This was observed on the surface of the rockslide and visible reingestion rates declined from spring to summer, as vegetation quality and quantity increased. Pelage maintenance acts increased gradually through the summer and possible causes for this increase are discussed. Sitting activity occupied between 40 and 60 percent of the time pikas were seen. They groomed themselves, called, and interacted vocally while sitting. Feeding activity occupied between 20 and 30 percent of the time pikas were seen in spring and early summer, decreasing in ♂♂ in July and in ♀♀ and juveniles in August with the onset of haying activity, because pikas fed while haying. Haying occupied between 15 and 35 percent of the time pikas were seen in late summer. The significance of haypiles is discussed.

Pikas lived in a paired arrangement. In the breeding season (April, May, and June), pair members' core areas overlapped extensively and the majority of interactions occurred within pikas' core areas between ♂♂. In spring, few agonistic interactions were seen, and the pikas were least vocal. However, long calls were heard most frequently at that time. The possible scent marking acts of cheek rubbing, urination, and defecation occurred mainly outside of pikas' core areas unless juveniles were present.

In July, ♂♂ had haypile oriented core areas and little overlap with their ♀♀. Agonistic interactions increased, occurring mainly outside of core areas. The majority of interactions were ♂-♀ and adult-juvenile ones. In August, ♀♀ and established juveniles had distinct haypile oriented core areas and no overlap of core areas with their "mates." Pikas were most vocal in August and the highest number of agonistic interactions were seen, mainly ♂-♀ and adult-juvenile ones, occurring mainly outside core areas. Agonistic interactions and vocality were highest when several juveniles were present and attempting to pair with single individuals.

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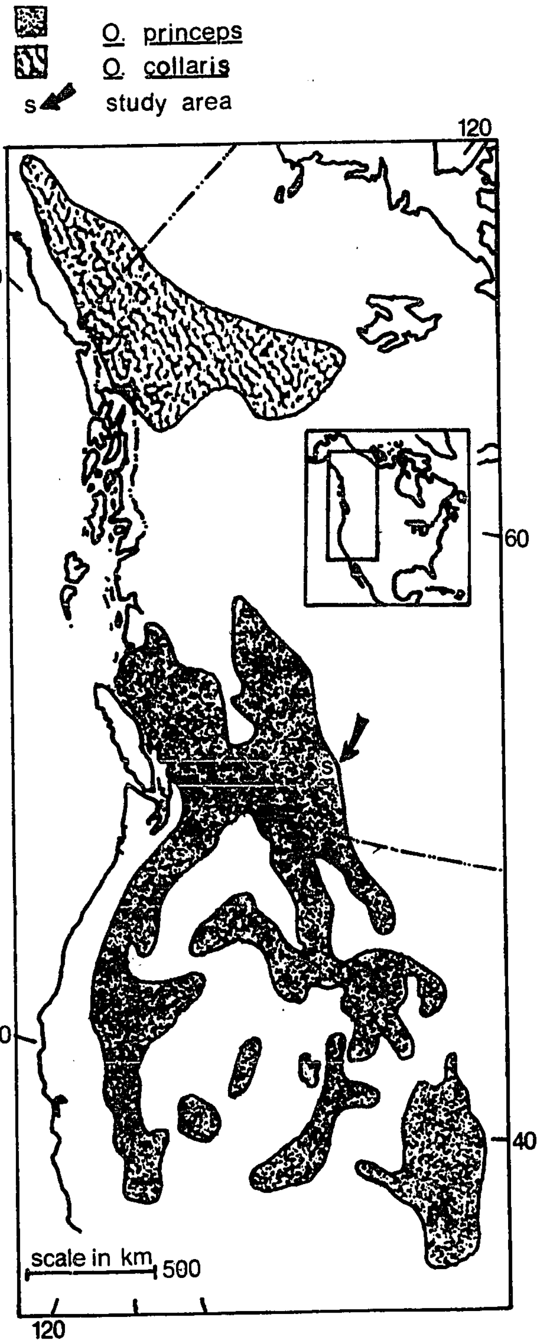
INTRODUCTION

Pikas (Family Ochotonidae) are mainly diurnal, small (approximately 120 g), sedentary, vocal mammals, known for their habit of caching vegetation in haypiles. Of the 14 recognized species of pika (Ellerman and Morrison-Scott 1951), only two are found in North America, occurring in discrete populations on talus slopes. The species studied, *Ochotona princeps*, ranges through British Columbia and western Alberta south to New Mexico, Arizona, Colorado, and California (Figure 1).

There have been few ethological studies of *O. princeps*. Severaid (1956) and Krear (1965) studied ecology, natural history, and ethology of *O. princeps*. Three asian species, the Himalayan pika (*O. roylei*, Kawamichi 1968, 1971a), the Japanese pika (*O. hyperborea yesoensis*, Kawamichi 1969, 1970), and the big eared pika (*O. macrotis*, Kawamichi 1971a) have been studied.

Descriptions of calls, home range overlap, and scent marking in *O. princeps* are incomplete. Krear (1965) describes six calls, Severaid (1956) seven or eight, Broadbooks (1965) three. Krear (1965) concluded that although each pika had its own fairly discrete home range, ♀♀ moved in with ♂♂ during the breeding season. Although Severaid (1956) did not observe one area for very long, he felt that pikas lived in family groups, composed of at least ♀ and young, later in summer. Kawamichi (1970) has shown that the Japanese pika generally lives in pairs.

Figure 1. Distribution of *Ochotona princeps* and *O. collaris* (from Hall and Kelson 1959, page 248.)



Although Severaid (1956), Krear (1965), Broadbooks (1965), and Kawamichi (1968, 1969, 1970, 1971a, b) mention seeing numerous fecal piles on talus inhabited by pikas, there is little discussion of this as possible scent marking. Harvey and Rosenberg (1960) describe a complex apocrine gland in the cheek of O. princeps, and Severaid (1956), Kilham (1958), Broadbooks (1965), and Krear (1965) noticed that pikas rubbed their cheeks on rocks, but could only speculate on the function of this act.

The purpose of my study was a qualitative and, where applicable, quantitative description of the behavior of the pika, with emphasis on social behavior and utilization of time and space. This study was conducted in the Kananaskis area, in the front range of the Rocky Mountains east of Banff National Park, Alberta. Field work was done during the spring and summer of 1969 and 1970.

1. DESCRIPTION OF STUDY AREAS

Observation was mainly done on two rockslides, the Kananaskis and Jumping Pound study areas. They are located at approximately 115°N, 51°W (Figure 1).

The Kananaskis study area (Figure 2) is located 24 km southwest of the University of Calgary Environmental Sciences Centre, bordered to the west by the Forestry Trunk Road and the Kananaskis River. The slope is west-facing and lies at an elevation of 1500 m. The rockslide measured 70 m by 30 m, with a vertical rise of 15-20 m. Pikas on this area were observed during May-August 1969 and April-May 1970.

This rockslide was generally surrounded by young spruce (*Picea* sp.), lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), and some willow (*Salix* sp.). Lower strata vegetation consisted of bear berry (*Arctostaphylos uva-ursi*), daisy fleabane (*Erigeron compositus*), grasses, stinging nettle (*Urtica gracilis*), gooseberry (*Ribes oxyacanthoides*), shrubby cinquefoil (*Potentilla fruticosa*), beard tongue (*Pentstemon* sp.), northern bedstraw (*Galium boreale*), and *Arnica* sp. The lower strata vegetation grew in open areas bordering and within the rockslide. Soil in the area is relatively dry and quite rocky.

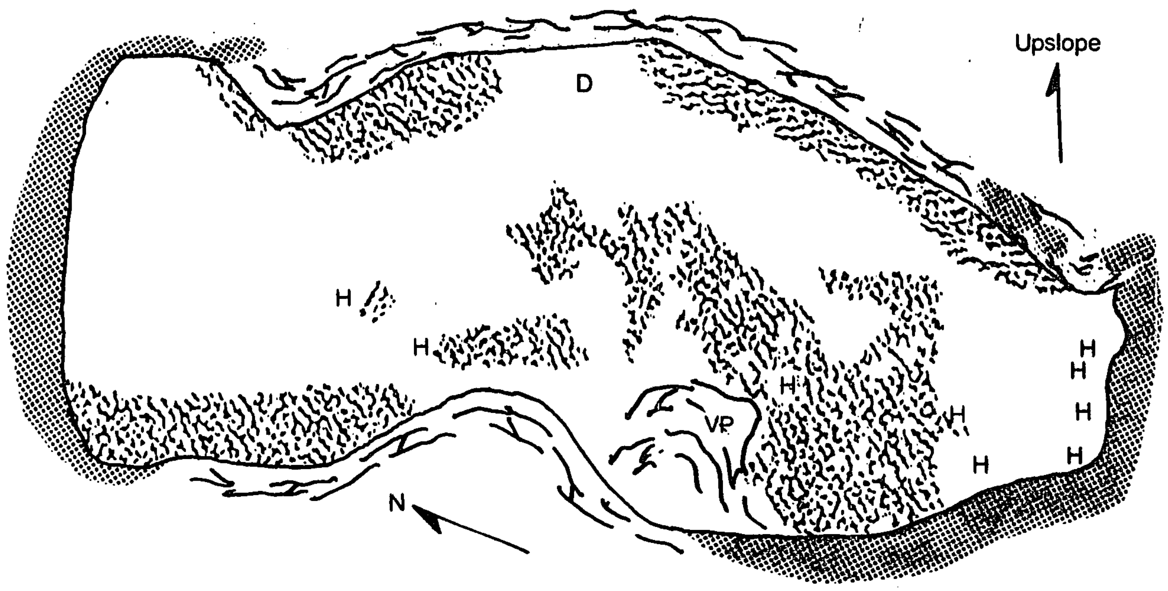
Other mammals resident or frequently seen travelling on this rockslide were wood rats (*Neotoma cinereus*), golden-mantled ground squirrels (*Spermophilus lateralis*),

Figure 2. Map of the Kananaskis study area

Scale : ⊢—⊣ 5 meters

VP	Observation point
H	Haypile
D	Deserted haypile
(white area)	Talus

▨	Vegetation and rocks within rockslide
▒	Vegetation bordering rockslide
⌶	Cliffs or sparsely vegetated rock outcrop
—	Edge of rockslide



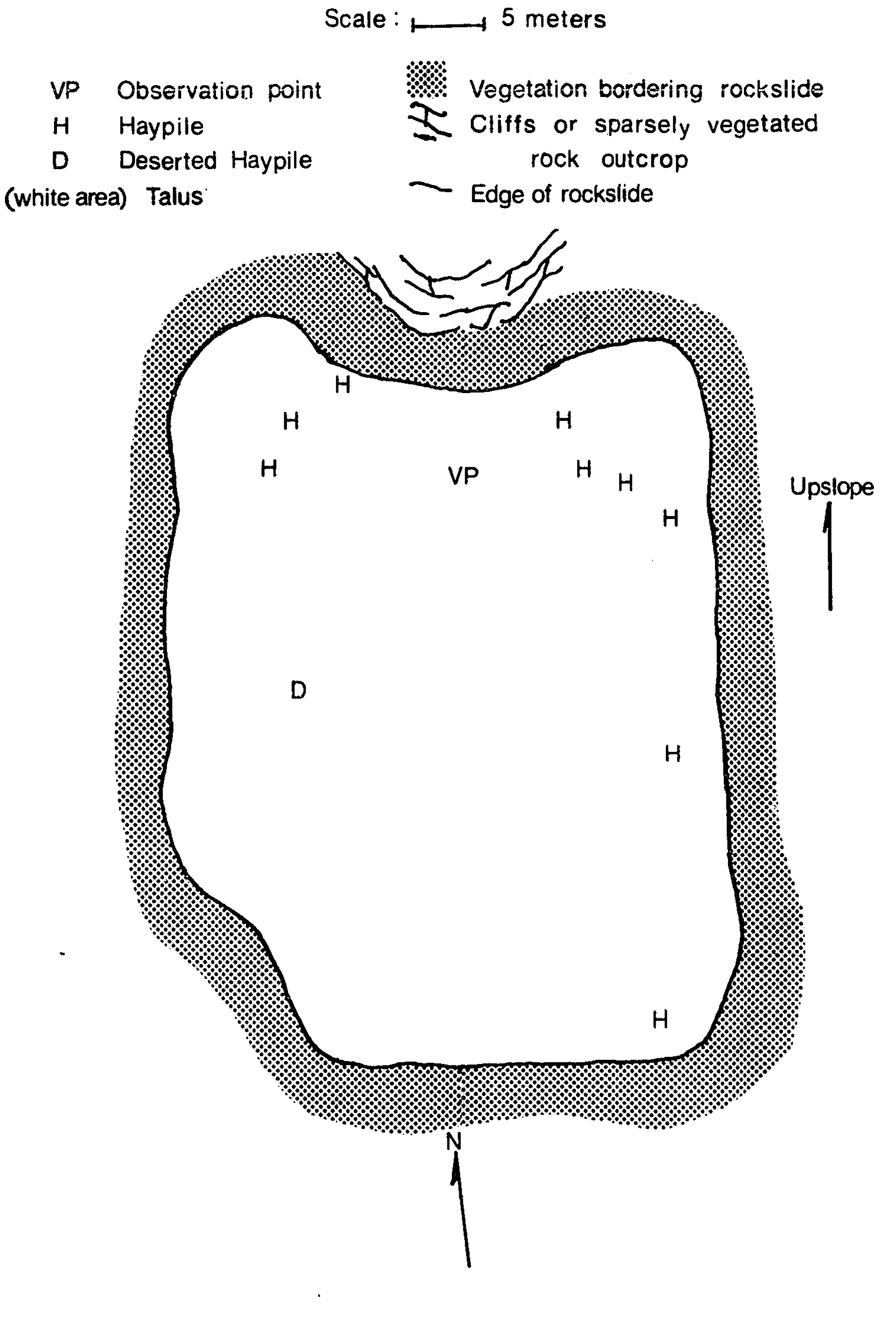
chipmunks (Eutamias sp.), and red squirrels (Tamiasciurus hudsonicus).

In 1969, one adult ♀ and two adult ♂ pikas were resident, and a ♂ offspring of the ♀ was present from July 8-August 4. An adult ♀ lived in a small patch of talus nearby; she was rarely seen but was visited regularly by one of the adult ♂♂. In October 1969 one adult ♂ disappeared; the other ♂ disappeared on May 11, 1970, and a marked ♂ from a nearby rockslide appeared on the study area May 15.

The Jumping Pound study area (Figure 3) lies by the Jumping Pound road, 6.8 km east of the Forestry Trunk road. The Jumping Pound road originates 1.6 km north of the Environmental Sciences Centre. The rockslide is exposed to the south at an elevation of 1500 m, and measures 45 m by 55 m, with a vertical rise of 25-30 m. A small patch of talus measuring 10 m by 25 m is located 10 m east of the main rockslide. Pikas were observed on this area in July-August 1969 and June-September 1970.

A forest of mature spruce, lodgepole pine, aspen, and balsam poplar (Populus balsamifera) borders this rockslide. The forest bordering the eastern and upper edge of the talus is more open than that of the Kananaskis study area, with an understory of bear berry, wild sweet pea (Lathyrus ochroleucus), wild licorice (Glycyrrhiza lepidota), wild vetch (Vicia americana), rose (Rosa sp.), gooseberry, grasses, false solomon's seal (Smilacina racemosa var. amplexicaulis), twisted stalk (Streptopus amplexifolius), wild white

Figure 3. Map of the Jumping Pound study area



geranium (Geranium richardsonii), northern bedstraw, fireweed (Epilobium angustifolium), Equisetum sp., stinging nettle, raspberry (Rubus strigosus), one-flowered wintergreen (Moneses uniflora), and paintbrush (Castilleja miniata).

The rockslide is in the bottom of a narrow valley and is wetter than the Kananaskis area; the bases of all low rockslides in the Jumping Pound flooded during spring runoff in 1969 and 1970.

Other mammals resident or frequently seen were wood rats, chipmunks, and red squirrels.

The 1969 population consisted of three adult ♂♂ and one adult ♀, and her offspring (one ♂, one ♀). The adult ♀ disappeared in mid-July and was replaced by her ♀ offspring. The juvenile ♂ disappeared soon after.

The three ♂♂ and the juvenile ♀ overwintered and this ♀ (then 11 months old) produced two ♂ offspring in early June, 1970. These young disappeared in late June and early July. A juvenile ♀ was introduced onto the rockslide in early August, and on August 4 the second litter of the yearling ♀ appeared, one ♂ and one ♀. The three adult ♂♂, the yearling ♀ and her offspring, and the introduced juvenile ♀ were all present at the termination of intensive observations on September 6, 1970. Table 1 shows the inhabitants of the two rockslides during this study. In all cases, number codes are used for individuals from the Jumping Pound study area (i.e. ♂1) and letter codes are used for individuals from the Kananaskis study area (i.e. ♀TE).

Table 1. Inhabitants of the study areas, 1969-70.

Kananaskis study area	May 1969	June 1969	July 1969	August 1969	April-May 1970
Adults	♂RR	♂RR	♂RR	♂RR	♂RR
	♂WR	♂WR	♂WR	♂WR	♂GR
	♀TE	♀TE	♀TE	♀TE	♀TE
Juveniles			♂LK		

Jumping Pound study area	June 1970	July 1970	August 1970	July-August 1969
Adults	♂1	♂1	♂1	♂1
	♂2	♂2	♂2	♂2
	♂3	♂3	♂3	♂3
	♀5	♀5	♀5	♀4
Juveniles	♂10		♂12	♀5
	♂11		♀13	♂6
			♀14	

2. METHODS

Most pikas on both study areas were trapped and individually marked with colored ear tags. Pikas were trapped with two sizes of Sherman traps (13 X 13 X 38 cm and 10 X 10 X 35 cm), placed about 3 m from a haypile, next to a rock that a pika frequently sat on, or near a fecal pile. Traps were prebaited for three days with a combination of willow leaves, vetch, and grasses. Trapping was done on an area until all individuals were tagged and when new juveniles appeared.

Until July 1969, trapping was done throughout the daylight hours; then, due to two deaths on other areas on hot afternoons, traps were run only in the early morning and late afternoon. Traps were checked every two to three hours and prebaited through the afternoon and overnight. In 1970, traps were run from 1700-1800 hours until 0900-1000 hours, as no trap deaths occurred overnight. Traps were checked at dusk, dawn, and 0900 or 1000, then prebaited for the day. The only other species caught in any numbers were wood rats.

Captured pikas were shaken into a bag drawn over the opened trap. The bag was then partially closed with a drawstring and sex determination and tagging done through the small opening. Sex was determined by manipulating the cloaca and distinguishing between a relatively long, thin penis in ♂♂ or a broader, flatter clitoris with a groove down the center in ♀♀. It is difficult to determine sex in young juveniles as their genitalia are not well developed.

Pikas were tagged with round colored plastic tags affixed through the ear cartilage by a numbered fingerling tag. Five colors of plastic were used. Tagging was done on the right ear in ♂♂ and the left ear in ♀♀. After two weeks of observation, individuals could be recognized by their coat patterns and calls as well.

Observation was conducted from one or two vantage points that gave as complete a view of the rockslide as was possible. No location on either rockslide gave an unobstructed view of the entire area and surrounding vegetation. Thus, some home ranges were more visible than others. Both study areas were marked with grid stakes at 10 m intervals.

Total observation time on these rockslides was approximately 450 hours. Observations were made with the unaided eye and through 10 X 40 binoculars. Data consisting of time of day (Mountain Standard Time), to the second whenever possible (for later derivation of duration of activities), individual pika, its activity and location (to a 5m by 5m area or specific location) were recorded on a portable tape recorder and later transcribed onto data sheets. Calls of pikas and activities of other species in the area were also recorded.

General weather conditions were recorded. Some aspects of behavior were documented photographically with a Konica

Super 8-6TL movie camera with telephoto zoom lens, and an Asahi Pentax 35 mm camera with normal and telephoto lenses.

By midsummer 1970, I had observed four ♂ juveniles on two rockslides, and one ♀, and all these ♂♂ disappeared about one month after weaning. I was curious to see whether (1) there was room for another ♀ on the Jumping Pound study area, and (2) ♀ juveniles were behaviorally different from ♂ juveniles. In early August 1970, a juvenile ♀ was introduced onto this rockslide.

Since observations were made on study areas with known individuals over two summers, some aspects of behavior could be analyzed quantitatively. For example, how frequently did an individual call? Did this frequency vary according to the sex and age of the pika, the time of day, weather, or the time of year? To permit the above analysis, detailed tally sheets were used. The number of times that each specific act or pattern was performed by one individual in a specific 5 m by 5 m area or at a specific location during each hour of the day (i.e. all short calls given by one pika while sitting on its haypile between 0900:00-0959:59 hours) was tallied, for each observation day. These tallies were then pooled into approximately one month time periods. These time periods were:

Kananaskis study area		Jumping Pound study area	
1969		1970	
	May 17-30		
	June 1-July 1		June 2-July 6
	July 2-August 4		July 7-August 2
	August 5-18		August 3-September 6
1970	April 22-May 21	1969	July 15-August 26

These time periods in spring differed because of the date of my arrival in the field and the accessibility of the study areas. Variation in later time periods are due to the timing of appearance of juveniles, as comparison of times when juveniles were not present on an area with times when they were present was desirable. The period of July 15-August 26, 1969 includes only three observation days in July; and in later sections is considered an August time period.

Analysis of data was done with the aid of desk calculators and an IBM 360 computer using APL. Programs used for sorting each individual's activities in each time period are presented in Appendix 1. Statistical methods were taken from Sokal and Rohlf (1969) and Steele and Torrie (1960). In all statistical tests $p \leq .05$ was considered significant.

I have divided the behavioral repertoire of the pika into two basic categories -- individual oriented behavior, including comfort and maintenance and food-getting behavior, and territorial and social behavior and structure, including vocalization, spatial and temporal use of home range, agonistic and related behavior, scent marking, and reproductive behavior. Some of these activities are not necessarily exclusive of others and may be discussed under either of the two basic categories.

3. GENERAL ACTIVITY

Severaid (1956), Krear (1965), and Kawamichi (1969) agree that although pikas can be seen or heard almost any time of day in spring and summer, they are most active in early morning and late afternoon. Haga (1960, p. 201) observed "During the summer months pikas show a preference for cool parts of the habitat." Dice (1927) and Kawamichi (1968) also mention this reaction to environmental conditions.

Severaid (1956), Krear (1965), and Kawamichi (1969) also observed that onset and termination of activity periods varied with day length. Krear (1965) and Kawamichi (1969) report that activity is decreased during high winds or stormy weather.

In late summer 1969, I noticed on clear mornings that activity levels decreased rapidly as direct sunlight reached the rockslides and did not begin again until the area was shaded or the sun low. Conversely, on cool or partly cloudy or overcast days, pikas seemed to be active throughout the day. Because this apparent variation in activity with weather was not recognized until late summer 1969, the weather records I made in 1969 were incomplete. More complete descriptions of weather conditions were taken in 1970 and the data are analyzed and presented below.

Data on the activity of pikas was classified as occurring during one of two general weather types: (1) clear or partly cloudy and hot at midday, or (2) partly cloudy or overcast, calm, and cool. The two study areas were treated separately and analysis was done separately for each individual, hour of day, and time period. The amount of time each pika was seen, expressed as a percentage of time spent observing for each hour of the day, was calculated and used as an index of observable activity. Data for all individuals on a study area during a particular time period in each weather condition were later averaged to give a mean percentage of time seen.

Individual activity percentages were transformed to arcsine angle (Sokal and Rohlf 1969, p. 380), and a three-way analysis of variance (anova) (Appendices 2 and 3) was run, comparing activity indices between and within individuals, time of day, and weather conditions.

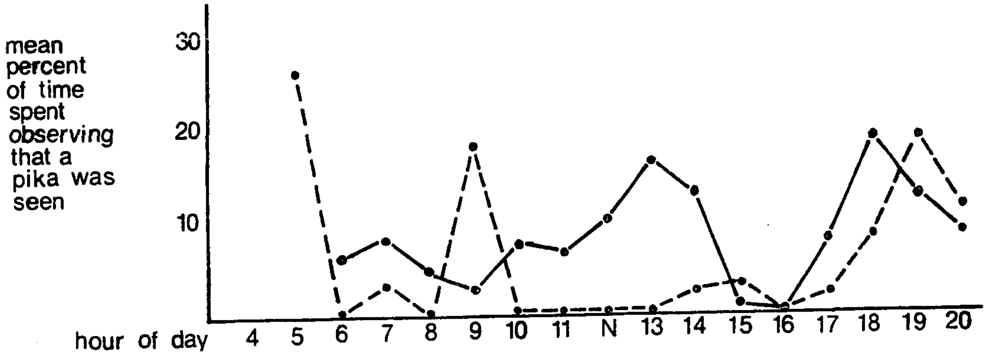
Figures 4 and 5 show the percent of observation time that a pika was seen (expressed as the weighted average of all individuals present) in each weather type during a one month time period. The anova on the activity levels from the Kananaskis study area, April 22-May 21, 1970 (Figure 4a) shows a significant difference in activity with time of day, and a significant interaction effect on activity of weather and time of day. It can be seen from Figure 4a that activity was higher at midday during clear or partly cloudy and warm weather.

Activity levels on the Jumping Pound study area during June 1-July 6, 1970 (Figure 4b) varied significantly with time of day, weather conditions, and showed a significant interaction effect on activity between time of day and

Figure 4. Pika activity indices during (a.) April-May and (b.) June, 1970, under two general types of weather.

a. Kananaskis study area, April 22-May 21, 1970

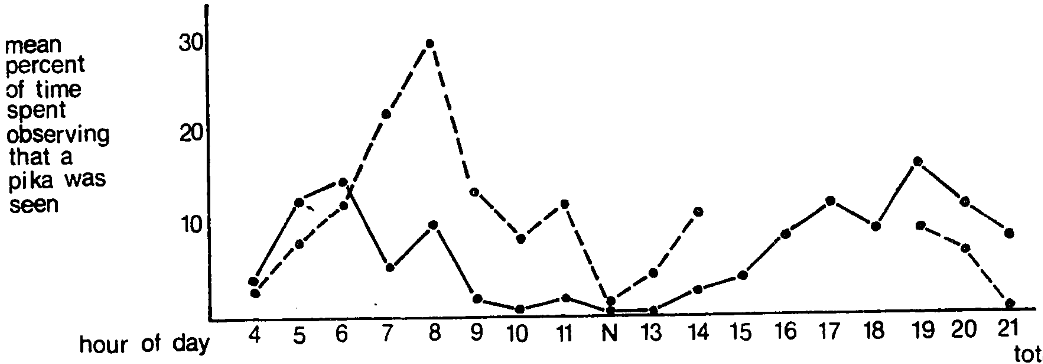
1 adult ♂, 1 adult ♀ present



time spent observing (min.)	4	5	6	7	8	9	10	11	N	13	14	15	16	17	18	19	20	total hours observation
————			60	105	145	175	257	300	230	180	180	195	197	70	80	101	67	39
– – – –		30	60	60	60	30	30	60	60	75	108	105	90	30	10	60	40	15

b. Jumping Pound study area, June 1 - July 6, 1970

3 adult ♂♂, 1 adult ♀, 2 juvenile ♂♂ present

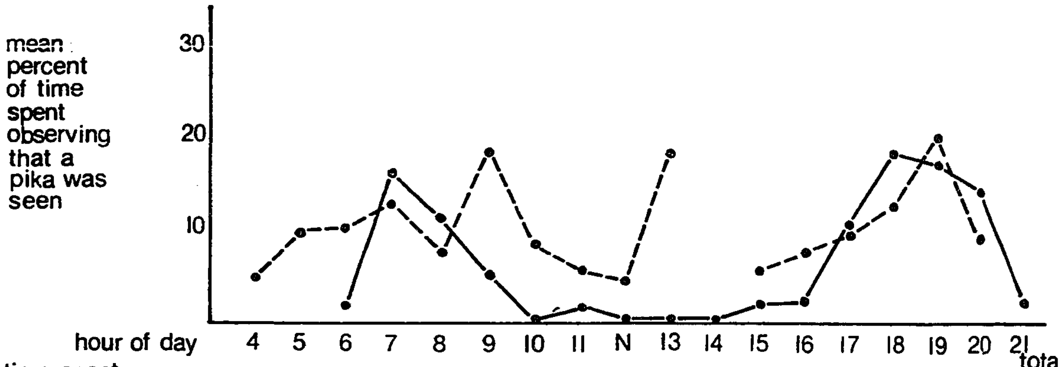


time spent observing (min.)	4	5	6	7	8	9	10	11	N	13	14	15	16	17	18	19	20	21	total hours observation
————	10	110	120	109	15	75	120	40	60	45	11	113	105	135	35	123	150	28	24
– – – –	25	60	60	30	15	60	60	55	38	121	60					70	75	65	13

weather types
———— clear to partly cloudy, warm to hot weather
– – – – partly cloudy to overcast, cool to cold weather

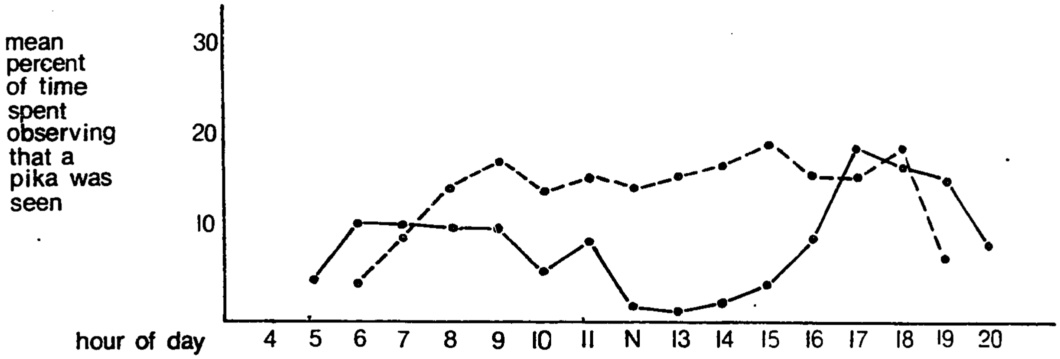
Figure 5 Pika activity indices during (a.) July and (b.) August, 1970, under two general types of weather.

a. Jumping Pound study area, July 7 – August 2, 1970
3 adult ♂♂, 1 adult ♀ present



time spent observing (min.)	4	5	6	7	8	9	10	11	N	13	14	15	16	17	18	19	20	21	total hours observation
———			30	165	77	165	75	60	60	60	60	120	120	157	195	196	175	30	29
– – – –	30	124	155	110	122	150	155	147	120	75		18	100	130	102	116	75		29

b. Jumping Pound study area, August 3 – September 6, 1970
3 adult ♂♂, 1 adult ♀, 1 juvenile ♂, 2 juvenile ♀♀ present



time spent observing (min.)	4	5	6	7	8	9	10	11	N	13	14	15	16	17	18	19	20	total hours observation
———		155	130	107	180	201	160	79	75	145	240	220	124	127	164	347	244	47
– – – –			25	32	60	60	101	155	90	57	60	60	55	115	75	35		16

weather types
——— clear to partly cloudy, warm to hot weather
– – – – partly cloudy to overcast, cool to cold weather

weather conditions. Activity levels in cool and cloudy weather were generally higher than those in clear and hot weather throughout the day, particularly in late morning.

During July 7-August 2, 1970 (Figure 5a), the pikas show two activity patterns according to weather conditions. On clear, warm days, the pikas displayed distinct morning and evening activity peaks; while on cool, cloudy days, their activity was more variable and higher at midday. Anova shows activity at different times of day, under different weather conditions, and an interaction effect on activity between time of day and weather conditions as significantly different. During August 3-September 6, 1970 (Figure 5b), the pikas again displayed two fairly distinct peaks in activity in early morning and evening on clear, warm days. On cool cloudy days, their activity was greater from midmorning to late afternoon. Again, anova shows that activity levels differ significantly according to time of day and weather conditions; there is also a significant interaction effect on activity of time of day and weather conditions.

These results agree closely with those of Kawamichi (1968, 1969) who showed that on clear days pikas exhibit strong bimodal activity peaks ("morning" and "evening" trips); but on cloudy, calm, and cool days, pikas were active throughout the day at a more variable level than in clear, warm weather.

These data also indicate a seasonal reversal in activity pattern with respect to weather conditions; in early spring pikas show high activity at midday on clear or partly cloudy and warm days, while later in summer they are more active at midday during partly cloudy or overcast and cool days. In late April and early May 1970, cloudy days were near freezing or below and snow flurries were not uncommon. Clear days were mild but rarely above approximately 60°F. Later in summer, clear or partly cloudy days were usually above 60°F and the rockslides heated considerably. In my study, the only two pikas that died in traps did so on hot afternoons. I checked traps regularly and in both cases all the fresh vegetation placed in the trap had been eaten (a large handful), and both pikas appeared to have died from water loss, as their abdomens were shrunken.

Smith (1971), working in California, placed pikas living at different elevations in exposed wire cages in vegetated areas bordering their home rockslides, and left them all day. Pikas living at low elevations did not survive, even though fresh vegetation was available through the cage floor. Pikas living at high elevations survived these conditions, although they were stressed. Thus, there is some evidence that pikas, at least those living at lower elevations, have a poor tolerance for high temperatures in summer.

Krear (1965) paid weekly visits to his study areas in autumn, winter, and spring, but saw little activity in midwinter when the areas were snow covered. Although Kawamichi (1971a) found that the Himalayan pika and the big eared pika were active in November-January in the Himalayas, the areas he studied were practically snow free, as were two other areas studied in 1968 for the Himalayan pika. The third area Kawamichi observed in 1968 was snow covered and the pikas were less active on the surface than on other areas; using instead an elaborate system of snow tunnels. Severaid (1956) and Krear (1965) describe snow tunnels.

I visited both of my study areas in mid-March 1970; the pikas were active on clear days in the Jumping Pound, which was snow free except for the very base of the rockslide. No activity was seen on the Kananaskis area, which was still snow covered. There was little evidence of surface activity on the Kananaskis area, and snow tunnels leading from the edge of the rockslide into surrounding vegetation were present. Tapper (pers. comm.) and Hobbs (pers. comm.) have also seen snow tunnels. The Jumping Pound area was visited in October 1970; it was snow free and the pikas were active at midday. Thus, in the winter months, pikas may avoid relatively low temperatures either by being active at midday in snow free areas or by becoming subnivean when snow is present.

4. INDIVIDUAL ORIENTED BEHAVIOR

4.1 Comfort and Maintenance Behavior.

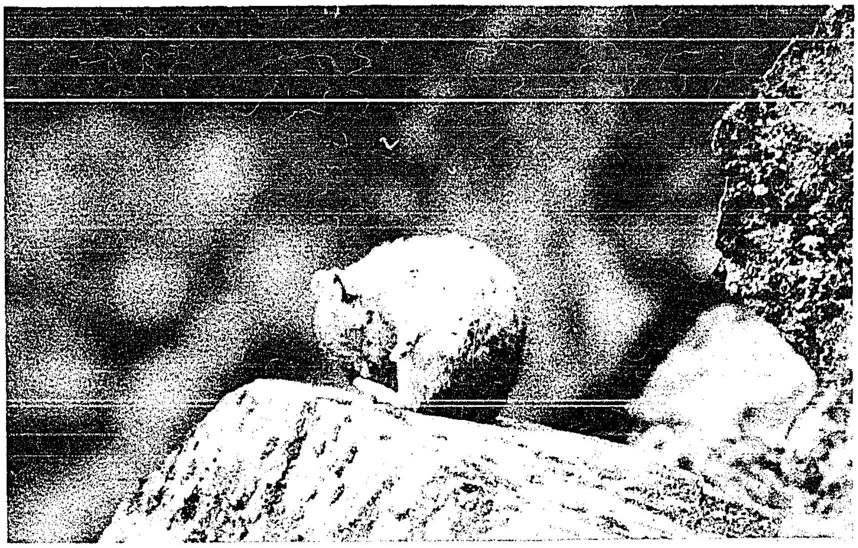
This section includes elimination and coprophagy, pelage maintenance, and use of "leisure time." A description of each pattern follows.

Eliminative Behavior and Coprophagy.

Pikas produce two types of feces; "cecal" feces, and pellets. These have been described by Severaid (1956), Haga (1960), Krear (1965), Broadbooks (1965), and Kawamichi (1971a). Cecal feces are about 4 mm by 20-30 mm, black, and are reingested. These are thought to be produced in the cecum and probably are of nutritional value to the animal, although this has not been investigated in pikas (for a discussion of coprophagy in rabbits, see Thacker and Brandt 1955).

Cecal feces are either reingested as they issue from the cloaca (seen by Krear (1965) in captive pikas), or voided in the nest or on a haypile and eaten later (saved, as described by Severaid 1956); as well, Krear (1965) saw cecal feces on haypiles and near nests of captive pikas. Severaid (1956) observed captive pikas carrying cecal feces and attaching them to the sides of nest boxes and tunnels. I did not see a wild pika close enough to be sure it was reingesting its cecal feces until 1970. The pika balances on its hind legs, brings its tail-cloacal apparatus forward, and bends its head down and inward into contact with the cloaca (Figure 6a). The cloaca appears everted. The diagnostic difference

Figure 6a. A pika reingesting it's cecal feces.



b. A fecal tower under an overhanging rock.

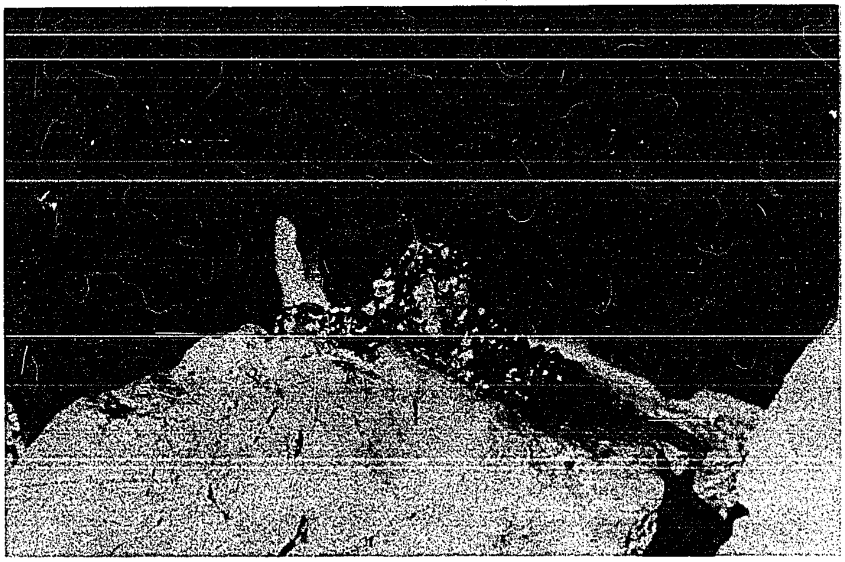


Figure 6a. A pika reingesting it's cecal feces.

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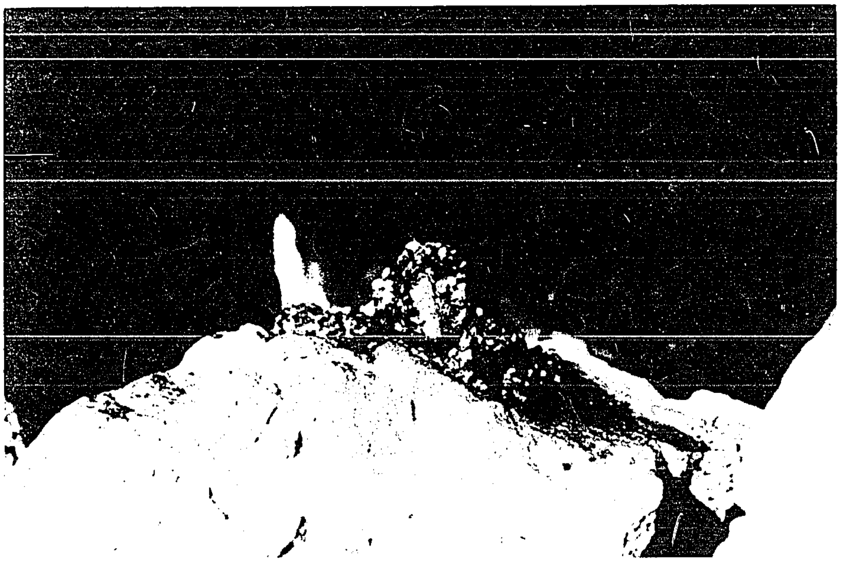


between reingestion and grooming of the stomach area is twofold: the pika always chews after refection and the head is usually bent more down and inward during refection.

The pellets are approximately 4 mm in diameter, and dark green in color. Fecal deposits of variable size, composed exclusively of pellets, were present on both rockslides. Such deposits have been reported by Severaid (1956), Broadbooks (1965), Krear (1965), and Kawamichi (1968, 1969, 1970a,b). Smaller pellet aggregations occur under overhanging rocks and occasionally on the edges of exposed rocks. Larger scattered piles, occurring in crevices between rocks, are common near haypiles. In addition, there were one or two large "fecal towers" present on each study area. The tower shown in Figure 6b was about 6 cm high and 4 cm in diameter.

When defecating on small fecal piles, the pika presses its posterior to the rock and deposits three to six pellets. The pellets are sticky and adhere to the rock. I have not seen pikas defecate on the larger, more scattered piles in the field, but captives would approach a deposit, elevate the posterior on stiff hind legs, and drop ten or more pellets onto the pile, sometimes urinating at the same time. These observations are in agreement with those of Krear (1965), who briefly discusses the fecal towers, postulating they may develop in winter as snow depth increases.

I saw pikas urinate in the field, although infrequently. On each occasion the pika urinated on a sheltered rock point or edge. The urine has a very strong, pungent odor and is rather viscous. It is sulphur-yellow upon release, changing quickly to brownish-yellow. Broadbooks (1965) states that conspicuous white encrustations on rocks near haypiles are due to accumulated pika urine. I am not certain of this for two reasons. Wood rats also urinate on such rocks, and the majority of sheltered rocks on my study areas had light colored encrustations, at least some of which may be due to natural weathering and redeposition from rocks above.

Pelage Maintenance.

Pikas shake, scratch, chew, and lick themselves often. When the body is shaken, it is done so vigorously that the front feet are lifted off the substrate. Body shaking was rarely seen, however, and head shaking was much more common and is described by Severaid (1956) and Krear (1965). Kawamichi (1969, 1971a) observed body shaking, calling it trembling, in the big eared pika and the Himalayan pika, but did not see this done by the Japanese pika.

Pikas scratch themselves with their hind feet, and can reach an area from the nose to the middle of the back and stomach. The head is extended and turned to the side when the head, ears, or neck are scratched (Severaid 1956, Krear 1965, Broadbooks 1965, Kawamichi 1968, 1969, 1971a).

A pika can chew, bite, and lick an area from its chest to tail, its front and hind legs and feet, and from the shoulders along the back and sides to the rump (in agreement with Severaid's (1956) and Krear's (1965) observations. Kawamichi (1969, 1971a) stated that biting and chewing of the fur was common in the big eared and Himalayan pikas, but was never seen in the Japanese pika. Pikas also lick the top and bottom of their paws and chew between their toes.

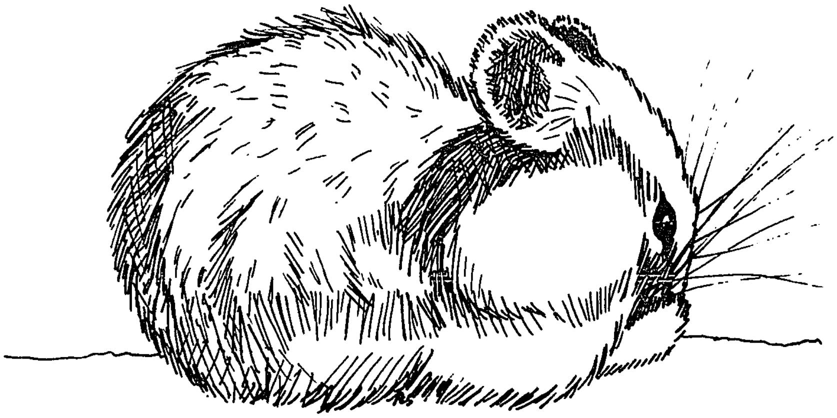
Pikas wash their faces from two positions, on their haunches on a slanted rock, or in a hunched over position (Figure 7a). In both positions the paws are brought alternately across the ears and face. The paw movement is more rapid when the pika is on its haunches. Severaid (1956), Broadbooks (1965), and Krear (1965) describe this pattern. Kawamichi (1969, 1971a) observed it in all three Asian pikas. I noticed that the front paws were frequently groomed after face washing; Krear (1965) reported this also.

Pikas lick their lips by moving the tongue in a figure-eight motion. This may be stimulated by mouth irritation, as captives licked their lips often after carrying off a discarded orange peel.

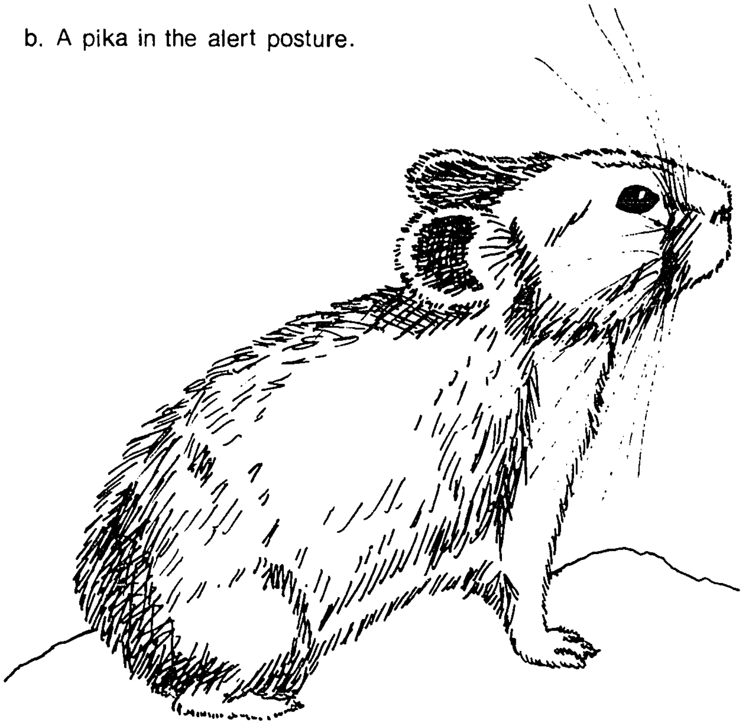
Sitting.

Pikas spend a portion of their time sitting on particular rocks, which I have named favorite places. Each pika has one or two favorite places. Loukashkin (1940) mentions this for the Manchurian pika (O. hyperborea mantchuria), and Allen (1938) saw this in the red pika (O. rutila). Severaid (1956) and Krear (1965) discuss these places; Severaid calls them porches. Kawamichi called them resting places (1968, 1969), then changed this to set in 1970 and

Figure 7a. A pika washing it's face in the hunched position.



b. A pika in the alert posture.



1971 publications. These favorite places are high rocks that afford a good view of the rockslide.

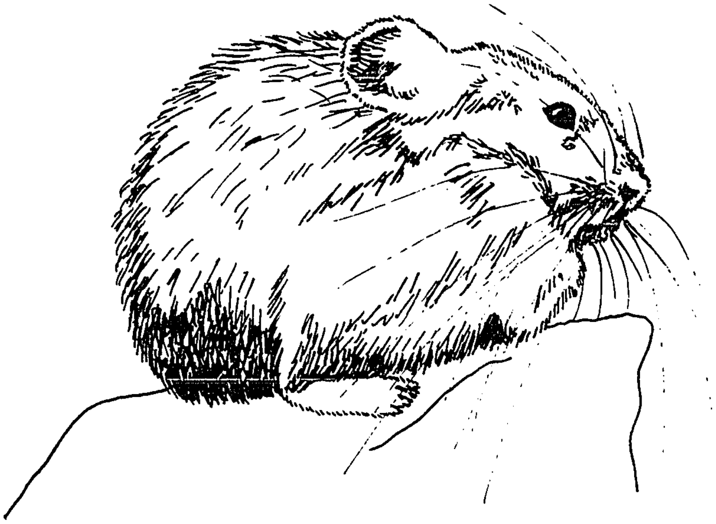
Kawamichi (1968) calls this sitting activity musing. I could distinguish five sitting positions: alert, normal, perched, propped, and basking. Pikas usually sit in the alert posture, with the head up and the feet visible. If alerted from a resting position, the pika initially raises its head in a series of jerks; if further alerted it props itself up on stiff front legs with the head high (Figure 7b). This is in agreement with Krear's (1965) description, and Kawamichi (1968) calls this warning musing.

In the normal position, when completely at ease, the pika lays its head back and down upon its shoulders; the feet may not be visible and the body appears spherical (Figure 8a). Hayward (1952), Severaid (1956), Krear (1965), and Kawamichi (1968, distinguishing between brief and deep musing) describe this position. I have observed individuals sitting in this position for 20 minutes, although usually much less. When settling into this posture the pika usually performs a series of small jerks or jumps before becoming motionless.

In the perched position, the hind legs are brought forward with the feet showing, and most of the weight seems to be on the posterior (Figure 8b). Pikas also perch on the edge of a rock with their posterior hanging over the edge.

Figure 8a. A pika in the normal sitting position.

b. A pika in the perched sitting position.



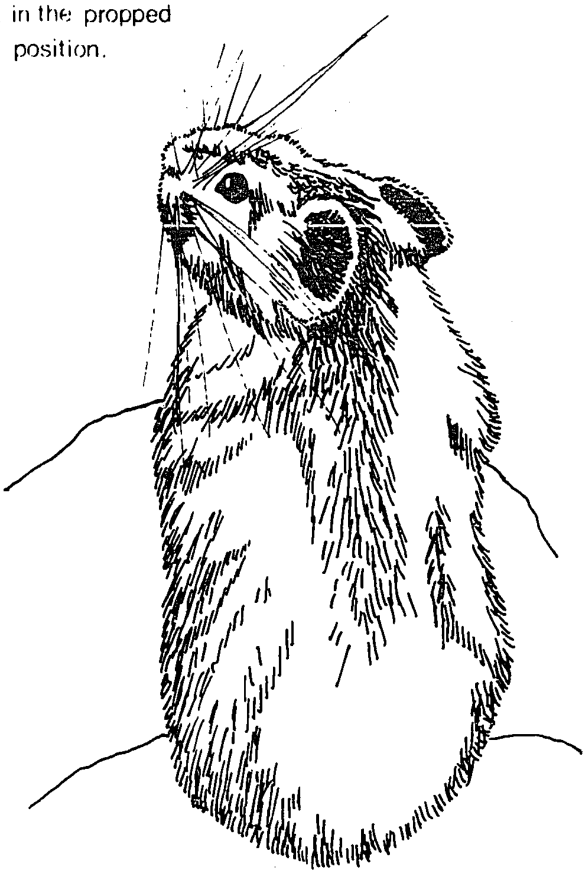
Pikas also sit partially propped with the front legs over a higher rock and the rest of the body supported at a lower level (Figure 9a).

In agreement with Krear's (seen in captives, 1965) observations, and those of Kawamichi (1969, dreamy musing), pikas were seen dozing while sitting on exposed rocks in the normal position. As well, I saw pikas dozing in the propped position. The animal's head would drop and the eyes partially or completely close, then the pika would rouse, raising its head, then doze again. From the propped position, one ♀ even slipped downwards and to one side, catching herself several times.

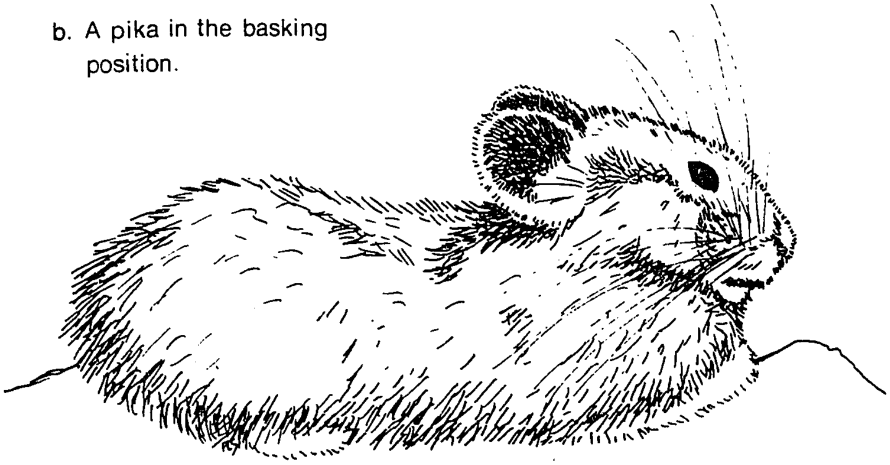
The basking position is distinct in that a pika flattens itself out on a rock with the head resting back upon the shoulders, the ears flattened and facing up (Figure 9b). Severaid (1956) and Krear (1965) describe this position, and Kawamichi (1969, 1971a) saw it in the Japanese pika and the Himalayan pika but not in the big eared pika. I never saw pikas rotating their bodies or turning around while sunning, as Kawamichi (1968, 1970) describes for the Japanese and Himalayan pikas.

Pikas sometimes stretch before moving off a rock after sitting. Stretching is done in several ways. The body can be arched in cat fashion, accompanied by a yawn, as Krear (1965) reported. The front end can be elevated on stiff front legs while the posterior is depressed and extended backwards. Pikas also stretch while moving slowly from

Figure 9a. A pika in the propped sitting position.



b. A pika in the basking position.



rock to rock; stopping momentarily with the forefeet on one rock and the hind feet on another, and depressing the back; or they may stop and stretch a front or hind leg.

Analysis and Discussion.

Because total observations for each month include different proportions of weather conditions, pooled data for each time period are not directly comparable on the basis of time spent observing; as well, variations in activity with hour of the day lessen such comparability. In an attempt to minimize the effect of these variables, duration and/or frequencies of acts or patterns (with a few exceptions) have been calculated on the basis of the amount of time an individual was seen, rather on time spent observing. Analysis of calls and of some interactions was done on the basis of time spent observing, as in the first case it was not necessary to see an individual to recognize its call and location, and in the second case, more than one individual was involved and it is difficult to envisage an acceptable time seen for two or more individuals.

The total time seen varied between individual pikas. It was assumed that the accuracy of information on frequency and/or duration of acts or patterns increased with the amount of time an individual was seen. Thus, in many cases, weighted averages were used. These were calculated by dividing the total number and/or duration of acts of all individuals by the total time all pikas were seen.

Frequency of visible refection of cecal feces is

Table 2. Frequencies of visible refection of cecal feces in 1970, expressed as number of acts/hour seen for each pika. Total time the individual was seen (hrs) is in parenthesis. Total refections seen = 152.

	April-May	June	July	August
Adults	♂GR 4.00(1.00)	♂1 3.44(0.58)	♂1 0 (0.15)	♂1 0 (0.37)
	♂RR 0.65(3.07)	♂2 4.22(3.55)	♂2 1.08(5.57)	♂2 1.03(8.70)
		♂3 3.62(8.56)	♂3 1.38(15.89)	♂3 1.01(13.90)
	♀TE 3.99(3.76)	♀5 2.11(2.37)	♀5 1.55(3.87)	♀5 1.48(8.09
Juveniles		♂10 1.14(0.88)		♂12 0.76(2.63)
		♂11 0.49(2.04)		♀13 0.66(1.51)
				♀14 0.27(7.48)

presented in Table 2. Only the 1970 data are presented, as this act was not confirmed until then. With one exception, adults show a rate of 2-4 refections/hour seen in April-May and June, decreasing to 1-2 refections/hour seen in July and August. Juveniles had a lower rate of refection than adults; and in June, juveniles had a higher rate than juveniles in August. I would expect juveniles to have a rate of refection comparable to or higher than adults, simply because they are growing. Krear (1965) thought that juveniles spent more time feeding than adults, and my data tend to show this also (see Food Getting Behavior).

The overall trend of a gradual decrease in refection in summer is logical, in that little fresh vegetation is available in spring, and pikas could make better use of food resources by reingesting feces more often. Later in summer when vegetation is abundant, maximal use of food might not be necessary.

Millar (pers. comm.) and I noted that captive pikas practically stopped eating the accumulated cecal feces in their cages when fed commercial rabbit chow, a high quality food source. Accumulations of dried cecal feces were common in and around haypiles in the field, as well as in nests in pens. These accumulations may be of some importance as a supplement in winter in nature. Broadbooks (1965) noticed marmot scats on one haypile and saw a pika feeding on them.

There is evidence that pellets and urine are used for scent marking and data pertaining to this are presented and discussed under Marking Behavior.

Frequencies expressed as weighted averages of some pooled pelage maintenance acts are presented for adults and juveniles in Table 3. Licking fur and licking paws are not included as they were seen only three times each. The May frequencies are least accurate, as this was the first month of field observations, and several maintenance acts were not yet identified at this time.

Seasonal variation in maintenance activities may be partly a reflection of changes in abundance and location of ectoparasites. Ear mites appear on adults in July and on juveniles in August (R. Hobbs, pers. comm.). Pooled frequencies of head-oriented acts correlate well with the appearance of mites for juveniles, but not as well for adults. Adults show an increase from April-May to June, and another increase in July. Juveniles show a doubled frequency of head-oriented acts in August. Thus, the observed overall increase of head-oriented acts through the summer does correspond in part to mite infections in adults and juveniles, and may be partly caused by such infections.

Frequencies of all scratching show a peak in late May or June in adults, while juveniles show a gradual increase to or slightly above adult levels in August. Frequencies of all chewing are less consistent, probably reflecting a fairly stable frequency for adults through the season and a gradual increase in juvenile frequencies until adult levels are reached in August.

Table 3. Weighted averages of some pooled pelage maintenance acts, expressed as the number of acts/hour seen. A = adults, J = juveniles. Total number of acts seen appears in parenthesis.

Acts		April-May	May	June	July	August
Shake head (107) Scratch face and ear (145) Wash face (210)	A	2.17	0.30	3.19	3.69	3.54
	J			2.09	2.63	5.09
All scratching (272)	A	1.28	3.14	2.41	2.00	1.86
	J			1.04	1.32	2.02
All chewing (401)	A	2.68	1.64	3.05	2.87	3.34
	J			1.04	1.97	3.42
All acts (1078)	A	6.00	5.08	7.68	8.01	8.06
	J			4.70	7.57	9.21

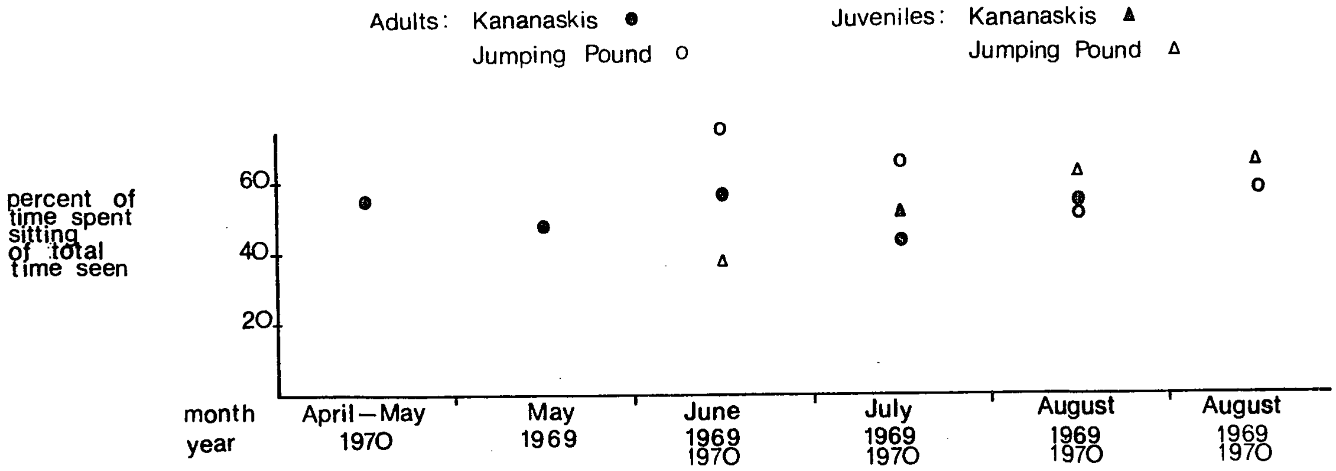
Frequency of all maintenance acts in adults and juveniles increases from early spring to late summer. Adult frequencies seem to level off in July and juvenile levels seem to reach a peak slightly higher than adults in August.

Adult ♂♂ begin to moult in late June or early July, and this process might require extra pelage care, thus a possible explanation for the observed increase in maintenance acts. The ♀♀ begin to moult about the same time as ♂♂ (S. Tapper, pers. comm.), but their moult proceeds at a slower rate until mid- or late July. The juveniles appeared to moult in late summer to a brown color, thus the gradual increase in maintenance acts that they display could be caused by a gradually building parasite load and onset of the moult in August.

A seasonal analysis of sitting is presented in Figure 10, expressed as weighted averages of percent of time spent sitting/time seen for each area. Data from the Kananaskis are most accurate, as sitting on the Jumping Pound is overestimated because feeding areas were not visible. Pikas were sitting between 40 and 60 percent of the time they were seen. Time spent sitting on the Jumping Pound is about 20 percent higher than the Kananaskis in June and July. In August, the time spent sitting on each study area agrees closely. Time seen feeding on both study areas is comparable in August (see Food Getting Behavior), due to the onset of intensive haying activity; thus the time budgets of the pikas in the two areas are comparable in August.

The percent of time spent in the normal position/total

Figure 10. Weighted averages of sitting time budgets, Kananaskis and Jumping Pound study areas, 1969 – 70



time spent sitting varies greatly (from zero to 25 percent) between individuals on the same rockslide and no trends whatsoever are evident within sex and age classes or between rockslides. I can only conclude that the amount of time spent in the normal position varies with the individual. Time spent basking/time spent sitting is lowest in April, May, and June, increasing in July to about 2-5 percent. The perched and propped positions were rarely taken (less than 1 percent of total time sitting); the propped position was seen throughout spring and summer, the perched position was seen only in July and August 1970.

Spatial distribution of sitting is discussed under Spatial and Temporal use of Home Range.

4.2. Food Getting Behavior.

Feeding.

When feeding, pikas move about in a series of short hops, looking around every few seconds. The pika clips off a few strands or pieces of vegetation at ground level by holding its head lateral to the ground. The head is raised and the leaf or leaves are gradually chewed into the mouth. On one area, pikas had actually beaten visible paths out onto the meadow bordering the rockslide. Broadbooks (1965) reports this for both O. princeps and the collared pika, O. collaris.

Krear (1965) never saw pikas using their forepaws for manipulation of food. I saw this done on three occasions. Pikas often gather a mouthful of food, carry it to a rock, and eat it there. If the strands were large or generally unwieldy, the pika gently lay a paw across the strand. This may have been to prevent movement while being chewed, as the chewing motion causes the strand or leaf to rotate. On another occasion, an adult ♂ was carrying a mouthful of grass that contained a twig. He batted at the twig with a forepaw until it fell out, apparently not wanting to drop the mouthful. Lastly, I watched an adult ♀ eating a lichen; she sat on her haunches holding the lichen between her forepaws.

Haying.

All pikas on my study areas used the same haypile sites both years. Resident adults had at least two caches; one adult ♂ had at least eight. The two juveniles that actively cached vegetation did so on deserted haypile sites.

When haying, the pika clips off vegetation as in feeding, keeping what it has already collected in its mouth as it gathers more. The pika runs to a haypile, stopping frequently to look around, and deposits and arranges the hay on the haypile. The pika then usually takes a vantage point, sits for a few seconds, calls, then returns to the haying area.

All haypiles in my study areas were in sheltered sites, usually under overhanging or large rocks. Pikas were never seen leaving freshly collected vegetation on rocks to dry. Broadbooks (1965), working at Bethel Ridge, central Washington, found that all haypiles were in exposed sites, and some were exposed throughout the winter. Near the East Fork, Toklat River in Alaska and in Rocky Mountain National Park, Broadbooks found that all haypiles were in sheltered sites. Krear

(1965) never saw an exposed haypile in his Colorado study area but did see exposed portions of haypiles in the Grand Tetons. Dalquest (1939), Loukashkin (1940), and A. Russell (pers. comm.) have seen pikas leave vegetation on exposed sites to dry. Hobbs (pers. comm.) has seen exposed haypiles in the Kananaskis area, DeBock (pers. comm.) has seen this in Kootenay National Park and Mt. Robson, and Gray (pers. comm.) has seen exposed haypiles in Manning Park, British Columbia. This variation in haypile placement may be influenced by exposure to wind, as Broadbooks (1965) mentions.

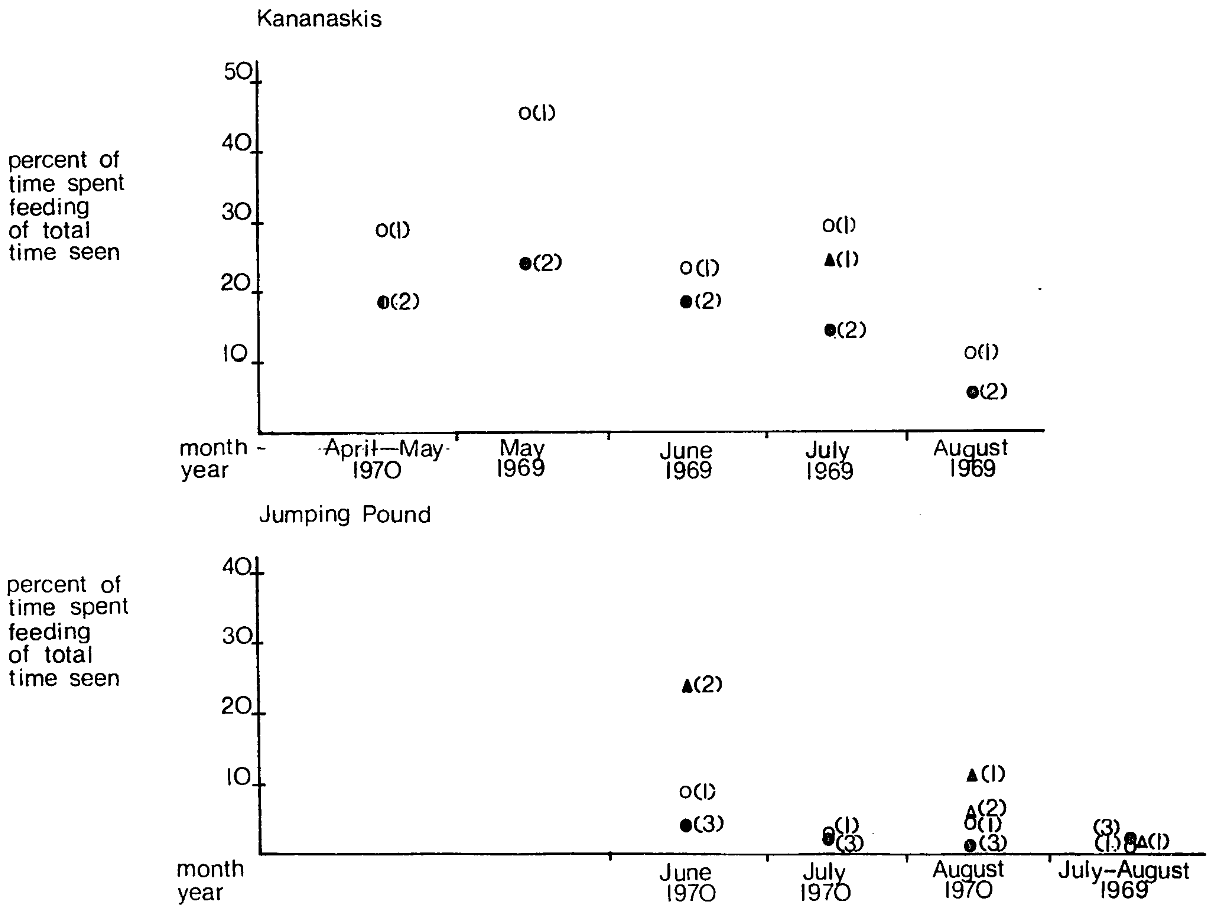
Severaid (1956) excavated one haypile complex in search of a nest in Bodie California, and found many small caches of hay as deep as 3 m below the surface. Hayward (1952) and Krear (1965) also mention the possibility of deep stores in the rocks. When weighing haypiles in the field, Millar (1971, p. 20) found that about 50 percent of the haypiles he located were inaccessible.

Analysis and Discussion.

Topography and lush understory (over 25 cm in midsummer) obscured feeding sites on the Jumping Pound study area. Feeding time budgets, expressed as pooled averages of percent of time spent feeding/time seen for each sex and age class are presented in Figure 11.

On the Kananaskis study area, the ♀ spent about 15 percent more time feeding in May 1969 than April-May 1970. The offspring of this ♀ appeared on July 8; thus the extra

Figure II. Weighted averages of feeding time budgets, Kananaskis and Jumping Pound study areas, 1969–70. The number of individuals used for each average appears in parenthesis. Sex and age classes are as follows: adult ♂♂, ●; adult ♀♀, o; juvenile ♂♂, ▲; juvenile ♀♀, ∆.



time spent feeding may have been related to her pregnancy. This ♀ was seen in courtship in 1970 on May 1, and assuming she was successfully bred on or around that date, she should have had a feeding time budget comparable to the previous year for the same time period (mid-May). During May 15-21, 1970 (four days of observation), she fed 39.5 percent of the time she was seen, compared to 27.9 percent overall for April-May 1970. During May 19-21, 1970 (two days of observation), she fed 45.0 percent of the time she was seen.

Millar (1971) reported that ♀♀ increased their fat reserves during pregnancy, and almost depleted those reserves during lactation. Although based on only one ♀ observed in two succeeding years, the suggestion that ♀♀ may meet the nutritional demands of pregnancy by increasing their food intake is worth considering. It is unlikely that this increased feeding time reflects vegetation availability, as earlier in late April and May 1970 this ♀ spent considerably less time feeding, and vegetation in late April and early May is just as sparse as in late May.

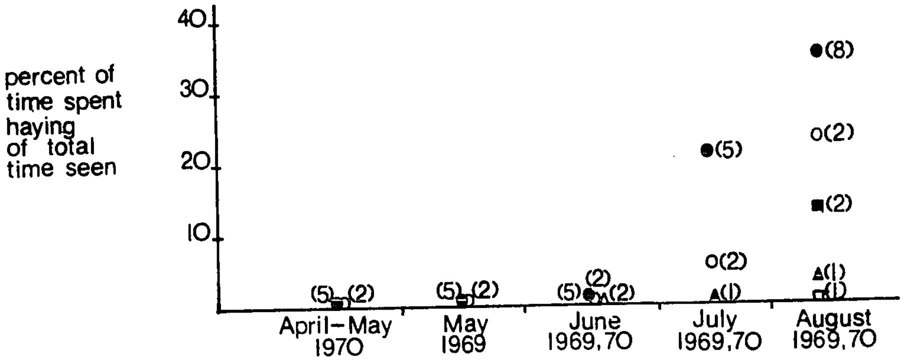
The time this ♀ spent feeding dropped to 22.7 percent in June 1969, when she was lactating. Millar (1971) analyzed vegetation on a "lush" meadow in the Sheep River, southern Alberta for total quantity, protein, phosphorus, and calcium content. He found that (1) the quantity of vegetation does not increase until early June, (2) protein and phosphorus content are highest in June, decreasing gradually through the summer, and (3) calcium content rose gradually through the summer. The decrease in feeding time displayed by this ♀ thus may reflect to some extent availability and quality of vegetation later in summer.

In July, this ♀ showed a slight increase in time spent feeding, likely not a meaningful one. However, in August, she showed a greater decrease in time spent feeding, this due to the initiation of haying (Figure 12), as pikas often fed for a short time before bringing vegetation back on a haying trip. Thus, there may not have been a change in actual time spent feeding in August. Feeding on haying trips was not recorded, as the pikas were difficult to see. The understory was over 10 cm and they usually gathered hay on remote parts of the rockslide and its borders, or beyond.

On the Jumping Pound study area, the ♀ began haying in July, even though she was nursing a litter at the time. In 1970, the pikas on the Jumping Pound began haying approximately two weeks earlier than those on the Kananaskis. This difference might be a reflection of the vegetation surrounding the rockslides, as it was more lush and came up more quickly in the Jumping Pound.

The ♂♂ on the Kananaskis area fed consistently less than the ♀. The difference between the two ♂♂ is due to the fact that ♂RR's home range was much less visible than that of ♂WR. This is also shown by the total amount of time each ♂ was seen in 1969; ♂WR was seen 18.23 hours total and ♂RR was seen 2.67 hours total. Following ♂WR's disappearance in October 1969, in April-May 1970, ♂RR ranged all over the

Figure 12. Weighted averages of haying time budgets, Kananaskis and Jumping Pound study areas, 1969–70. The number of individuals used for each average appears in parenthesis. Sex and age classes are as follows: adult ♂♂, ●; adult ♀♀, ○; juvenile ♂♂ with haypiles, ▲; juvenile ♂♂ without haypiles, △; juvenile ♀♀ with haypiles, ■; juvenile ♀♀ without haypiles, □.



rockslide and was seen 3.07 hours total. Feeding areas used by ♂WR in 1969 and ♂RR in 1970 were perhaps less visible than the areas used by the ♀. Thus, the difference in feeding time budget between the ♂♂ and the ♀ may in part be an artifact.

The ♂♂ fed most in May, with a gradual decline in July and August, concurrent with the onset of haying. The ♂ present from May 15-21, 1970, ♂GR, fed 40.2 percent of the time he was seen. Feeding time by ♂RR was only 13.6 percent of the time seen during May 1-11, and only 3.1 percent of the time he was seen from April 22-30, 1970. The data on ♂RR are probably more accurate than those on ♂GR for the following reasons: (1) ♂RR was seen three times as much as ♂GR, and (2) as ♂GR first appeared on the study area on May 15, he was in an unfamiliar environment and probably under stress -- the high feeding time may have been displacement activity.

The slight drop shown by ♂♂ in feeding time in June, concurrent with a drop shown by the ♀, might be for the same reasons, food availability and quality. The amount of time spent feeding/time seen is consistent in June and July for both ♂♂. Millar's (1971) data show that ♂♂ begin building up fat reserves in early July. As ♂WR was already haying approximately 15 percent of the time he was seen in July, the actual amount of time he fed may have increased in July. Although the feeding time of ♂WR decreased to 7.6 percent in August, he was haying 33.9 percent of the time he was seen.

The only juveniles that hayed consistently were ones that became successfully established on an area. On the Jumping Pound study area, ♀5 hayed an identical amount in 1969 and 1970 (she was a juvenile in 1969). In 1970, the juvenile ♀14 paired with ♂2, and spent 8.5 percent of the time she was seen haying. The juvenile ♂LK on the Kananaskis study area in 1969 took over a deserted haypile but made only a few haying trips.

The other juveniles seen in this study made a few haying trips but spent little time haying, and they had neither established haypiles nor "defended" home ranges.

The number of haying trips/hour seen serves as an index to the amount of time spent haying, with the exception of the ♀ on the Kananaskis study area; her haying areas were closer to her haypile than those of the ♂♂.

Pikas spent about 10 percent more time haying on the Jumping Pound area than those on the Kananaskis area. The Jumping Pound data are biased by the lack of feeding data; this bias is also shown in the sitting time budgets, presented earlier. Pikas on both study areas show the same increase in haying from July to August.

The Kananaskis study area was visited twice in September 1969. The pikas were still haying on September 11, and had stopped haying on September 28 but were still fairly active. The Jumping Pound area was visited in October 1970, no haying activity was seen and the pikas were not very active. Both study areas were free of snow during these visits.

In spring 1970, all haypiles on the Jumping Pound study area appeared little used, while those on the Kananaskis study area appeared moderately used. The actual amount of hay (if any) stored deep in the rocks is unknown, as is the extent of use of these stores, if present. Remnants of snow tunnels were present on the Kananaskis study area in late April 1970, and on north and west-facing rockslides near the Jumping Pound study area. The Jumping Pound was visited in March 1970 and was practically free of snow, while there was still 0.5 m of snow on the road below. In early spring, vegetation bordering or within both study areas appeared heavily grazed, particularly mat and rosette plants, such as fleabane.

Millar (1971, p. 50) removed all haypiles from three rockslides along the Sheep River in autumn, added 1000 g of material to haypiles on another area, and left one area as a control. The following spring and summer he found no difference in survival and reproductive success among these areas. However, on areas that were left with haypiles, he found that all haypiles were depleted in spring.

The areas Millar used for manipulations were at 2100 m elevation, and from his description, less lush than my study areas. From the above, it appears that although haypiles may be depleted in winter, they are not absolutely necessary to winter survival and reproductive success.

Two possibilities should be considered here: (1) some amount, perhaps a critical one, of hay is stored deep in the rocks, or (2) pikas forage extensively in winter and haypiles might only be necessary as an emergency supply when forage is temporarily unavailable, such as after a sudden wet snowfall or thaw, or when extreme low temperatures and very little snow are present in winter.

5. TERRITORIAL AND SOCIAL STRUCTURE

This section includes temporal and spatial use of home range, vocalization, agonistic and related behavior, reproductive and maternal behavior, and marking.

5.1 Spatial and Temporal use of Home Range.

Although previous authors agree that an individual pika has a fairly definite home range (Severaid 1956, Krear 1965, Broadbooks 1965, and Millar 1971), detailed documentation of ranges is lacking. Actual utilization of home range for various activities and relationships between individuals and possible seasonal changes in home ranges have not been reported.

Figures 13-23 show utilization of home range by each pika in each month, expressed as percent of time the individual spent in a 5 m by 5 m portion of the rockslide out of the total time it was seen.

Intensive use, or core areas: areas in which a pika spent over 4 percent of the time it was seen, are shown as S, F, or a combination of the two, indicating their use for mostly sitting, mostly feeding, or both, respectively. A dot following an S indicates that most sitting was on one rock (a favorite place). Feeding and sitting areas are not shown on the Jumping Pound maps, as these data are biased in favor of sitting. Each pika's haypiles are shown as an H.

First of all, it is evident from these range maps that pikas live in a paired arrangement. On the Kananaskis in

Figure 13. Individual utilization of home range, Kananaskis study area, May 17-31, 1969

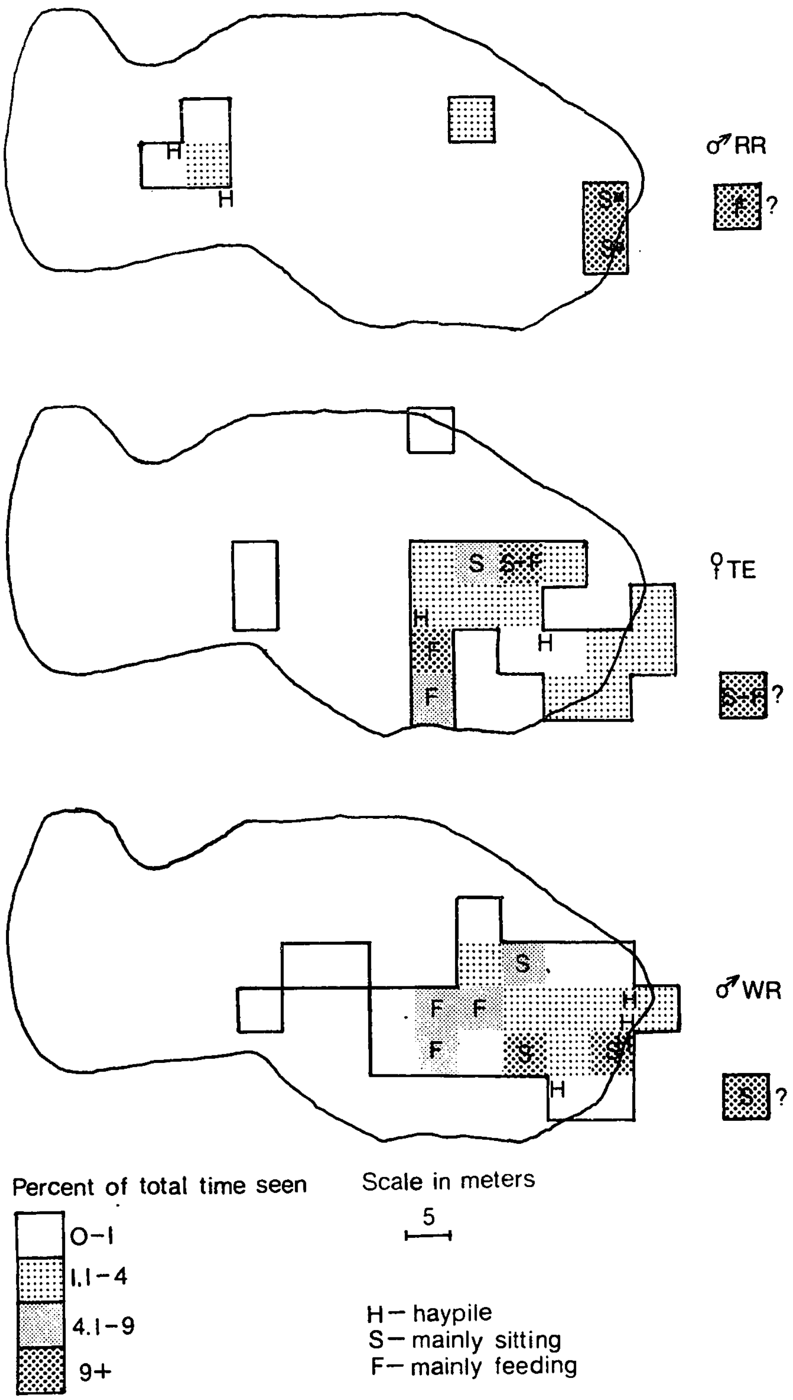


Figure 14. Individual utilization of home range, Kananaskis study area, June 1– July 1, 1969.

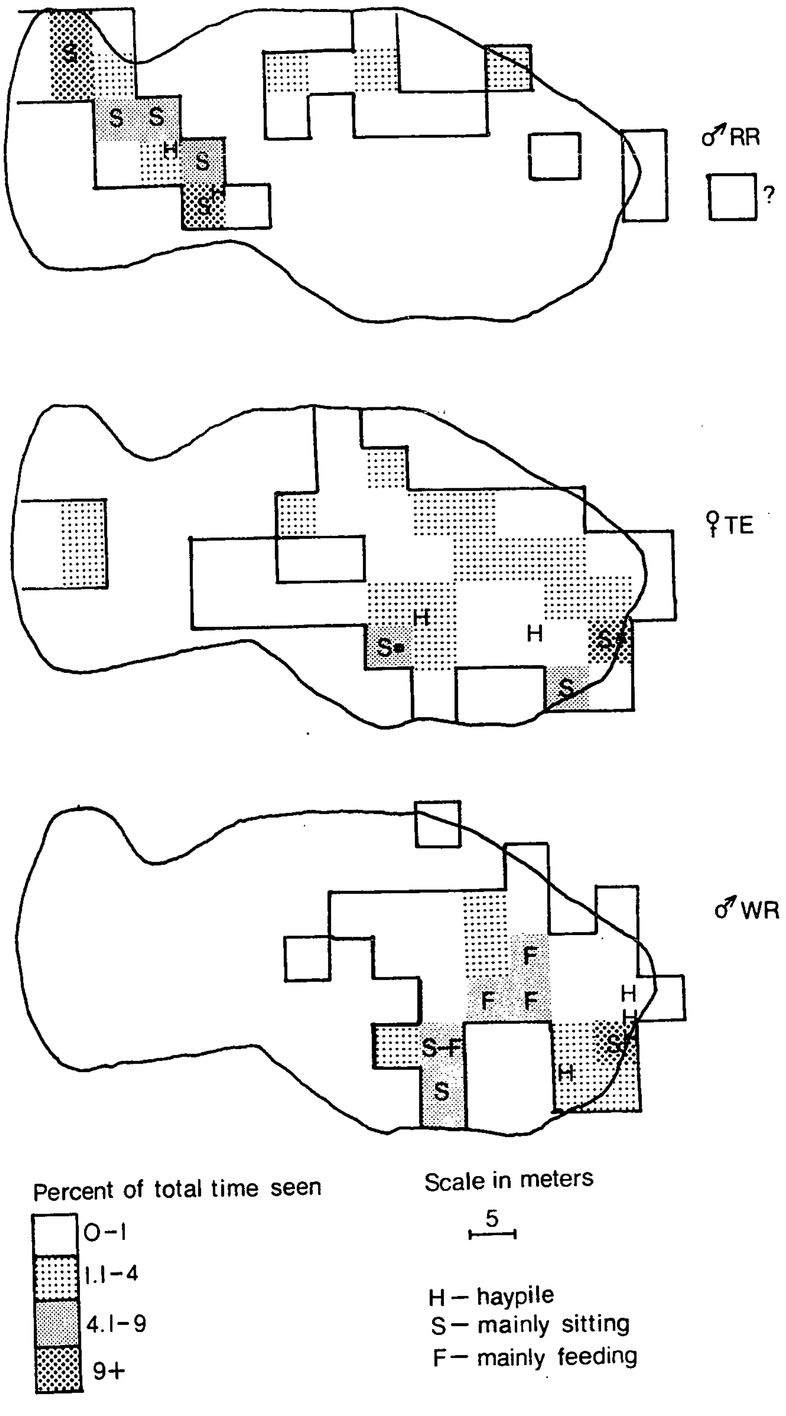


Figure 15. Individual utilization of home range, Kananaskis study area, July 2– August 4, 1969.

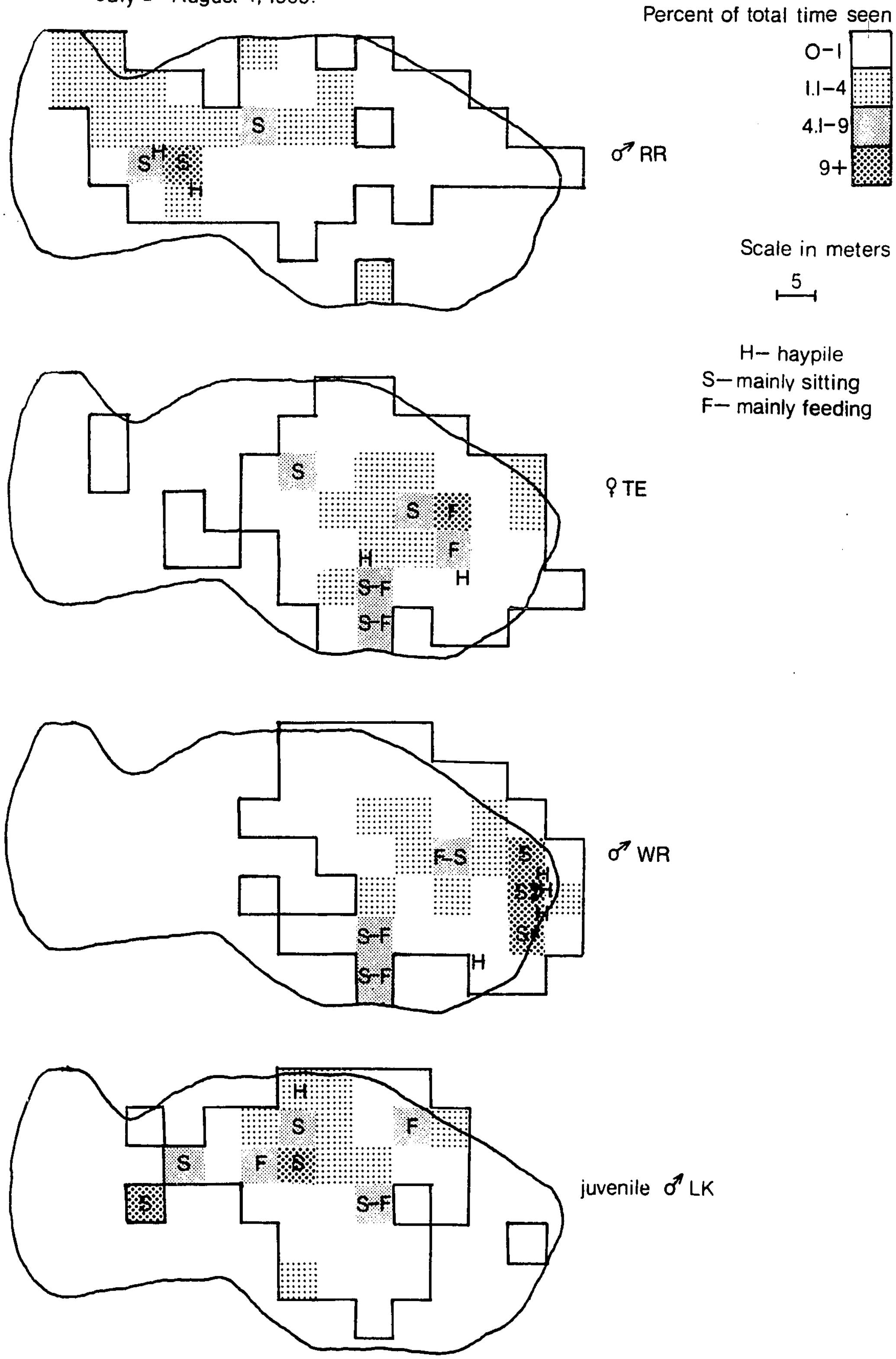


Figure 16. Individual utilization of home range, Kananaskis study area, August 5 – 18, 1969.

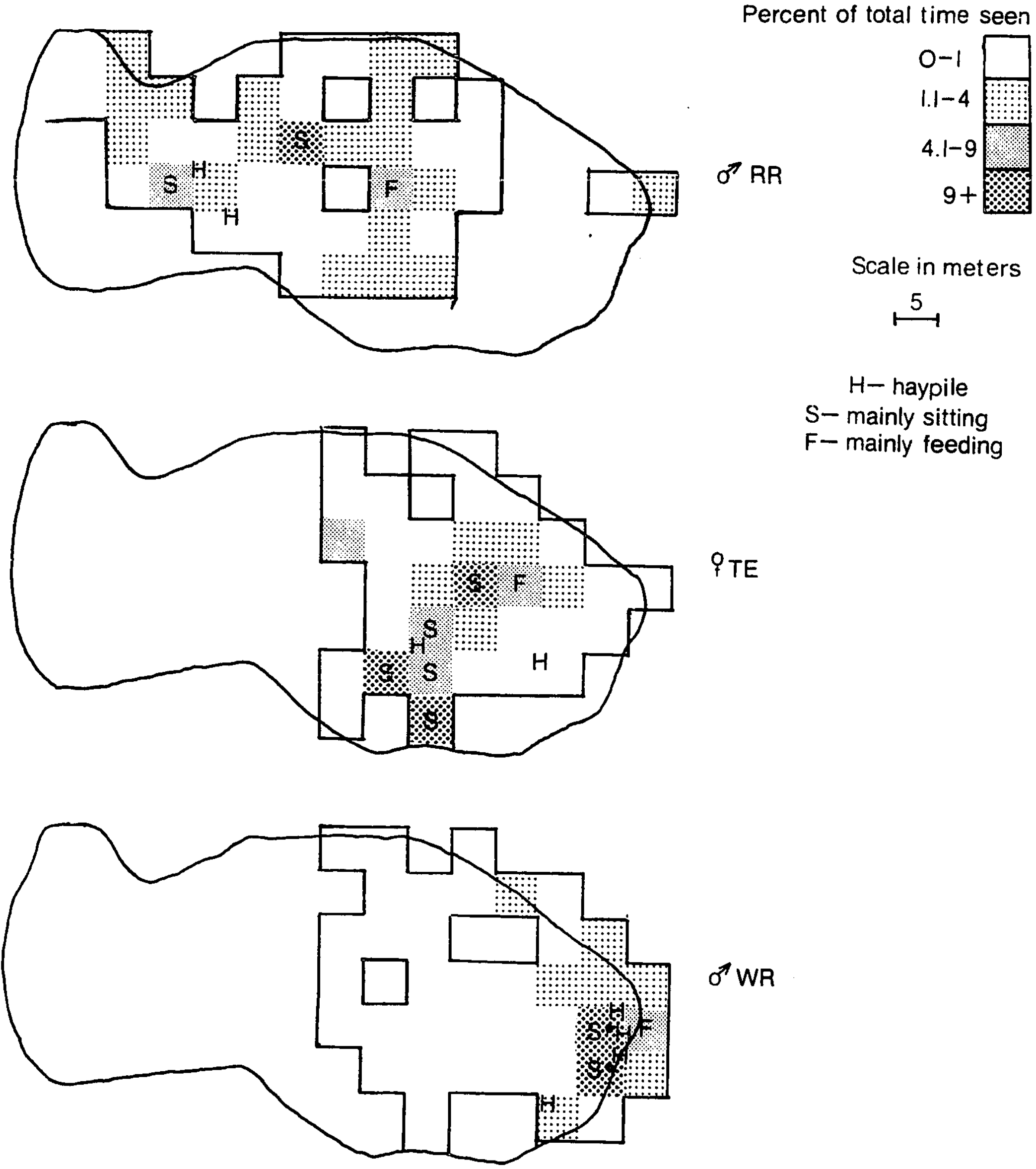


Figure 17. Individual utilization of home range, Kananaskis study area, April 22–May 21, 1970.

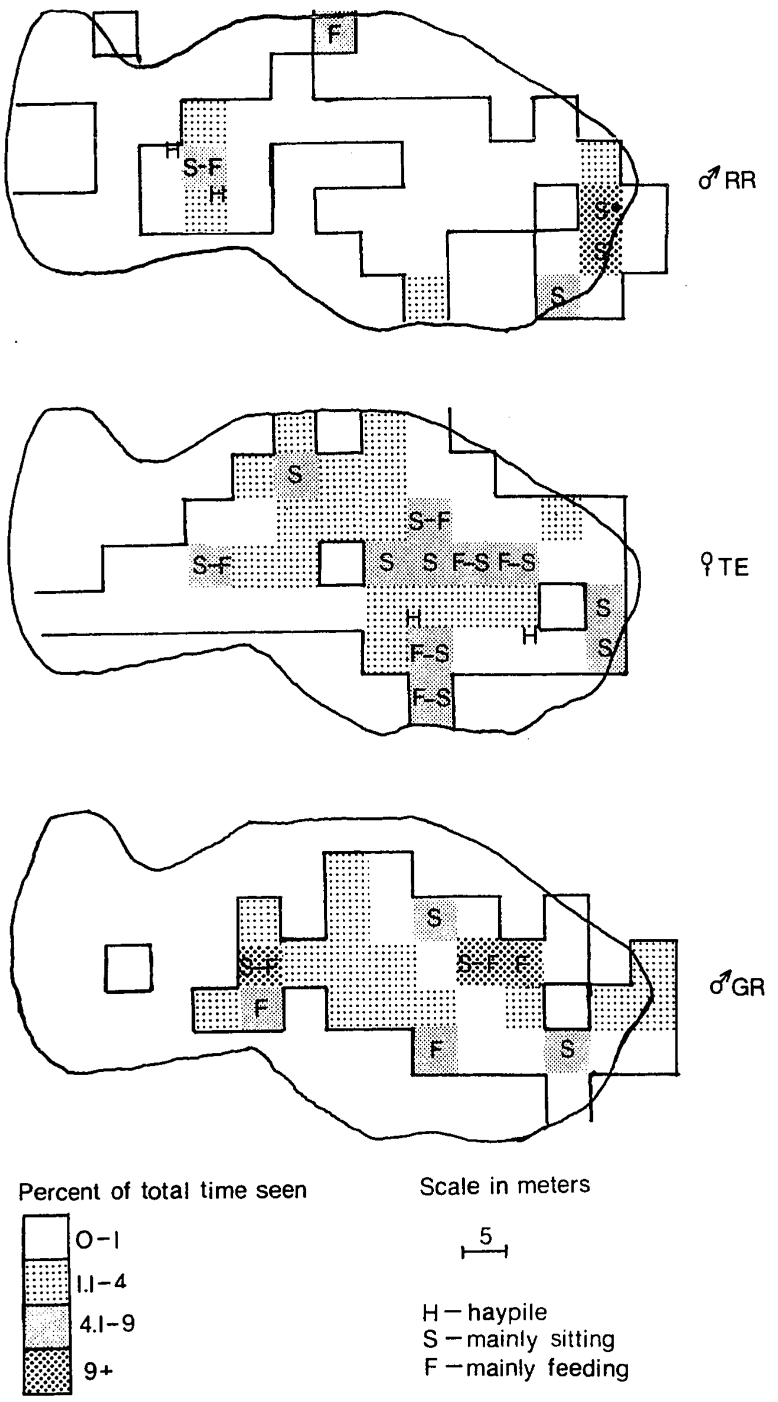


Figure 18. Individual utilization of home range, Jumping Pound study area, June 2 - July 6, 1970.

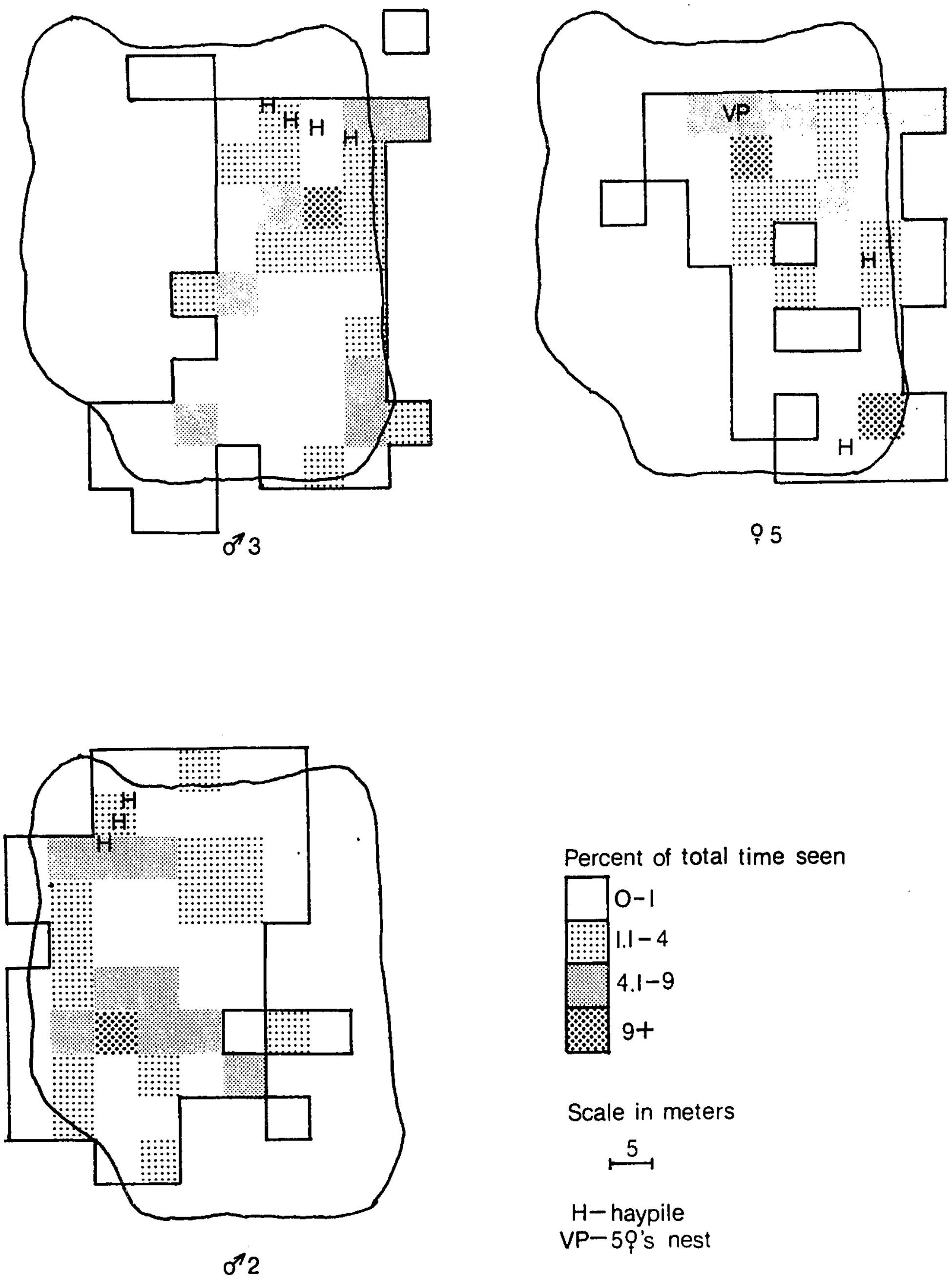
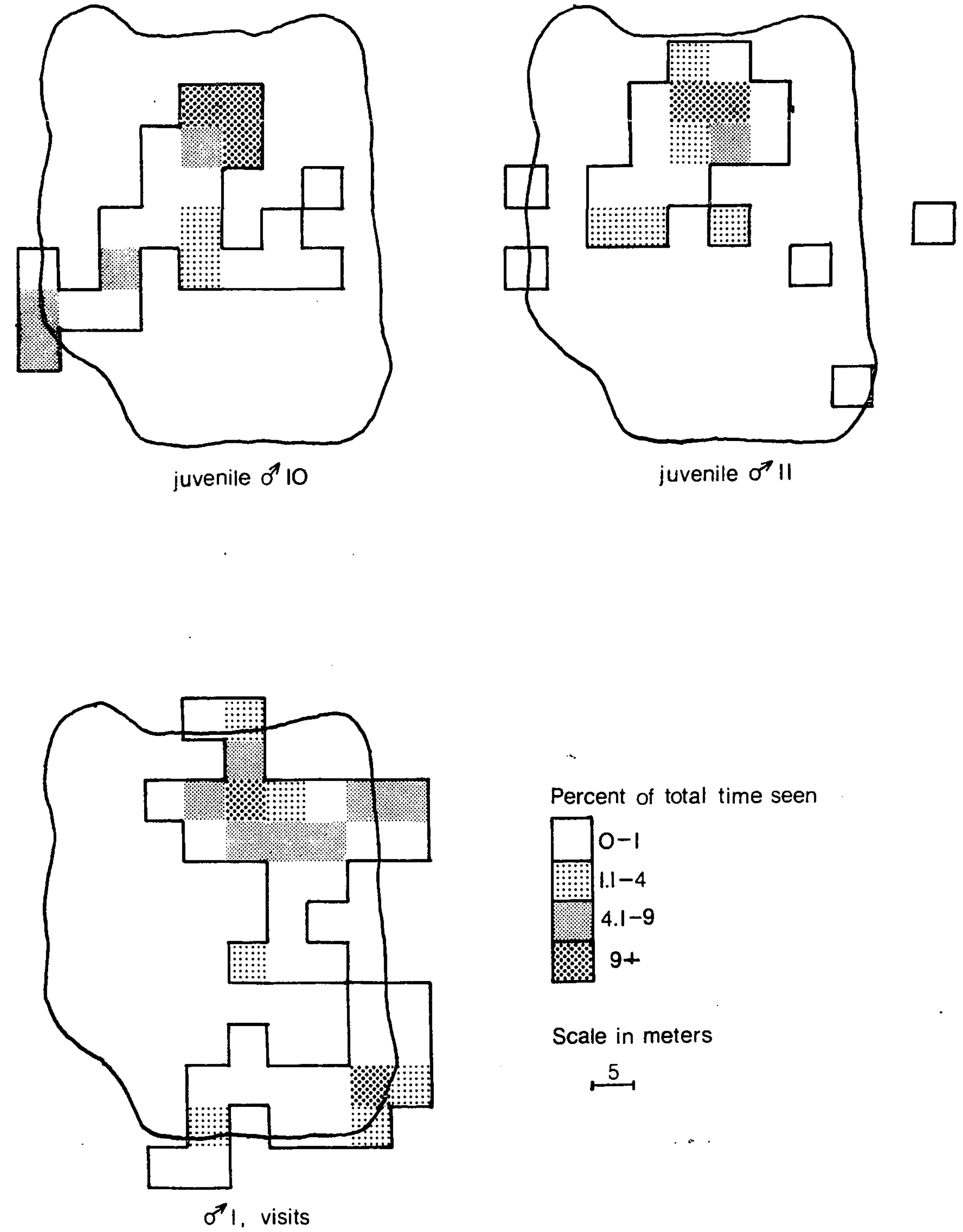


Figure 19. Individual utilization of home range, Jumping Pound study area, June 2 - July 6, 1970.



juvenile ♂ 10

juvenile ♂ 11

♂ 1, visits

Figure 20. Individual utilization of home range, Jumping Pound study area, July 7–August 2, 1970.

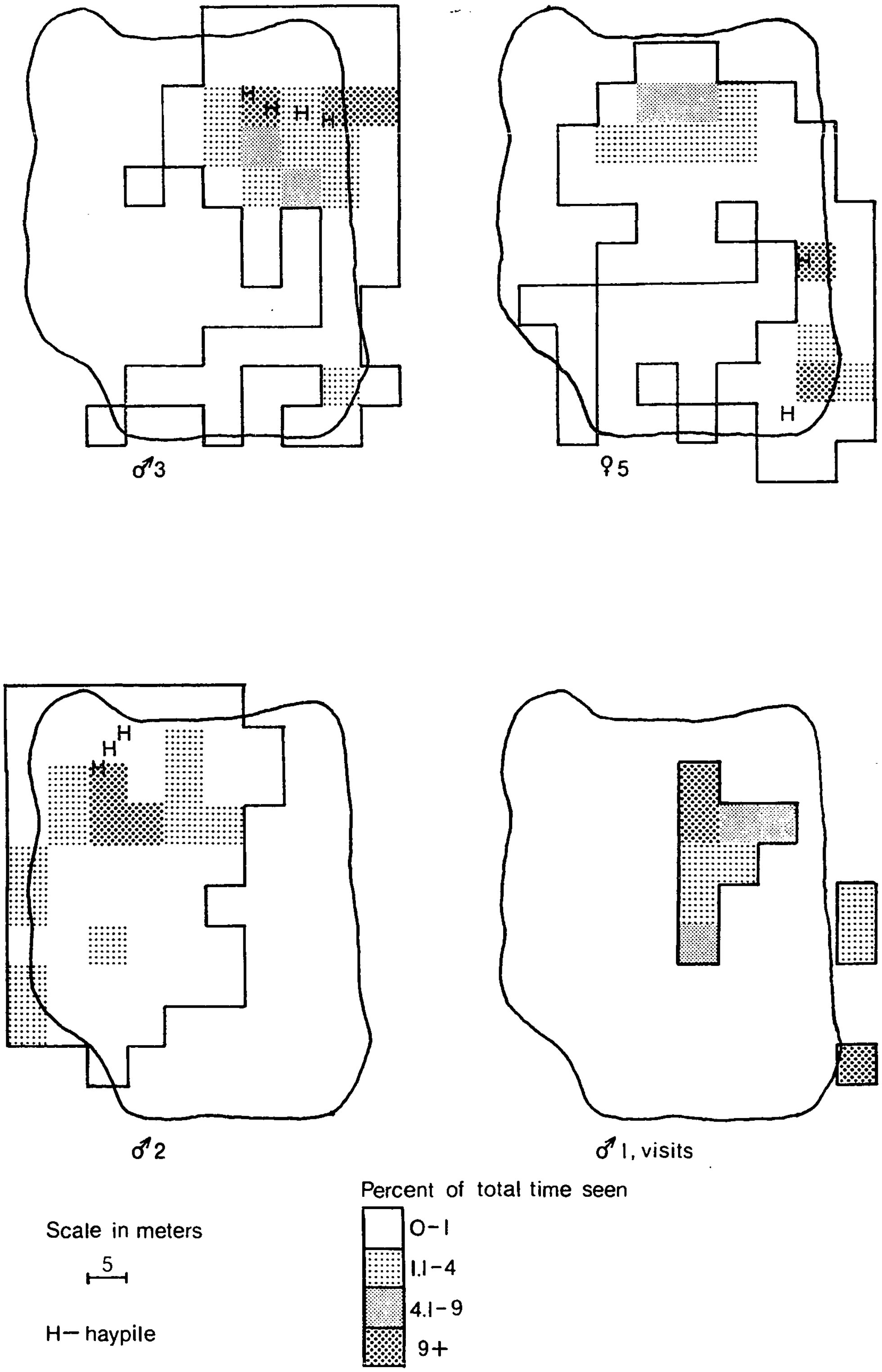


Figure 21. Individual utilization of home range, Jumping Pound study area, August 3- September 6, 1970.

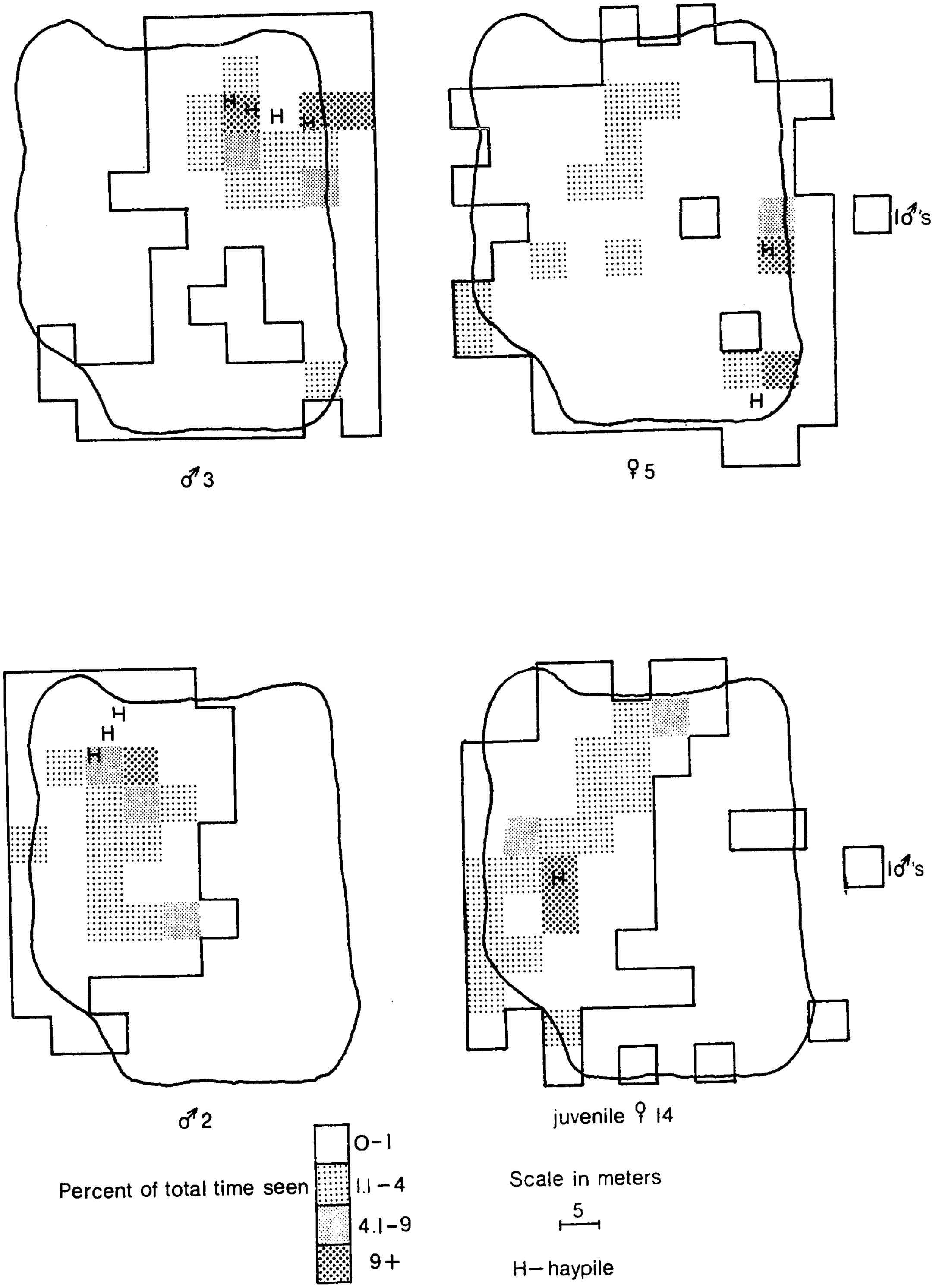
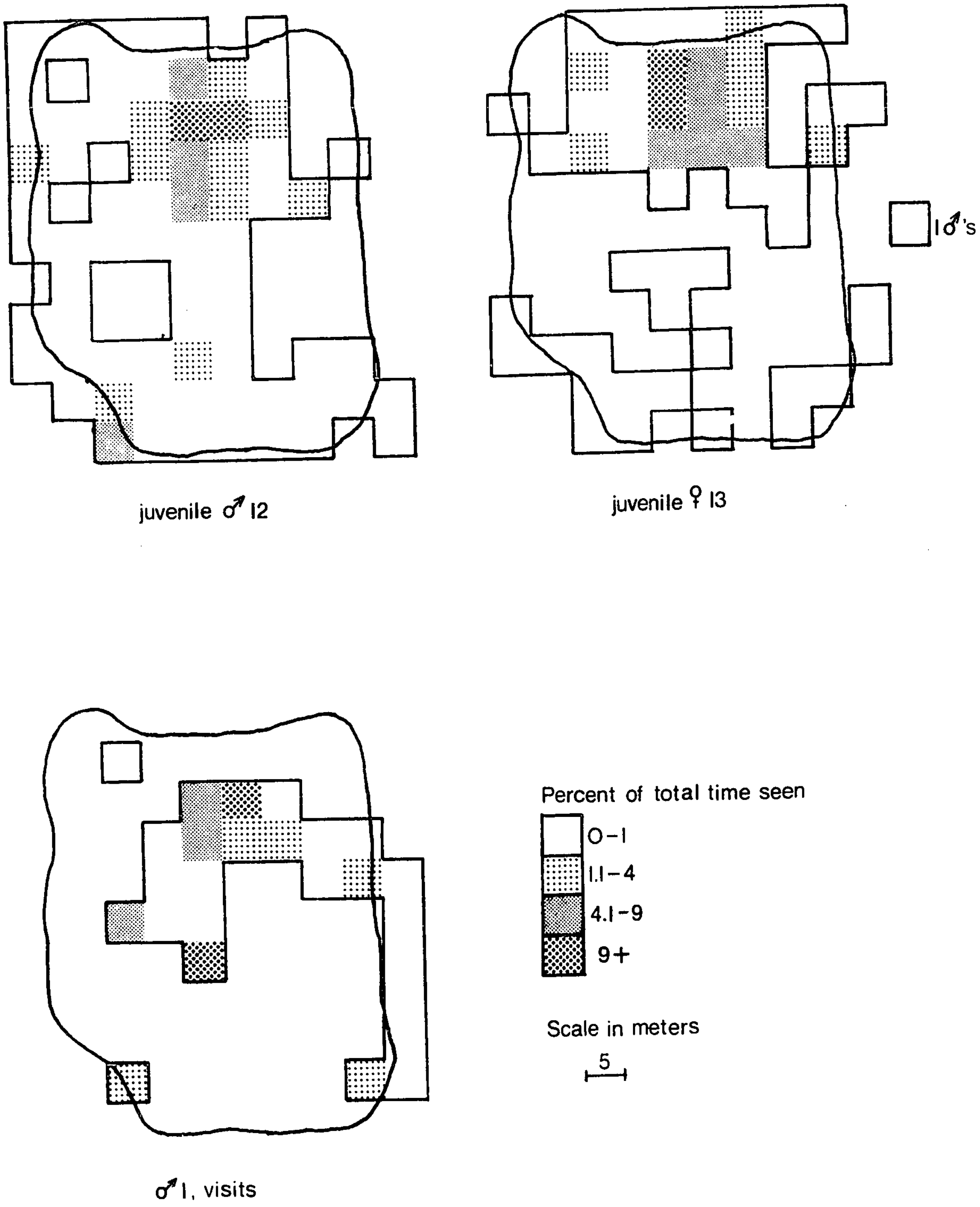


Figure 22. Individual utilization of home range, Jumping Pound study area, August 3 - September 6, 1970.

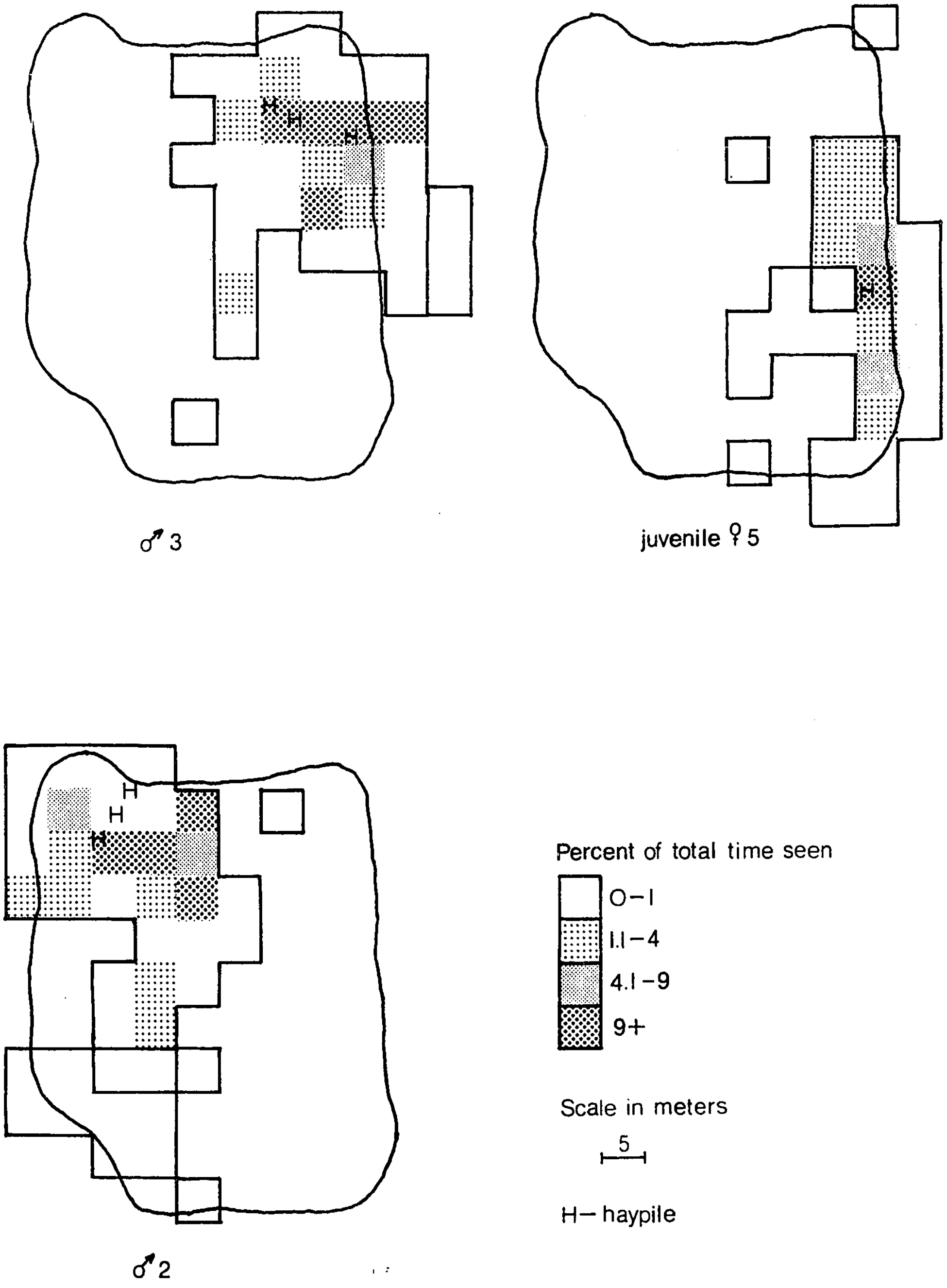


juvenile ♂ 12

juvenile ♀ 13

♂ 1, visits

Figure 23. Individual utilization of home range, Jumping Pound study area, July 15 – August 26, 1969.



1969, ♂WR and ♀TE showed heavily overlapping ranges (particularly in spring). This is also shown by ♂RR-♀TE and ♂GR-♀TE in 1970 on the Kananaskis, and on the Jumping Pound by ♂3-♀5 in 1969 and 1970, and by ♂2-♀14 in 1970. In addition, ♀5 and ♀13 spent a significant portion of their time with ♂1 in August 1970 and were considered partially paired to him.

Kananaskis study area.

May 1969 ranges (Figure 13) are incomplete, probably underestimating range sizes for ♂WR and ♀TE, and innacurate for ♂RR, who was seen only 0.28 hours total. The pair ♂WR-♀TE show many overlapping or adjoining intensively used areas. June 1969 (Figure 14) shows larger ranges for all pikas, with scattered core areas and fewer overlapping intensively used areas between the pair ♂WR-♀TE. The two ♂♂ centered some activity around their haypiles, while the ♀ did not.

July 1969 ranges (Figure 15) are larger still for all pikas. Three factors contributed to this: the presence of a juvenile ♂, the initiation of haying by adult ♂♂, and greater time spent observing and achievement of consistent observational techniques by the observer. There is perhaps an increase in overlapping and adjoinining intensively used areas between the pair ♂WR-♀TE, although ♂WR spent a larger amount of time near his haypiles. A few days after his appearance, the juvenile ♂LK settled in the abandoned haypile, with a home range situated roughly between the two adult ♂♂. The apparent intensive use of two areas by the juvenile ♂LK well within ♂RR's range is entirely from the day he emerged and is not representative of his later home range. The range of ♂LK was overlapped heavily by the adult ♂♂, and ♀TE showed a shift in range toward ♂LK.

August 1969 ranges (Figure 16) are smaller for all pikas, with complete separation of intensively used areas between the pair ♂WR-♀TE. The single ♂RR was seen only 0.44 hours in August and his range is probably innacurate.

All individuals had large ranges with scattered intensively used areas in April-May 1970 (Figure 17). The pair ♂WR-♀TE exhibit overlapping sitting areas, but little overlap in feeding areas. It appears that ♂RR had taken over ♂WR's old range (Figures 13-16) as well as retaining some of his old range. The range of ♂GR (the ♂ that replaced ♂RR) is large, showing scattered areas of intensive use and heavy overlap with ♀TE. During the time he was present, he was still exploring the area and did not adopt a haypile complex.

Jumping Pound study area.

Adult ranges are large in June 1970 (Figure 18) and similar to those of the Kananaskis, having scattered intensive use areas. Both ♂♂ centered some activity around their haypiles, while the ♀ did not, in agreement with the situation on the Kananaskis study area. The pair ♂3-♀5 show overlapping and adjoining areas of intensive use. A large amount of time was spent by ♀5 within the upper part of ♂3's home range. She was caring for her young, which were located under VP; she bred again in mid-June, and may have been attracted to the juveniles later in June, as ♀TE showed a shift toward her offspring after it had been weaned.

The downward shift shown by ♂2 (compare to Figure 23) may have been a response to the activities of the juveniles, ♂10 and ♂11 (Figure 19). Both juveniles had restricted ranges, centered around their birthplace, but they spent slightly more time within ♂2's range than within that of the pair ♂3-♀5. Visiting activities of ♂1 appear centered around VP and the base of the rockslide. Two things probably drew him to the area around VP; the juveniles, and the presence of at least four well-defined and rather traditionally used fecal piles. When ♂1 visited the main rockslide, he often contributed to these piles (see Marking Behavior).

July 1970 ranges (Figure 20) show little change in size. Shifts in intensively used areas, however, are apparent for all pikas. Both ♂♂ centered activity around their haypiles, concurrent with the onset of haying. The ♀ also centered some activity around her haypile to a lesser extent, spending some time with her offspring. Visiting by ♂1 dropped in July, but visits were still centered around VP. The pair ♂3-♀5 showed little overlap of intensively used areas, in contrast to the pair ♂WR-♀TE on the Kananaskis study area. This earlier separation of ranges of pair members might be due to the earlier initiation of haying on the Jumping Pound.

All residents showed distinct haypile oriented core areas in August 1970 (Figure 21). Both pairs (♂3-♀5 and ♂2-♀14) show no overlap in intensively used areas. The downward shift shown by ♂2 is undoubtedly a response to ♀14, who settled in an abandoned haypile. A high number of agonistic interactions was seen between this pair. The expanded range of ♀5 is probably a response to the presence of ♀14, and perhaps that of the other two juveniles, ♂12 and ♀13 (Figure 22). The ranges of these juveniles were large, but again concentrated around VP, similar to those of ♂10 and ♂11 in June 1970 (Figure 19). Visits by ♂1 increased in August, indicating that he was attracted to the juveniles.

Ranges in August 1969 (Figure 23) were small, with each pika having a well defined core area. The pair ♂3-♀5 showed no overlap in intensively used areas, an arrangement similar to that of the same pair in August 1970 (Figure 21) and of the pair ♂WR-♀TE on the Kananaskis in August 1969 (Figure 17).

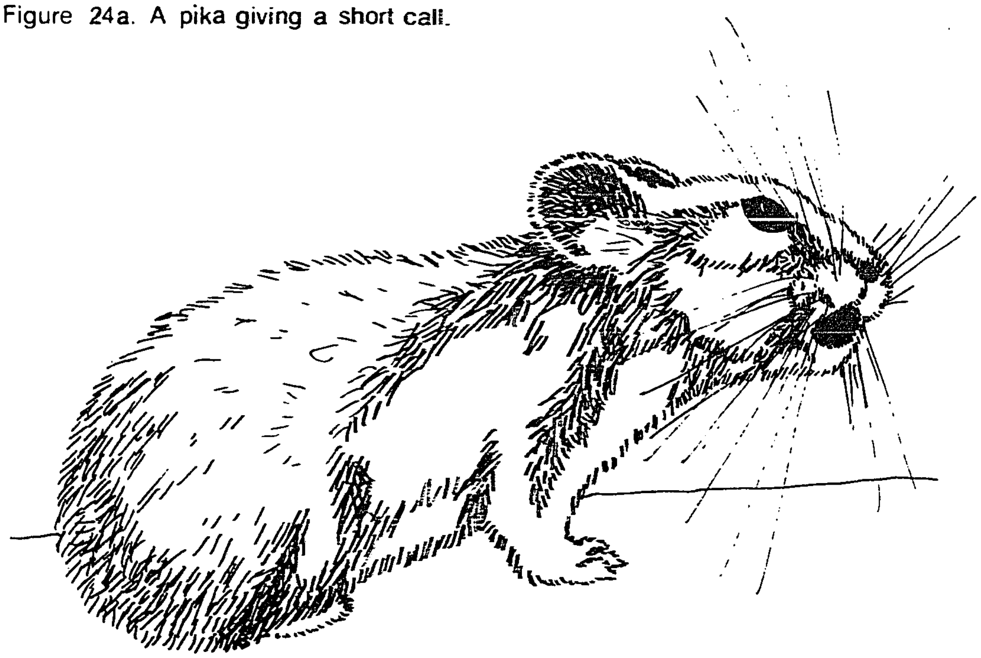
5.2 Vocalization and Agonistic Behavior.

The pikas in my study areas were heard to give six distinct types of calls. All these were given in more than one context. Five different agonistic patterns were distinguished and are described and discussed below.

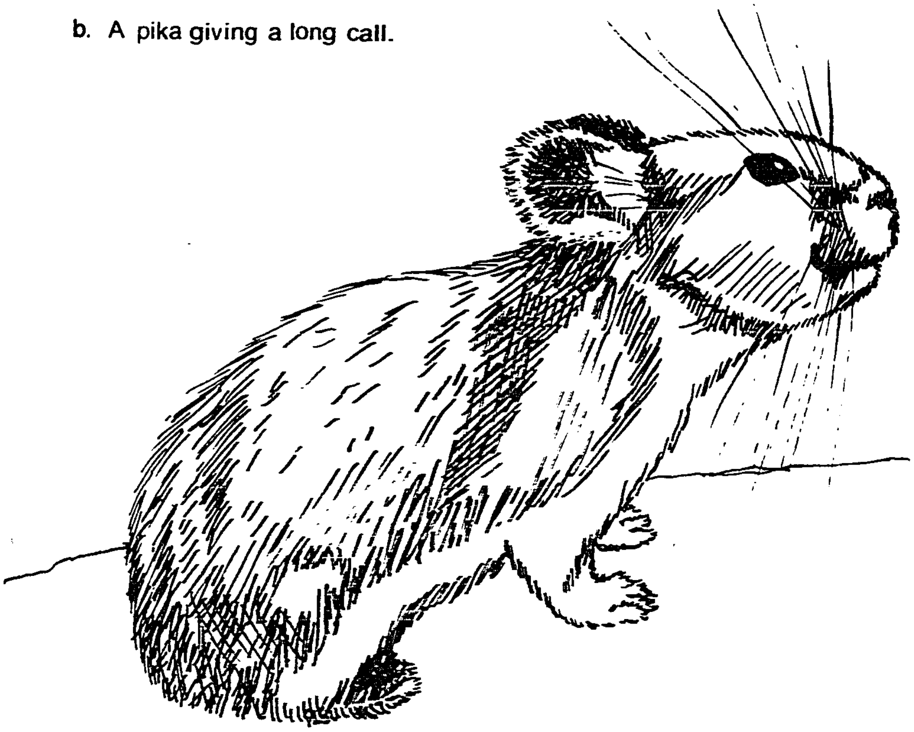
Short call.

This is the most frequent call. It is a single short "ANK!", given as the pika's feet are planted squarely and its head is thrust vigorously forward (Figure 24a). The short call is given by all sex and age classes. Howell (1924), Severaid (1956), Kilham (1958), Krear (1965), Broadbooks (1965), and Kawamichi (1968) describe this call. Krear (1965) distinguished four types of short call: a territorial declaration call, a dominant chase call, a

Figure 24a. A pika giving a short call.



b. A pika giving a long call.



subordinate chase call, and an alarm call. I agree only partially with his classification.

The most frequent short call given is Krear's (1965) territorial declaration call -- it is fairly high pitched (this varies with the individual), lasting about 1/4 to 1/2 second. This call is given while a pika is sitting, or before or after a haying trip. When given by a resting pika, others often reply and an exchange of calls ensues. These exchanges are not mentioned by Krear (1965) or other authors. For tallying data, the criteria used for a call exchange were that: (1) at least two individuals participated, (2) total calls given was more than two, and (3) the interval between calls was less than 30 seconds.

Later in summer in both years on both study areas, many short calls were briefer (around 1/4 second) and more forceful than the territorial declaration call. These were given when a pika was approached too closely by another, or sometimes when another was merely sighted or heard. Sometimes a call exchange followed if the invader did not retreat, and occasionally the invader was chased. This could also be given by a pika that stopped for a moment while chasing another. Krear (1965) described this pattern and named the call the dominant chase call. In recording data, no distinction was made between the territorial declaration call and the dominant chase call, as there are gradations between the two.

The third variation is much lower pitched than other short calls and very brief. It sounds like a muffled, cut-off short call and was usually given as a pika was moving. Pikas gave this in three situations: when surprised, when chased by another, or when chasing another. This is Krear's (1965) subordinate chase call. Krear never heard both participants of a chase give this; he heard it only from the pika being chased. Because of this difference I refer to this as the chase call.

The fourth type is the alarm call, given in response to a potential predator or other disturbance. The pikas responded to any potential mammalian predator, any bird flicker-sized or larger, and to alarm calls of other resident birds and mammals. The alarm call had a sharper sound, and may be higher pitched than other short calls. This is also mentioned by Krear (1965) in his description. Alarm calls were excluded from calculations of call frequencies.

The fifth type I could distinguish has not been previously reported. It was only given by one individual, ♀14, who established successfully on the Jumping Pound study area, pairing with ♂2; but not without meeting hostility. She was chased many times by ♂2, with the chases often preceded by a call duel. The ♀ would sit on her favorite rock, the ♂ just below his haypile. The ♂ would approach, calling, she would reply and finally be chased. During these call exchanges, particularly as the ♂ approached, her calls became lower pitched, dropping off at the end, and were longer than other short calls (1/2 second or more). This call was distinctive, and I would describe it as a plaintive sound. It may be associated with the pairing process; however, it did not appear to be of appeasement value, as ♀14 was generally chased whether she gave this call or not.

♂ Long Call.

Severaid (1956), Krear (1965), and Broadbooks (1965) describe this call. It is actually a long chattering series of calls that decrease in pitch and increase in interval as the call proceeds. It is given by ♂♂, from much the same position as the short call except the head is not as vigorously extended. The head is thrust forward slightly and the ears flip as each component is given (Figure 24b). It lasts from 10-20 seconds and is usually followed by one or more short calls. In spring and early summer, ♂♂ participate in long call exchanges. One evening on the Kananaskis study area in May 1969, the two ♂♂ "exchanged" calls for about a half-hour, giving long calls at intervals of 1-2 minutes. These exchanges are also described by Severaid (1956) and Krear (1965). Although heard all summer, long calls were most commonly heard in April, May, and June.

♀ Long Call.

Only Severaid (1956) reported hearing ♀♀ giving long calls. This resembles the ♂'s long call, but is shorter (3-4 seconds long) and has between four and seven components. I heard four different adult ♀♀ give this call. It was given in two contexts, when a ♀ was apparently in heat (see Reproductive and Maternal Behavior) and later in summer, during interactions with ♂♂; likely as appeasement when a ♀ encountered a ♂ within his home range, as in these cases the ♀ was allowed to remain near the ♂ and was not chased.

Chattering.

This is produced by rapid chattering of the teeth, and is probably Severaid's (1956) "purring." It is given during courtship by both ♂♂ and ♀♀. I also heard a ♀ chattering in conjunction with giving long calls in the same situation as described above for ♀ long calls. Pikas usually chatter while they are moving.

Submission Call.

This call is given by all sex and age classes (Tapper, Millar, Samuels, (pers. comm's.) have heard adults give it), although in my study areas it was given mainly by juveniles, as Krear (1965) reported. It is a whining noise, repeated several times, and very similar to the sounds guinea pigs make. Pikas give the submission call when under stress, particularly if they are approached or have been chased by another.

Agonistic Interactions.

Five patterns were distinguished: call exchange or duel, approach, interruption, chase, and attack. The call exchange was the most common pattern and has been described under vocalization. Exchanges occur between and within all sex and age classes. Territorial declaration calls, dominant chase calls, and long calls may be given in call exchanges. Duels often result in an approach and/or chase, particularly later in summer. The outcome of approaches varied about equally between the approachee withdrawing, the approachee being chased, or the approacher retreating.

Late in summer, ♀♀ interrupted ♂'s long calls with short calls, characteristically the dominant chase call. A ♂ was heard interrupting another ♂ only three times; this was done by juvenile ♂♂ only. Twice in late summer, a ♂ giving a long call was well within the home range of a ♀ and about 1-2 m from her. The ♂ gave the long call when approached by the ♀, the ♀ interrupted with a dominant chase call and chased the ♂ out of her home range.

Chases vary in length and intensity and are accompanied by chase calls and dominant chase calls. The pikas move quickly through the rocks, stopping occasionally, and sometimes even out into the surrounding vegetation. The longest chase I saw lasted 5 minutes, the shortest a few seconds. Krear (1965) and Broadbooks (1965) also describe chases. Chases occur between and within all sex and age classes.

Only two attacks were seen; both involved juveniles on the Jumping Pound study area. In June 1970, ♂11 attacked his smaller brother, ♂10, by jumping onto him from above. The juvenile ♂10 retreated immediately and disappeared from the study area a few days later. In August 1970, ♀14 had been chased and approached repeatedly by ♂3; she moved to a rock overhanging ♂3's regular haying route through the area, lying with her head down. When ♂3 (apparently unaware of her presence) moved beneath her a few minutes later, she jumped onto him, kicking with her hind legs. The ♂ retreated immediately, giving chase calls. He stopped 3 m away, faced ♀14, then chased her into ♂2's range.

Krear (1965) saw part of one prolonged fight; none were seen during my study; although there was evidence that some fighting may have occurred. A few days after the second attack described above, ♀14 had fresh blood stains below her left ear. These were not likely from her ear tag as she had been tagged a month before. In addition, a juvenile ♀ was trapped on a nearby rockslide in the Jumping Pound in early August and she had several round bare patches on her rump. Severaid (1956) mentioned that occasionally when a pair of pikas were in the same cage, one started pulling fur out of the other's rump and they had to be separated. Dice (1927) also observed this in captive pikas.

Analysis and Discussion.

Distribution of calling throughout the day reflects general activity closely and thus is not presented here. A seasonal analysis of average call frequencies for individuals is presented in Table 4. These frequencies were calculated by averaging the call frequencies of the hours of the day, as the distribution of observations throughout the day varied between months.

In April 1970, and May and June 1969, the ♂♂ were much more vocal than the ♀ on the Kananaskis study area. In July

Table 4. A seasonal analysis of average call frequencies for each individual, expressed as mean number of calls/hour observed. Paired individuals are shown with an asterisk.

		April-May 1970	May 1969	June 1969	July 1969	August 1969	July-August
Kananaskis study area							
Adults	♂RR	4.6*	5.4	5.9	3.9	6.9	
	♂WR		6.7*	4.8*	4.6*	14.0*	
	♂GR	2.0*					
	♀TE	0.6*	1.5*	2.4*	4.8*	9.8*	
Juveniles	♂LK				2.1		
Jumping Pound study area				1970	1970	1970	1969
Adults	♂1			3.6	7.9	9.8*	5.8
	♂2			5.0	7.8	13.5*	4.6
	♂3			3.9*	7.0*	11.7*	7.9*
	♀5			3.1*	6.5*	12.1*	7.3*(juvenile)
Juveniles	♂10			0.9			
	♂11			0.5			
	♂12					3.3	
	♀13					3.2*	
	♀14					21.7*	

and August, the ♂♂ and ♀ had similar call rates, with a definite peak in calling in August 1969. The juvenile ♂ present in July called less often than the adults.

On the Jumping Pound study area, all adults had similar call rates, increasing through the summer to a peak in August 1970. The juveniles present in June and August 1970 had much lower call rates than the adults, with the exception of ♀14. This ♀ was one of two juveniles seen to establish successfully (the other being ♀5 in August 1969), and was the most vocal individual encountered during this study.

Paired pikas (shown with asterisks in Table 4) are more vocal than unpaired ones in August. Information on April-July is inconclusive. This increased calling by paired pikas is concurrent with the August separation of intensive use areas of pair members, and certainly one of the contributing factors to separation, as discussed below.

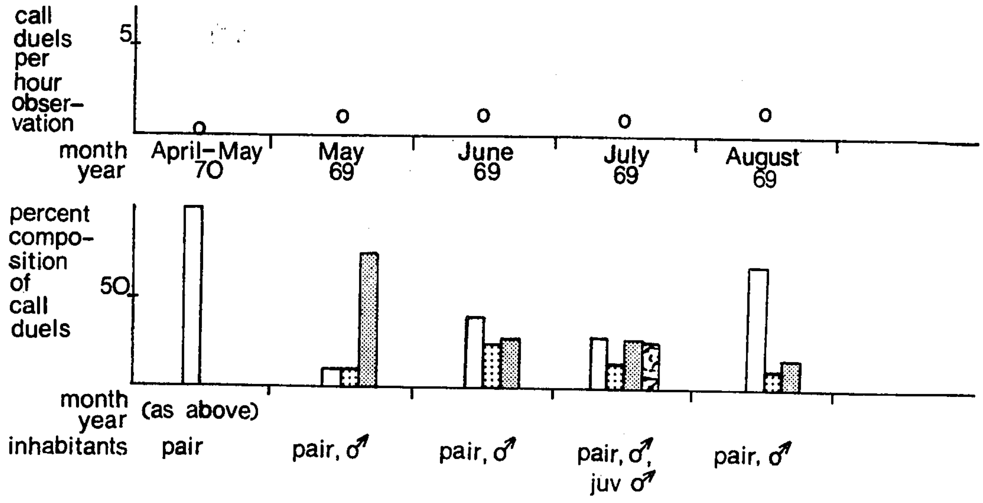
For analysis, call duels were separated into single call duels (two participants) and multiple call duels (more than two participants). The majority of exchanges heard were single ones. The results are summarized in Figure 25, where total call duels heard per hour observation and percent composition of single call duels is presented for both study areas. The juveniles ♀5 (1969) and ♀14 were members of pairs and were included in that category rather than considered juveniles, and considered ♀♀ in other interactions.

Figure 25. A seasonal analysis of occurrence and composition of call duels.

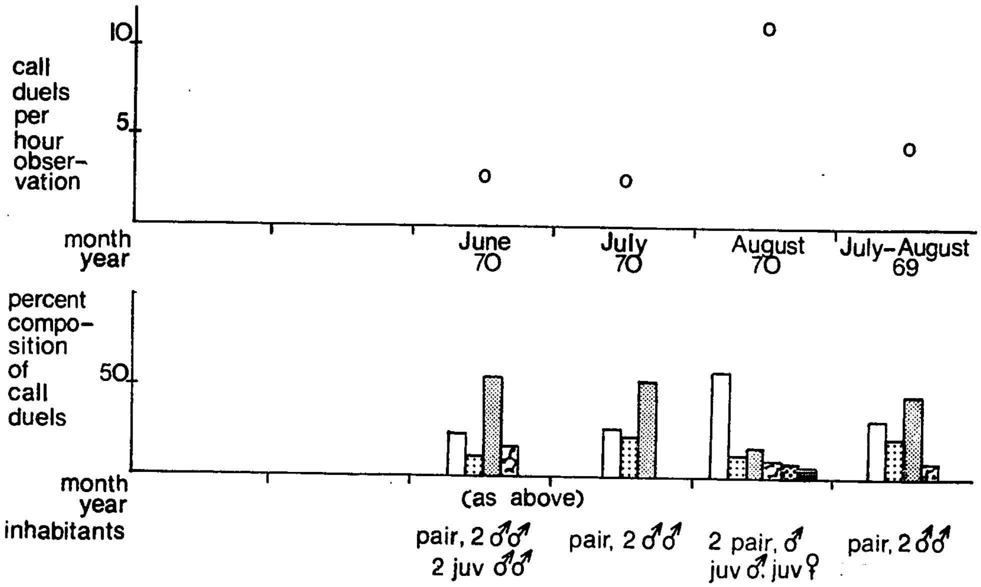
Participants:

pairs	□	♀–♀	⊠
♂–♀	⊞	adult–juvenile	▨
♂–♂	▩	juvenile–juvenile	■

Kananaskis study area



Jumping Pound study area



With the exception of the Jumping Pound study area in August 1969, there is a decrease in ♂-♂ interactions and an increase in pair interactions through the summer. Maximum ♂-♂ interactions occur during the breeding season and maximum pair interactions occur in August. The higher overall rate of call duels on the Jumping Pound is probably a reflection of the number of pikas present. In July-August 1969 on the Jumping Pound, the juvenile ♀5 was involved in 57/124 call duels, in June 1970, the two juvenile ♂♂ were involved in only 14/95 call duels, and in August 1970, ♀14 was involved in 254/527 call duels, ♀13 in 36/527, and ♂12 in 21/527 call duels. Thus, when juvenile ♀♀ were present on an area and pairing with ♂♂, they were involved in approximately 50 percent of the call duels that occur, accounting in part for the observed increase in this interaction during July-August 1969 and August 1970.

The increase in call duel rate in August 1970 on the Jumping Pound area is due to a combination of the high number of pikas on the rockslide, two juvenile ♀♀ attempting to pair with ♂♂, and the adult ♀ attempting to pair with another ♂ while still paired with her original ♂.

A seasonal analysis of interruptions is presented in Table 5. Although an infrequent interaction, interruptions occur most often in August, and 83 percent of the interruptions heard were between paired or pairing individuals. In August 1970, the juvenile ♀13 was spending some time with ♂1, as was ♀5, and in this analysis both were considered as

Table 5. Total interruptions (n = 46) heard on both study areas, 1969-70. Those occurring within pairs are marked with an asterisk.

	Individual	April-May	May	June	July	August
Kananaskis study area	♀TE	0	0	0	4*	0
Jumping Pound study area	♀5			2	1	5*, 1(1969) 10*, 13*(1970)
	♀14					1
	♀13					6*
	♂12					3

One interruption was heard in late April 1971 on the Jumping Pound study area. From the behavior of the pikas at that time, I am certain that the ♀♀ had already bred.

partially paired or pairing with ♂1. This indicates increased antagonism between pair members in late summer, and several times interruptions were followed by chases.

Frequency and composition of approaches is summarized in Figure 26. The frequency of approaches was generally low, less than one per hour observed throughout the summer on both study areas. These interactions were calculated on the basis of time spent observing rather than time seen. A total of 130 approaches were seen: 57 percent between pairs, 10.8 percent between non pairs, 25 percent between adults and juveniles, 2 percent between ♂♂, and 1 percent between ♀♀. Approaches between pair members are probably sexual in April and May. Most approaches involve pairs throughout the summer, and adults and juveniles when juveniles are present.

Some approaches were not followed by chases or submission calls. On these occasions the approach may have been between animals of equal "status" or between pikas that were quite familiar with each other and/or on neutral ground.

Composition and frequency of chases are summarized in Figure 27. Only 16 chases were seen on the Kananaskis study area in 1969-70, seven of these between the pair ♂WR-♀TE, the ♀ losing every chase. In July, the ♀ lost two chases to the single ♂RR, and chased ♂LK twice. The juvenile ♂LK also lost three chases to ♂WR, never winning any chase. When he was present, this juvenile was involved in the majority of chases seen.

On the Jumping Pound study area, 247 chases were seen

Figure 26. A seasonal analysis of occurrence and composition of approaches.

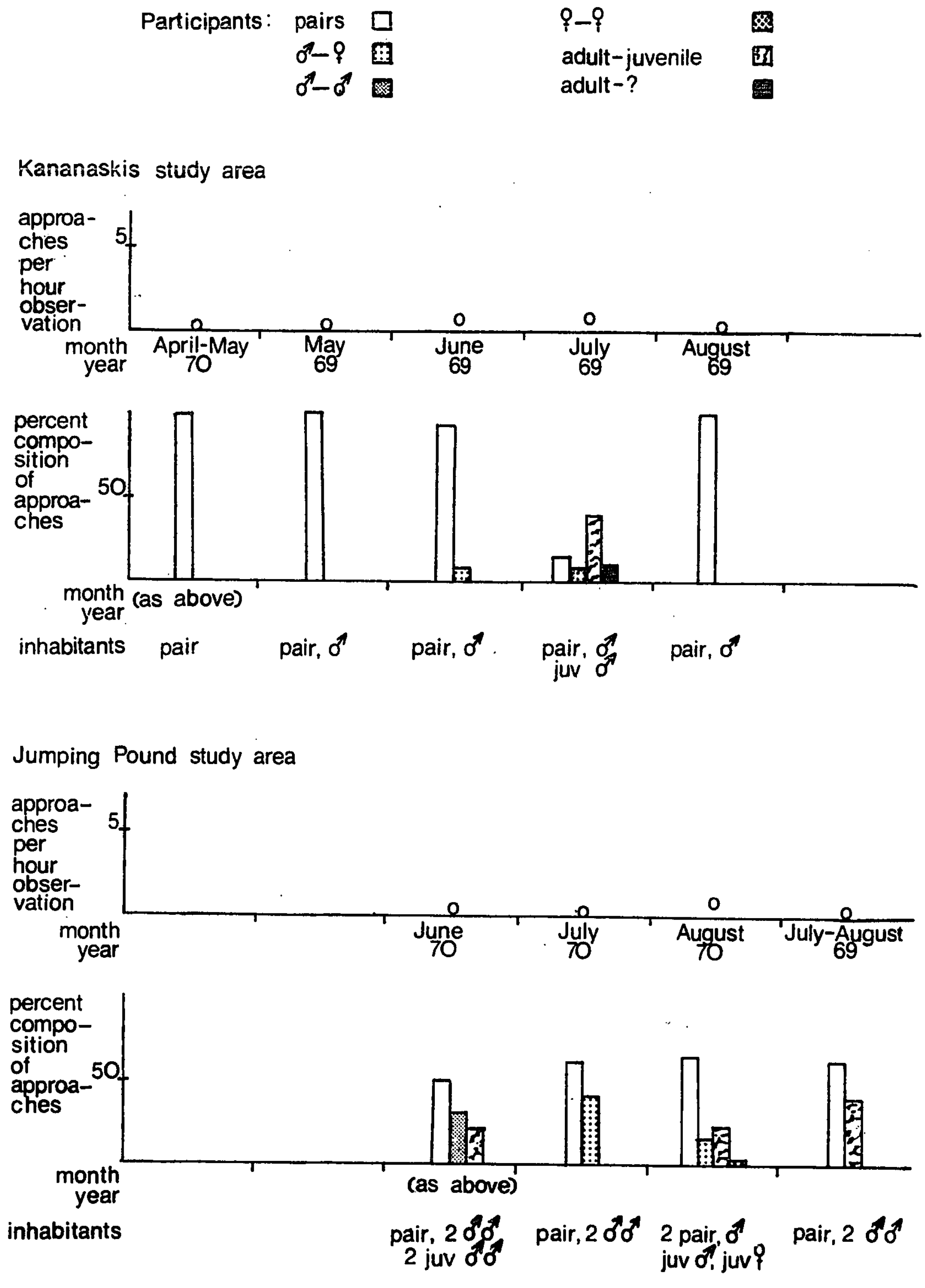
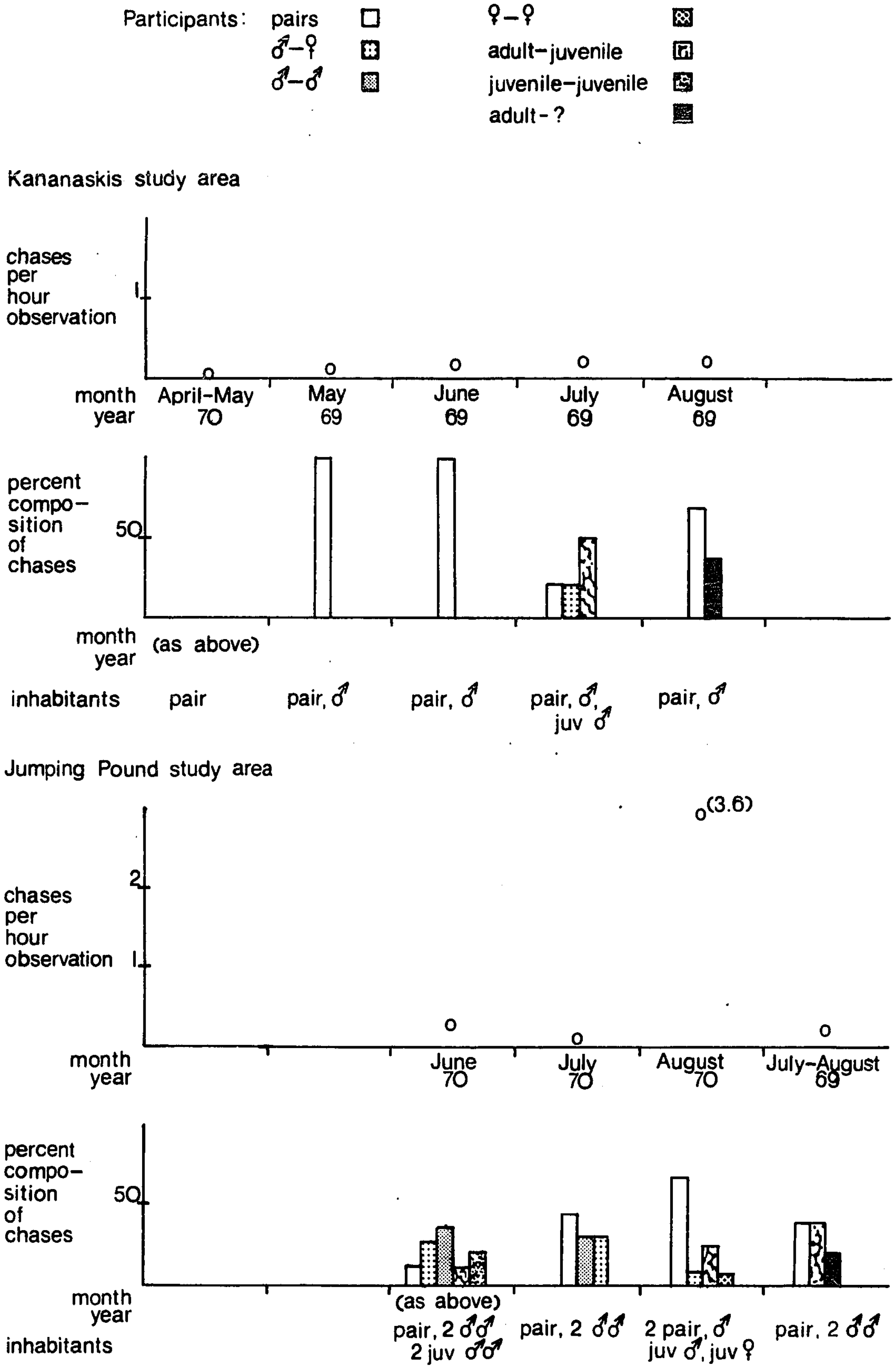


Figure 27. A seasonal analysis of occurrence and composition of chases.



in 1969-70. In July-August 1969, the juvenile ♀5 lost all her chases, two to her ♂ and one to her mother, ♀4. In June 1970, only one of the 11 chases seen was between pair members. All four of the ♂-♂ chases in June involved the visiting ♂1. Many of ♂1's visits resulted in his being chased off the rockslide when he was discovered by the resident adults. This ♂ won two and lost five chases. The adult ♀5 won two chases (against ♂11) and lost two (one to ♂3 and one to another ♂). The juvenile ♂10 won three chases, one against ♂1 and two against ♂11. These juveniles were inconspicuous and nonvocal when compared to the others seen in this study, and were involved in relatively few interactions with the adults.

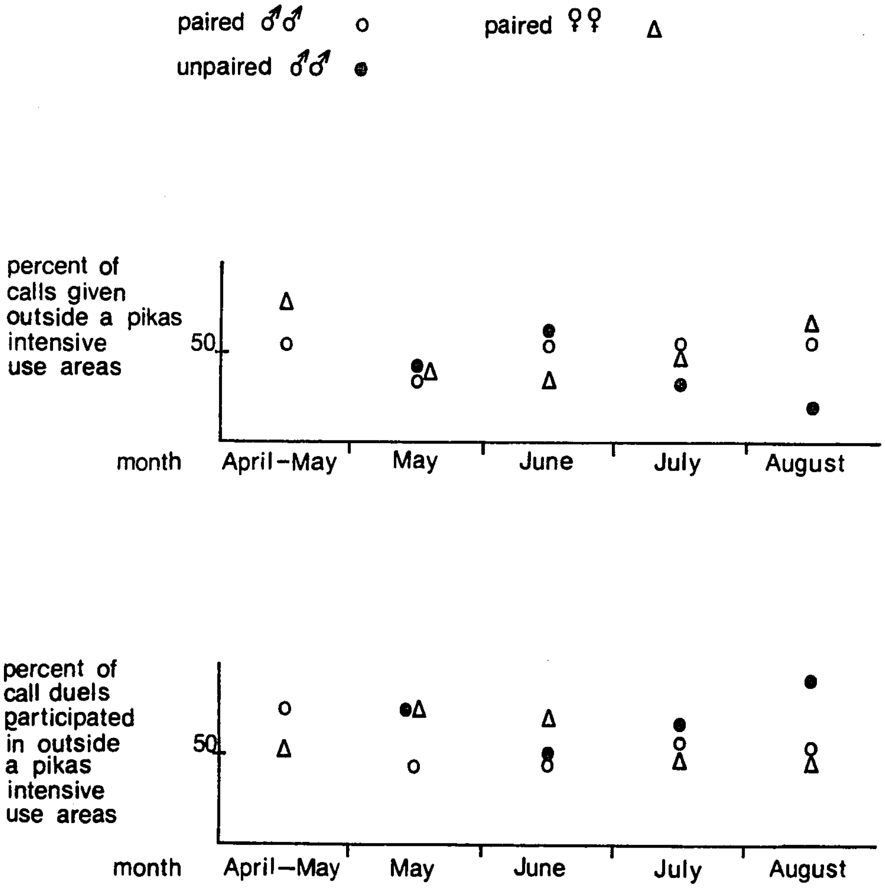
Chases were perhaps less frequent in July. The ♀5 won two chases and lost one against ♂3. She won and lost one against ♂1. The ♂♂ 2 and 3 each chased each other once.

In August, 224 chases were observed, an extraordinary increase over July. The juvenile ♀14 was considered an established pair member, as she had a fixed home range and haypile, she was twice as vocal as the adults, and she won some chases against ♂2 and other adults, indicating that she was defending her home range. Out of the 224 chases seen, 124 involved ♀14. A total of 184 of the chases seen involved ♀14 or a juvenile; accounting for the increase in chases in August on this study area. The ♀♀ 13 and 14 were involved in 153 of the 224 chases recorded. These juveniles were generally more conspicuous and vocal than the others seen in this study. In addition, the ♀♀ 5 and 13 were partially paired with ♂1, and accounted for some chases.

Thus, the high number of chases on the Jumping Pound study area in August is due to a combination of (1) vocal and conspicuous juveniles, (2) several juvenile and adult ♀♀ either pairing or attempting to pair with ♂♂, and (3) the general phenomenon of increased aggression between pair members in August, displayed by the pikas on both rockslides in both years. From the frequencies and outcomes of the above agonistic patterns, the intensity of threat implied increases from call duel - approach - chase - fight. The status of interruption is not clear, as on several occasions it resulted in a chase, but generally did not.

Figure 28 shows a seasonal analysis of the relationship of calling (calls and call duels) to intensive use areas for all individuals and months, expressed as percent of calls given and call duels participated in outside the individual's intensive use area. Both rockslides are combined in this analysis. Individuals here are classed as single ♂♂, paired ♂♂, and paired ♀♀. Unpaired juveniles are not included in this analysis. Single ♂♂ show perhaps a peak in calls outside of intensive use areas in June, followed by a decline through July and August. Pair members appear to call more outside of intensive use areas in April-May, dropping in late May and rising to a second peak in August. The percent of calls given within intensive use areas by ♀♀ declines

Figure 28. A seasonal analysis of the relationship of all calls and call duels to intensive use areas.



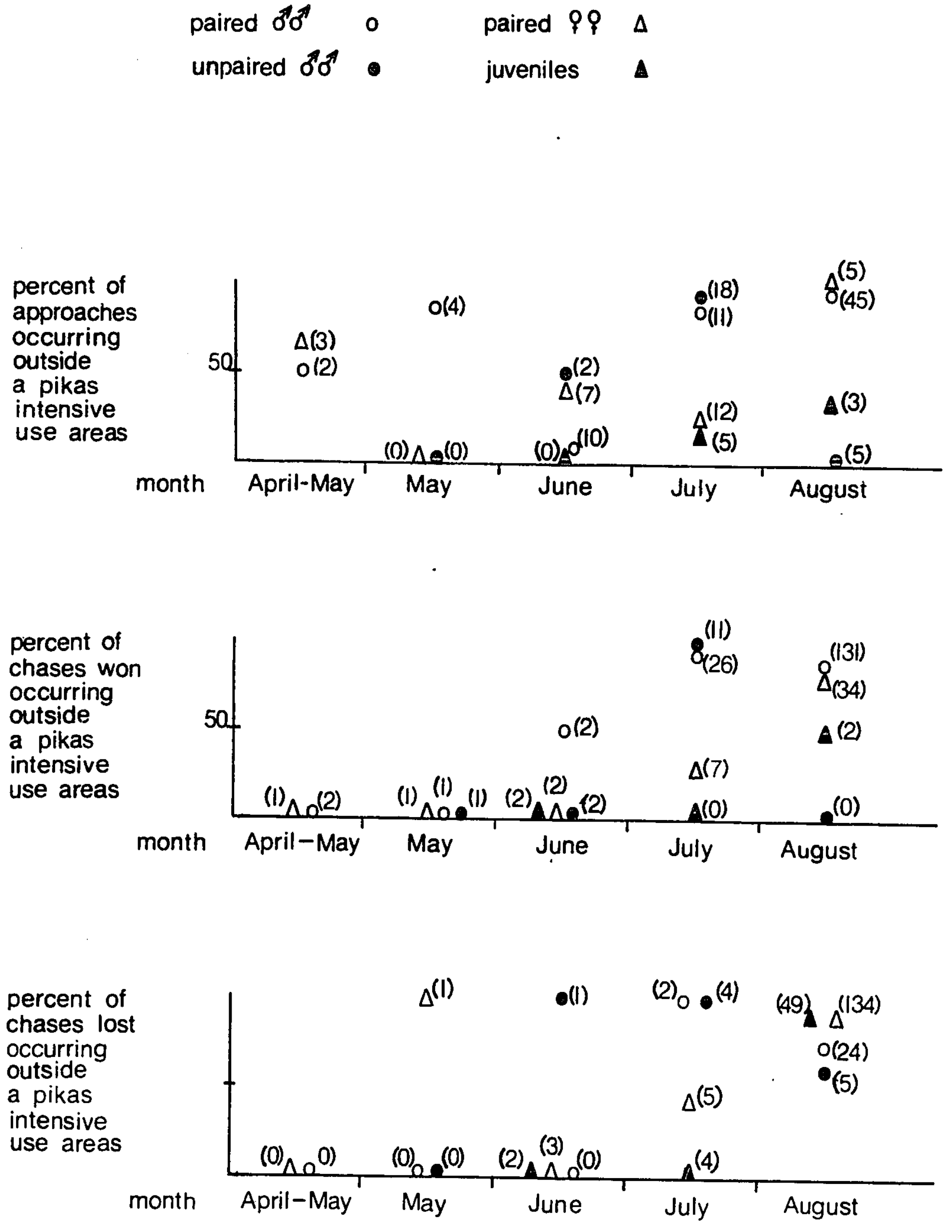
during the breeding season. Paired ♂♂ and ♀♀ show a gradual decrease through the summer in call duels participated in outside of their intensive use areas. Single ♂♂, however, show a high level of call duels outside core areas in May, decreasing in June, then increasing steadily through July and August to a level much higher than paired individuals.

The pair ♂2-♀14 on the Jumping Pound study area in August 1970 called and duelled more frequently and were involved in more interactions outside their intensively used areas than were ♂3-♀5. While ♀14 was in the process of pairing with ♂2 and establishing her home range, both pikas were more actively defending larger portions of their home ranges vocally than the other residents.

Figure 29 shows a seasonal analysis of approaches, chases won, and chases lost in relation to intensive use areas. Paired ♂♂, unpaired ♂♂, paired ♀♀, and unpaired juveniles are grouped and averages shown. Sample sizes for April, May, and June are small; the July and August sample sizes are larger. Interactions occurring outside core areas increase to a peak in July and August (with the exception of call duels, (Figure 28), which may decrease slightly in paired pikas in August).

The outcome of chases does not appear to depend greatly on whether a chase occurs within or outside of an individual's core areas, as 76 percent of all chases won and 81 percent of all chases lost occurred outside a pika's core areas.

Figure 29. A seasonal analysis of the relationship of approaches, chases won, and chases lost to intensive use areas (number of interactions in parenthesis).



Thus, late summer separation of core areas is effected by a general increase in antagonism, particularly between paired individuals, and expansion of an individual's actively defended area to outside of its core area.

5.3 Reproductive and Maternal Behavior.

The breeding season lasts from mid-April to early July (Millar 1971). The ♀♀ conceive two litters, but typically only the first is successfully weaned (Krear 1965, Millar 1971). The gestation period is about 30 days (Severaid 1956), and the young are weaned at 3-4 weeks (Severaid 1956, Millar 1971). On the Jumping Pound study area, however, the yearling ♀5 produced two litters in 1970. The first appeared on June 11, the second on August 4, thus she must have bred in early April and early June. This rockslide is south-facing, and clear of snow in late winter. The lack of snow on the area and surrounding slope may have provided increased food, perhaps bringing this ♀ into breeding condition early. The ♂♂ go out of breeding condition in late June or early July, although some adult ♂♂ are incapable of breeding in early June (Millar 1971).

Courtship.

I have seen part of courtship only twice, both times in 1970. On May 1, on the Kananaskis study area, I first heard a ♀ giving long calls. Before the ♀ gave these calls, she was seen sitting on the same rock with ♂RR. Krear (1965) reported seeing ♂♂ and ♀♀ sitting on the same rock in spring also. The ♂ remained close to the ♀, responding to her calls with his own many times. The ♂ approached the ♀ several times, then fed voraciously. This was probably displacement feeding arising from the conflict between his sexual drive versus approaching the ♀ too closely.

On July 1, in the Jumping Pound, a captive adult ♀ began giving long calls in the evening. I was observing on the Jumping Pound study area at the time (about 70 m away) and all three resident ♂♂ responded to her with long calls. One adult ♂ made his way to the base of the rockslide, giving long calls, which were answered by the ♀. This ♂ then disappeared into the vegetation at the base of the rockslide, calling all the while. He crossed the road and went to the pens that contained the ♀. I moved to the pens and continued to observe. The ♂ ran along the outside of the pens, chattering, accompanied by the ♀ on the inside. The pair stopped frequently and nosed through the wire. The ♀ gave a long call, and as her call ended the ♂ gave a long call. These calls were given so close together they sounded like one. This call "duet" could easily be mistaken for a single call given by the ♂ if the observer was not very close.

This sequence was repeated several times. The ♂ also made several excursions around the pens; chattering, calling, and moving noisily through the vegetation. The ♀ sat on her small rockpile or in a corner while the ♂ was away. This ♂ visited the ♀ on four evenings. I was unable to trap the ♂ to place him in the pen, and copulation was never observed, although Severaid (1956), Krear (1965), and Millar (pers. comm.) report seeing copulations.

Care of the Young.

Like rabbits, pikas are born unfurred and with their eyes closed. They are weaned at 24-28 days of age at a weight of about 45 g (Millar 1971). The ♀♀ reared their young far from their haypiles, usually at the edge of their home range. Tapper (pers. comm.) noticed this also. On the Kananaskis study area, the juvenile ♂LK first appeared near ♂RR's haypile; and on the Jumping Pound, ♀5 raised both litters beneath the rock I used as an observation place. Muffled sounds were heard from the nest before the juveniles appeared.

Since ♀5's second litter appeared on August 4, their approximate birthdate is the first week of July. Visits by ♀5 to the nest that were seen between July 2 and August 4 are presented in Table 6. On July 2, ♀5 gave several long calls, and since pikas have a post-partum estrus (Severaid 1960), she probably gave birth around July 1. Although these data are at best sketchy, it appears that ♀5 visited her young at intervals of 2-3 hours during daylight. Occasionally she was seen carrying dried leaves or grass into the nest, perhaps as bedding material.

5.4 Marking Behavior.

Kleiman (1966, p 167) states that "Scent marking has been defined as urination, defecation, or rubbing of certain

Table 6. Visits by ♀5 to her nest during July 2-August 4, 1970.

Date	Hours of Observation	Hour of Day of Visit	Time spent in Nest (min)
July 2	9-13, 16-18, 19-21	10, 13	4:30, 4:00
July 4	9-13	10	6:00
July 6	16	--	
July 7	12-17, 18-21	13	2:00+, noises heard
July 8	9-12	10	4:30
July 13	7-10, 11-13	12	1:30+
July 17	5-8, 10-11, 11-20	7	1:30 (?)
July 18	8-11, 17-20	8, 10	♀5 sitting on VP as I approach, ?
July 22	4-6, 15-18	16	5:00
July 23	6-8, 9, 17-20	--	
July 29	15-19	16, 18	0:30, 2:15
August 1	17-20	18	?
August 2	9-13	One juvenile peeked at me momentarily, then returned to the nest.	
August 4	Juveniles emerge.		

areas of the body which is (1) oriented to specific objects, (2) elicited by familiar conspicuous landmarks and novel objects or odours, and (3) repeated frequently on the same object."

Urination and defecation have been described under eliminative behavior. Most sites of elimination were sheltered and not visible to me, and elimination was rarely seen. In midsummer 1970, defecation was first seen on an exposed rock. An adult ♀ stopped on a flat rock, sniffed its outer edge, turned around and squatted, sniffed the edge again, then moved off. I checked the site immediately and found three fresh pellets on the rock edge, coated with a light yellow substance (urine?) that more or less glued them to the rock. Six or fewer pellets were deposited by pikas when elimination was seen on exposed sites and the site checked. However, this is not true of elimination in sheltered sites, as both captive and wild pikas were seen releasing more than ten pellets in some sheltered sites and corners of pens and cages.

Several sheltered and exposed elimination sites were visible to me, and different pikas used these sites. Before eliminating, the pika usually sniffed the area thoroughly, in the process knocking off some of the feces already present.

Harvey and Rosenberg (1960, p. 213) describe the cheek gland of *O. princeps* as "unique in having the coiled tubules of the apocrine portion embedded in a highly basophilic cell mass variable in size in different reproductive states of the animal." This cell mass is described as largest and most basophilic in estrous ♀♀ and reproductively active ♂♂.

Kilham (1958), Krear (1965), and Broadbooks (1965) saw pikas rub their cheeks on rocks, and suggested a scent marking function for this act. The act consists of a quick forward movement of the head along the edge of a rock or stick, sometimes preceded by sniffing of the object. There were several "traditional" rubbing places on the study areas, these were seen being rubbed by several individuals, in some instances the same site was rubbed by different individuals in the same day.

The smaller fecal deposits, if not conspicuous, are familiar to pikas, as they were visited and defecated on fairly regularly. Some cheek rubbing sites were rather conspicuous -- one was a stick protruding over a flat rock. Other sites rubbed were pyramid-shaped rock corners.

Traps set on prebait often had urine spots or a few pellets glued to the doors. Since traps were washed after a capture, they might have presented a novel object and/or odor to a pika. Finally, when the first captive pika was placed in her pen, her water supply was a plastic cottage cheese carton sunk into the ground. This was unsatisfactory as she literally filled the carton with feces. The captives also made fecal piles in corners of their pens, but only in corners adjoined by an inhabited pen.

Frequencies of cheek rubbing and sniffing, expressed as weighted averages of number of acts/hour seen are presented in Figure 30. The ♂1 was not included in this analysis as he was infrequently seen and displayed an erratic frequency of cheek rubbing. The frequency of cheek rubbing by adult ♂♂ did not change greatly from April-August. Adult ♀♀ show a peak in cheek rubbing in July, coincidental with the separation of intensively used areas. Juvenile ♂♂ rub more often than all others, and juvenile ♀♀ rub about as much as adults. Sniffing was not recognized in the field until June 1969, accounting for the low frequency observed in May. Sniffing frequencies generally reflect those of rubbing for all sex and age classes.

The relationship of defecation, urination, and rubbing to core areas is presented in Table 7 for each individual and month. Adults and successfully established juvenile ♀♀ rub mainly outside areas of intensive use. The proportion of rubbing by adults within intensively used areas is higher when juveniles are present and in August, when intensive use areas are discrete. Unpaired juveniles rub predominately within intensively used areas.

Most rubbing occurs around borders of home range core areas. The presence of juveniles may stimulate adults to rub the areas occupied by juveniles.

Thus, from this study, urination, defecation, and cheek rubbing by pikas do display characteristics of marking behavior.

Figure 30. A seasonal analysis of weighted averages of cheek rubbing and sniffing.

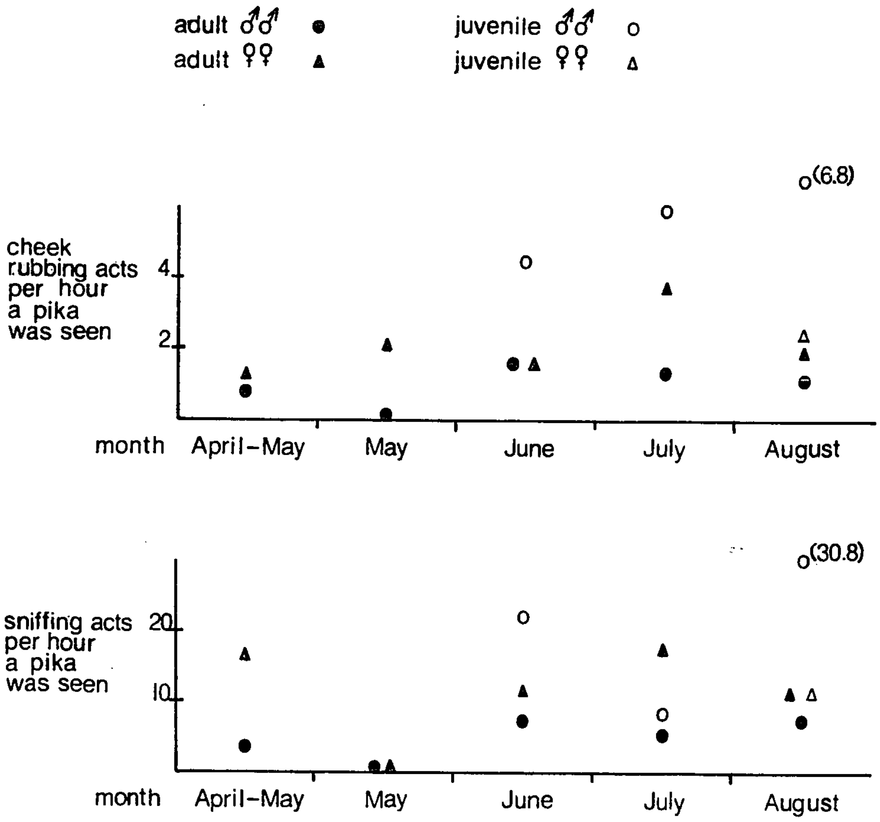


Table 7. Cheek rubbing, urination, and defecation sites in relation to core areas for each individual.

Kananaskis study area		April-May		May		June		July		August		
		in	out	in	out	in	out	in	out	in	out	
Adults	♂GR	1	0									
	♂RR	1	1	0	0	0	1	2	10	0	1	
	♂WR			0	0	3	7	11	8	0	3	
	♀TE	0	4	1	4	0	5	3	15	7	1	
Juveniles	♂LK							12	6			
Jumping Pound study area												
Adults	♂2					1	7	0	5	5	9	(1970)
										2	0	(1969)
	♂3					2	5	1	6	3	8	(1970)
										8	1	(1969)
	♀5					4	1	4	10	1	16	(1970)
										0	1	(1969)
Juveniles	♀14									4	23	
	♀13									2	2	
	♂10					4	0					
	♂11					6	0					
	♂12									18	3	

6. CONCLUDING DISCUSSION

Like most wild species, pikas show variable activity under different weather conditions. In summer, pikas avoid the hottest parts of the day, and although information is scarce, may also avoid the coldest parts of the day in the colder months.

Surface water was not available for most of the summer on either study area (with the exception of the Jumping Pound area during spring runoff). Unless water trickled beneath the rocks, or ice remained under the rockslides all summer, the only water available to the pikas was rainwater and that in the vegetation they ate. Pikas are physiologically adapted to conserve water (MacArthur, pers. comm.) and their urine is very concentrated. These adaptations, however, are apparently not sufficient to keep them alive at high temperatures (over approximately 75°F) for very long without water, as the two pikas that died did so on hot afternoons. Thus, susceptibility to heat stress is likely the reason for the pikas' avoiding the hottest part of the day in summer.

Avoidance of extreme cold in winter is one method of energy conservation, as a high quality food source is least available at this time. The gradual decrease observed in rate of refection of cecal feces from early spring to summer corresponds to the increase in food quality and quantity. I would expect reingestion to be most frequent in winter. Accumulations of cecal feces were present in the nests of penned pikas, and these might be eaten in the wild in winter as a supplement.

Pelage maintenance acts increase gradually through the summer; this increase may be caused by irritation by ectoparasites and pelage moults. Sitting occupied between 40 and 60 percent of the time pikas were seen; pikas groom, call, and interact (through call duels and interruptions) while sitting. They are fairly alert while sitting, and were aware of a potential predator or other disturbance before I was in most cases. Pikas almost always gave alarm calls immediately, alerting the other individuals. One pika was usually up and around, perhaps serving as a "sentry." Pikas responded to the alarm calls of ground squirrels, chipmunks, red squirrels, and marmots (Marmota caligata, seen on other areas), and some passerine birds, and vice-versa. Thus, the alarm call functions in both inter- and intraspecific communication. Pikas always responded to avian predators with a quick volley of alarm calls and rapid disappearance from the rockslide surface. However, the response varied when a weasel (Mustela frenata or M. rixosa) appeared. The pikas either reacted as above, or silently took high vantage points and watched the weasel, ducking into the rocks only if approached. The second type of response was the most common one seen. I never saw a weasel catch a pika, although Tapper (pers. comm.) did.

Feeding occupied about 20 to 30 percent of the time a pika was seen in spring and early summer. When haying began, observable feeding time dropped, as the pikas fed while haying, and haying areas were generally not visible. Haying occupied about 20 percent of the time pikas were seen. Sitting activity averaged about 50 percent of the time pikas were seen in the haying season. Haying areas of individual pikas did not overlap greatly and the edges of the haying areas were usually close to the pikas' core areas. A few chases were seen in haying areas when the occupant encountered an invader.

How did haying behavior evolve, and what is the selective advantage (or advantages) for such behavior? Before pikas began intensive haying activity, in both spring and summer, they often went out to feeding areas and brought vegetation back onto the rockslide before eating it. The pika usually sat on a favorite place or other high rock while feeding. This pattern was more common in early summer, when understory vegetation height increased, obscuring the pikas' vision. The pika probably felt more secure on the rockslide, as it's vision was not obscured and the animal was much closer to well-known escape terrain; thus this type of behavior probably reduces exposure to predation and would be of selective advantage.

The second part of the pattern, that of actively caching large quantities of vegetation, is more difficult to explain. Pikas were seen caching mouthfuls of vegetation in many places within their home ranges in spring and early summer. They also sometimes ate only part of what they had brought, leaving the rest. This often happened when the pika was feeding on its favorite place. Most favorite places were large, high rocks. A cache could have accumulated in such places, and the dried material may have been used initially as an emergency food source.

From Millar's (1971) experiments, haypiles do not appear necessary to winter survival or reproductive success, although these experiments should be repeated over several years and involving more animals. It seems illogical that pikas should spend between 10 and 30 percent of the time they are seen haying in late summer if haypiles are not necessary for winter survival or reproductive success. Also, the possibility of deep, inaccessible caches of the type that Severaid (1956) found cannot be ignored -- these may be some critical amount necessary in most winters, or necessary perhaps when weather conditions are not favorable for extensive winter foraging, as in years of little snowfall and extremely cold weather.

Haypiles may also have a social function. On the areas I studied and a number of others visited, ♂♂ had more numerous and more conspicuous haypiles than ♀♀. Hobbs (pers. comm.) noticed this also. It is possible that these conspicuous haypiles are some sort of display, most likely a "statement of occupancy" to other ♂♂, and perhaps also as an attraction to ♀♀. Kawamichi (1971b) feels that ranges stabilize after haying ceases in autumn, and that pair members probably share haypiles in winter.

Table 8 shows a summary of the spatial and social shifts observed during April-August in this study. During the breeding season (April, May, and June), pair members were tolerant of each other and ranges overlapped extensively. Few sexual interactions were observed in this study, accounting for the low frequency of interactions seen in spring. Call duels occurred mainly between ♂♂, and might have been competitions for ♀♀. Long calls were most frequent during this period. Other agonistic interactions occurred mainly between ♂♂, but few were seen. In June ♂♂ and ♀♀ cheek rubbed, urinated, and defecated mostly outside their core areas (unless juveniles were present), and most interactions occurred within core areas.

In July, ♂♂ began haying and showed distinct haypile-oriented core areas with little overlap of their ♀♀'s core areas. Long calls were less frequent, and ♂-♀ and adult-juvenile interactions predominated. Interactions and cheek rubbing, urination, and defecation occurred mostly outside core areas. When juveniles were present, single ♂♂ began cheek rubbing, urinating, and defecating within their core areas as well. Agonistic interactions increased slightly.

In August, ♀♀ and some juveniles began haying, showing haypile-oriented core areas. There was no overlap of core areas between pair members. Interactions occurred mainly between ♂♂ and ♀♀ and adults and juveniles; all occurred mainly outside core areas. The number of agonistic interactions increased greatly when several juveniles were present

Table 8. A summarization of spatial and social events taking place during April-August during this study.

Month	Ranges	Reproductive	Interactions	Food	Marking	Calling	Agonistic
April-May	Large, scattered overlapping core areas	Breeding	Mostly ♂-♂ inside core areas		♀♀ outside core areas ♂♂ ?	Generally increasing	Generally increasing
May	Large, scattered overlapping core areas	Breeding	Mostly ♂-♂ inside core areas		♀♀ outside core areas ♂♂ ?		
June	Large, scattered still, less overlap	Breeding	Less ♂-♂, some ♂-♀, mostly inside core areas		♀♀ outside ♀♀ inside (juveniles present) ♂♂ outside ♂♂ slight increase inside (juveniles present)		
July	♂♂ have haypile oriented core areas some ♀♀ have same, little core area overlap	non-Breeding	♂-♀, adult-juvenile, mostly outside core areas	Haying ♂♂	♀♀ outside ♂♂ outside single ♂♂ increase inside (juveniles present)		
August	Distinct core areas, large ranges when juveniles present, no overlap of adult core areas	non-Breeding	♂-♀, adult-juvenile, mostly outside core areas	all Haying	♀♀ inside, outside with juveniles ♂♂ outside, inside with juveniles		

and attempting to pair with single individuals. The ♀♀ cheek rub, urinate, and defecate mostly inside their core areas when juveniles are absent, and mostly outside their core areas when juveniles are present. The ♂♂ cheek rub, urinate, and defecate mostly outside their core areas when juveniles are absent, and mostly inside when juveniles are present. The pikas were most vocal, and agonistic interactions were most frequent in August, particularly when juveniles were present.

This shift indicates increased defense of core areas; a direct response to the juveniles, as it occurred whenever juveniles were present and did not when they were absent.

The outcome of social interactions did not appear to be dependent on the site of the interaction with established adults. From the outcomes of agonistic interactions, ♂♂ are generally dominant over ♀♀, and adults are dominant over juveniles. The juvenile ♀14 did win some chases while becoming established, and the first ones she won were in or very near her core areas; thus the outcome of an interaction appears to be somewhat site dependent during establishment.

Pikas have a fairly complex social communication system, using calls, direct threats, and perhaps scent. All the calls appear to have different meanings according to the context in which they are given. The intensity of threat implied in agonistic behavior patterns, derived from the overall frequencies of the patterns and the sequence in which they were seen is (interruption≤?)<call duel<approach<chase<fight.

The social and spatial arrangement of the pika thus possesses characteristics of both territoriality and a dominance hierarchy.

Why do pikas live in pairs? This is of advantage to reproductive success, as in many areas in early spring, snow still covers the rockslides, restricting movement, and ♂♂ are readily available to receptive ♀♀ if they are paired. Later on, while ♀♀ are pregnant and caring for young in the nest, the ♂ still uses the entire range of the pair, and may actually "defend" the area against invasion by pikas from less optimal habitat.

In spring and early summer, ♂♂ called, interacted, and cheek rubbed, urinated, and defecated throughout the range of the pair. Since most interactions during this time were between ♂♂, it can be assumed that ♂♂ were competing with each other for ♀♀, even though they were already paired. Tapper (pers. comm.) found that some ♂♂'s ranges were largest during the breeding season, overlapping the ranges of neighboring pairs and extending even further in some instances.

Range separation between ♂♂ and ♀♀ later in summer appears to be brought about by defense of a larger area by each individual. This separation occurs the same time that ♀♀ begin haying, and from this study, the initiation of haying does not appear dependent upon the timing of appearance of juveniles, as pikas on the Jumping Pound in 1970 began haying in mid-July and weaned young appeared in early

August. The fact that pikas on the Jumping Pound began haying earlier in both years than those on the Kananaskis, and that vegetation on the Jumping Pound came up more quickly and was more lush, indicates that the state of the vegetation itself may trigger haying behavior.

The function of cheek rubbing, urination, and defecation is likely marking, as all display characteristics of marking behavior. Confirmation of this must be left to intensive field, and if possible, laboratory experiments.

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Appendix 1. Programs used for sorting in and sorting out data on the activities of an individual pika in one month.

```
        ∇SORTIN[⎕]∇
     ∇ R SORTIN C;D
[1]     D←⎕
[2]     →(D[1]>1)/4
[3]     M←(R,C)⍴0
[4]     M[D[1];]←D
[5]     →(D[1]<R)/1
     ∇



        ∇SORTOUT[⎕]∇
     ∇ SORTOUT Z;A;B;C;D;G
[1]     'WHAT COLUMN(S) DO YOU WANT TO GRADE-UP?'
[2]     G←⎕
[3]     →((⍴G)>1)/L1
[4]     →(G=0)/L10
[5]     Z←Z[(⍋Z[;G]);]
[6]     →L10
[7]    L1:Z←Z[(⍋Z[;G[2]]);]
[8]     Z←Z[(⍋Z[;G[1]]);]
[9]    L10:⎕←⎕←⎕←⎕←⎕←''
[10]   L2:'WHAT COLUMN(S) DO YOU WANT TO DISPLAY?'
[11]    A←⎕
[12]    'WHICH DATA COLUMN(S) ARE YOU INTERESTED IN?'
[13]    B←⎕
[14]    →((⍴B)>1)/L3
[15]    →((+/(C←((Z[;B])>0)/⍳(⍴Z)[1]))=0)/L4
[16]    →L7
[17]   L3:→((+/+/Z[;B]>0)=0)/L4
[18]    →('N'=(⍞,⎕←'DO YOU WISH CONCURRENT OCCURRENCE OF DATA?')[1])/L9
[19]    →((D←⍴B)=2)/L11
[20]    'HOW MANY COLUMNS MUST HAVE DATA IN THEM?'
[21]    D←⎕
[22]   L11:→((+/(C←((D)≤+/(Z[;B]>0))/⍳(⍴Z)[1]))=0)/L4
[23]    →L7
[24]   L9:→((+/(C←((+/Z[;B])>0)/⍳(⍴Z)[1]))=0)/L4
[25]   L7:⎕←⎕←''
[26]    A,[1] Z[C;A]
[ 27]   →L10
[28]   L4:⎕←⎕←''
[29]    'THIS BEHAVIOR NEVER OCCURRED'
[30]    →L10
     ∇
```

To exit from this program, use a→.

Data were entered in an eight column matrix, including: row number, specific act, other participant(s) if an interaction, frequency of the act, duration of the act, location of the act, specific location of the act, and hour of day. All were in numerical code.

These programs were developed by Len Mottus of the University of Alberta.

Appendices 2 and 3. Programs for arcsine transformation, sum of squares, and multiway analysis of variance used on activity data.

```
      ∇ARCSINE[⎕]∇
    ∇ ARCSINE Z
[1]   M←((-1)○(Z*0.5))×360÷○2
    ∇
```

Arcsine program courtesy of Len Mottus, University of Alberta.

```
      ∇SS[⎕]∇
    ∇ S←Y SS R;DIM;K;ZEROS;ONES
[1]   →(K=ONES←K-ρZEROS←(Y=0)/⍳K←ρDIM←ρR)/4
[2]   R←+/[(⍳0)ρZEROS[ρZEROS]] R
[3]   →(0≠ρZEROS←¯1↓ZEROS)/2
[4]   R←R*2
[5]   R←+/R
[6]   →(0<ONES←ONES-1)/5
[7]   S←R÷×/(Y=0)/DIM
    ∇
```

```
      ∇ANOVA[⎕]∇
    ∇ T←ANOVA D;DIM;N;REPS;K;R;CT;V;I;S
[1]   N←(ρDIM←ρD)-1
[2]   T←((R←(2*N)+2×K←(REPS←DIM[1])≥2),4)ρ0
[3]   CT←((N+1)ρ0) SS D
[4]   T[R; 2 3]←((×/DIM)-1),((N+1)ρ1) SS D
[5]   →(REPS=1)/7
[6]   T[1; 2 3]←(REPS-1),((⍳(N+1))≤1) SS D
[7]   D←+/[1] D
[8]   DIM←1↓DIM
[9]   V←⌊((2*(N+1)-⍳N)∘.|⍳S)÷(2*N-⍳N)∘.×(S←(2*N)-1)ρ1
[10]  V[;⍳(2*N)-1]←V[;(+/(X∘.>X)+((⍳ρX)∘.≥⍳ρX)∧X∘.=X)⍳⍳ρX←+/[1] V]
[11]  I←1
[12]  T[I+K; 2 3]←(×/((V[;I]=1)/DIM-1)),(V[;I] SS D)÷REPS
[13]  →((2*N)>I←I+1)/12
[14]  T[;3]←T[;3]-CT
[15]  →(N=1)/20
[16]  I←2
[17]  DV←(Kρ0),(X←(~(~CT)∨.∧S)∧(CT←V[;I])∨.∧S←V[;⍳I-1]),(R-(I+K-1))ρ0
[18]  T[I+K;3]←T[I+K;3]-+/T[;3]×DV
[19]  →((2*N)>I←I+1)/17
[20]  →(REPS=1)/23
[21]  T[R-1;2]←T[R;2]-+/[1] T[⍳(R-2);2]
[22]  T[R-1;3]←T[R;3]-+/[1] T[⍳(R-2);3]
[23]  T[⍳(R-1);4]←T[⍳(R-1);3]÷T[⍳(R-1);2]
[24]  I←1
[25]  T[I+K;1]←10⊥V[;I]
[26]  →((2*N)>I←I+1)/25
    ∇
```

Anova and SS programs are from the University of Alberta Computing Science Library.