SOCIAL BEHAVIOUR OF A COLONY OF THE YELLOW-BELLIED MARMOT *(Marmota flaviventris)*

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The yellow-bellied marmot has many characteristics that lend themselves to the study of social behaviour and its role in the ecology of a species. These animals are diurnal and can be observed directly, they can be trapped readily and marked, and they live in relatively compact groups.

This study was conducted from June 18th, through August 30th, 1955; July 12th through August 24th, 1956; June 10th through August 23rd, 1957; and June 14th through August 21st, 1961, as project number 82 of the Jackson Hole Biological Research Station. Only adult behaviour will be described unless otherwise indicated.

Dr. L. Floyd Clarke, Director of the Jackson Hole Biological Research Station, provided living and research facilities. I wish to thank the many members of the National Park Service whose co-operation made it possible to conduct the study inside national parks where the animals are not molested.

The study was supported by the New York Zoological Society, the Gans Fund of Bethany College, West Virginia, and the National Science Foundation.

Study Area

The marmot colony selected for detailed study is located inside the southern boundary of Yellowstone National Park along a river terrace (Fig. 1) on the east side of the Snake River and slightly south of the junction of the Lewis River with the Snake River at an elevation of about 6,880 feet. Old bridge foundations form the central point of colony activity. The colony extends about 1,500 feet in a north-south direction and about 500 feet in an east-west direction, covering about 17 acres. The area was mapped by taking compass sights between burrows and pacing off the distance. Each burrow-system was numbered (Fig. 2).

The flat east of the bank was covered with a low-growing sagebrush interspersed with grasses. The bank had only a few grasses and forbs (Fig. 1). The flood plain west of the bank and south of a line drawn between burrows 48 and 60 (Fig. 2) was covered with a dense growth of timothy and white clover (*Trifolium repens*).

The colony is split into two sections by a small stream of warm water flowing from hot springs north of the colony. The stream usually formed a barrier to movement in June, but thereafter animals were able to cross on three small logs that protruded from the bottom of the stream west of B1 (the capital B plus a number will be used throughout the paper to designate a particular burrow-system).

Methods

The marmots were observed from a tower erected at the top of the bank northeast of B1 (Fig. 2). The activity and position of each animal were recorded every hour on a map of the colony and other observations were recorded in a notebook.

Animals were trapped with wire traps manufactured by the National Live Trap Company of Tomahawk, Wisconsin. A variety of baits, apples, honey, peanut butter, clover and oats, was tried. Oats and clover were more successful than the others and were used exclusively after the first year. Each animal was colour marked for field identification with Nyanzol A fur dye (Fitzwater, 1943) and was given permanent identification by means of a size 3 self-piercing strap tag. During the four years of the study there were three known cases of tags being lost. Two of these occurred in retrapped animals who snagged the ear tag on the wire of the cage. Other animals were observed with tags hanging loose. Whenever such an animal was retrapped, it was retagged.

Organization of the Colony

Burrow System

There were two types of burrows in the colony. One type I designated the home-burrow. The home-burrow is where an animal normally spends the night, the place to which it will retreat when danger threatens, and the burrow where the young live. The home-burrow appears

to have a strong psychological value, as a marmot will make every attempt to return to its home-burrow when an alarm call is sounded. I designated all other burrows in the colony as auxiliary burrows. They serve as places of refuge when an animal is unable to return to the home-burrow. There is no certain way to distinguish a home-burrow from an auxiliary burrow except by the activity of the animals. However, home-burrows always have at least three openings and auxiliary burrows commonly have two and sometimes only one opening.

The burrows are connected by a trail system. The trails were formed by the marmots repeatedly travelling the same path so that the vegetation was eliminated. Once formed, the trails provide a familiar and direct route of travel. Their significance is illustrated by the following experiment. Most trapped animals were marked near a home-burrow and when released, dashed into the nearest opening. Some animals were trapped near auxiliary burrows or in trails and when released, dashed directly to an entrance. However, when a marmot was released away from a trail, the animal bounded in any direction, first to the left, then to the right, until it came across a trail, then dashed directly to a burrow. The burrow which it entered frequently was not the one closest to it, but was determined by which trail the animal happened to find. The trails eventually lead to feeding areas. Couch (1930) also reported trails between the burrows and the presence of "temporary burrows under isolated rocks or excavations". These

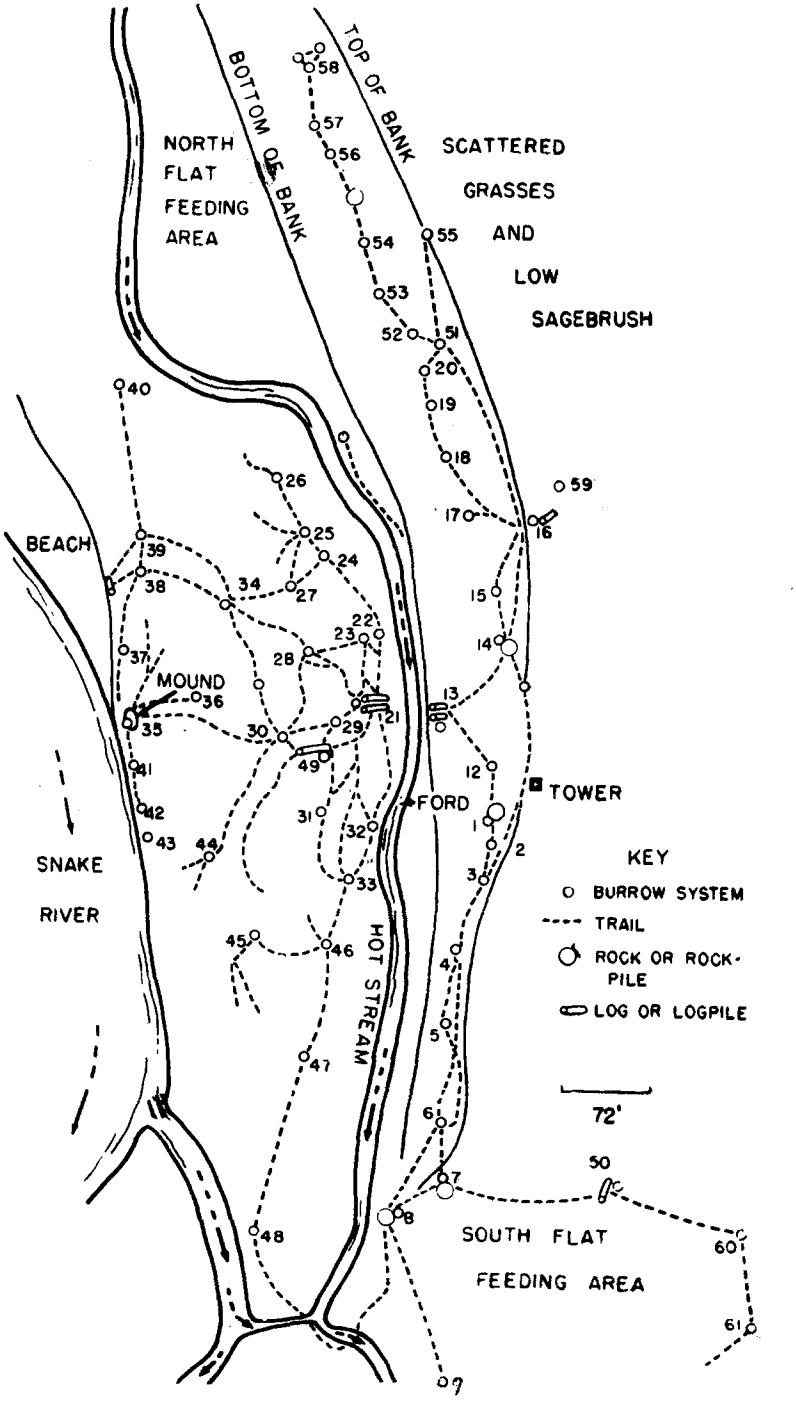

Fig. 2. A map of the colony showing the burrow systems, trails, major rocks and log piles and major feeding areas east of the hot creek. North is at the top of the page.

PLATE V

Fig. 1. A view of the colony to the south from B16 under the log in the foreground. The Snake River is at the upper right corner. The hot creek that divides the colony into East and West sections flows from the right centre to upper middle of the picture and passes between the logs making up B13 on the left and the logs making up B21 on the right. The meadow to the right of the hot creek is clover and timothy. The flat above the bank on the left is covered with a low-growing sagebrush and a few scattered grasses.

temporary burrows seem to be the same as the auxiliary burrows described above. Trails or pathways linking burrows also were reported for the striped ground squirrel (Evans, 1951) and for *M. marmota* (Bopp, 1954, 1955b, 1956).

Distributions of Adults and Litters

Fourteen of 19 litters over the four years were concentrated in the central part of the colony at burrows 1, 13, 14, and 21 (Fig. 2, Table I). These burrows are centrally located and all have either logs or large rocks under which the burrows are located. There were no logs or rocks at burrow 30, where there was one litter

Table I. The Distribution of Adults, Yearlings and Litters for Each Year of Study.

Burrow number	Number of adults and litters			
	1955	1956	1957	1961
1	1A, 1L	1A, 1L	1A, 1L	1A, 1L
3	1A, 1L	2A	1A, 1L	
13	1A, 1L	1A		1Y
14	1A		1A	1A, 1L
16	1Y	1Y	1Y	
21	5A, 2L	5A, 2L	4A, 1L	3A,2Y, 1L
25	1A	1A	1A	
26	1A			
29	1Y			
30	2A, 1L		1A	
35	2A, 1L	1A	1A, 1L	1A
40	1A			
51			1Y	1Y
58	1A, 1L		1A, 1L	1Y
59			1Y	

A—adults. Y—yearlings. L—Litter.

in four years. There were litters in two of the four years at burrows 35 and 58. These also have rocks under which the burrows are located, but they are on the periphery of the colony. The location of adults shows the same central concentration (Table I). Although some of the peripheral burrows were inhabited by adults, only one of these had adults all four years of the study. Therefore, the most successful (as measured by persistence of use) burrows are those with large objects under which the marmots burrow and are those located in the central part of the colony. A similar grouping of burrows has been observed in the red squirrel (Layne, 1954), and the striped ground squirrel (Evans, 1951) and in the alpine marmot of Europe (Bopp, 1954).

Sex Ratio

Of 33 adults whose sex was identified, two were males. Only one male was identified in any year. Thus the colony consists of a male with a harem. Sex ratio of 54 young, determined in 1956, 1957, and 1961 was 1·16♂:1♀ for the three years.

Home Range

The home ranges of eight females in 1957 (Fig. 3) show three patterns. Three home ranges are essentially separate, several have slight overlap, and several have major overlap. Burt (1943) considered overlap to be neutral range; however, "neutral" range does not adequately describe the complex relationships among marmots. For example, the home range of ♀TEST was almost completely overlapped by the home range of ♀635. During June, frequent encounters between these animals showed ♀635 dominant to ♀TEST, who usually left the area. By July a pattern was established so that the two utilized essentially the same home range, but occupied different parts of the home range at the same time, or visited the same area at different times. The temporal separation of dominant and subordinate animals utilizing the same home range also was shown by other marmots.

The shape of the home range seemed to depend primarily on the location of the feeding area utilized by the animal. The home ranges of the animals east of the hot creek were roughly flask-shaped; the home range of ♀627 was oval.

The size of the home range primarily depended on the nearness of the feeding area (Fig. 3, Table II). Females on the east side of the hot creek had the largest home ranges and went farther to feeding areas. Females 629, F35, and 1278 had smaller home ranges and all lived near feeding areas.

However, agonistic behaviour and the density of the population modified size and shape of some home ranges. Some animals travelled a greater distance to feeding areas when the population was more dense as evidence by the

largest mean size of home range in 1955 (Table II). Blair (1953) reported that there was probably less ranging where food was dense but did not find any evidence that population density influenced the size of individual home ranges.

Home ranges underwent some seasonal changes. Some of the animals crossed from the east to the west side of the hot creek when the water level dropped. During the first two weeks of August when some animals hibernated several of the remaining animals frequented areas that were avoided earlier.

There were also year to year changes in home range that were correlated with changes in the individuals inhabiting near-by burrow systems.

Behavioural Patterns

Daily Activity Cycle

Although the daily activity cycle was different for each individual, a generalized population cycle, in its main outline, is applicable to any adult member of the colony (Fig. 4). The pattern is based on 26 days of records in 1956, 19 days in 1957, and 43 days in 1961.

Emergence from the burrow was roughly correlated with the time when the first rays of the sun reached the colony area. However, this period of major emergence extended over at least an hour and some of the less active animals appeared even later. On four cloudy days the animals appeared at about the same time as on sunny days. Because many of the burrows did not face the sun and were often under rocks or logs, it does not seem likely that light was responsible directly for initiating activity. As many animals defecated

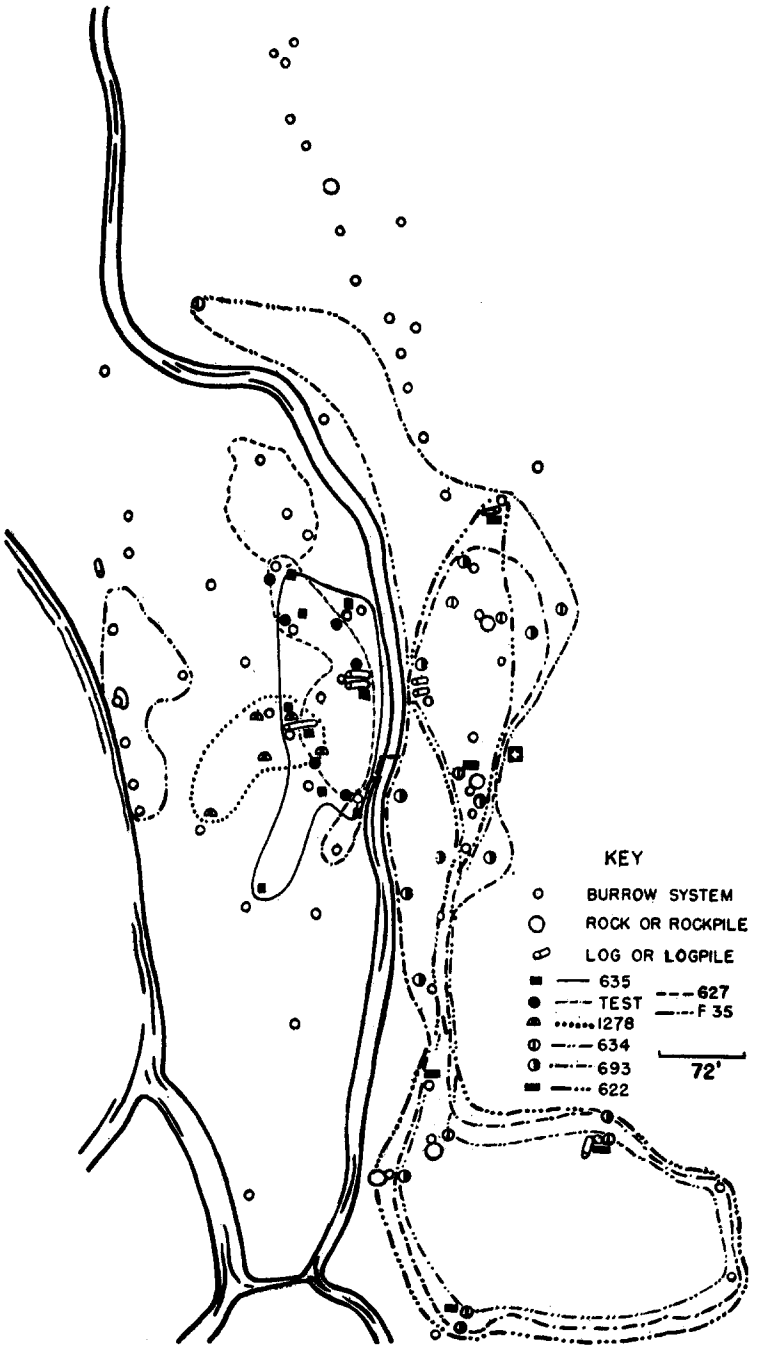

Fig. 3. The home ranges of eight adult females in July and early August of 1957. Symbols for each animal are placed in areas frequently visited. The lines indicate the boundaries of the home ranges. Note that the home range of ♀693 extends across the hot creek.

Table II. The Population and Home Ranges of *M. flaviventris* on the Study Area. Home Range is for Adults only for the Month of July. Home Range is Reported as the Maximum Distance in feet that an Animal Ordinarily Travelled from its Home-burrow to its Feeding Area.

	1955	1956	1957	1961
Population:				
Adult	17	12	11	8
Yearling	3	1	3	5
Young	45	18	25	12
Range of size of home range:				
East of hot creek	108—720	144—468	108—468	180—432
West of hot creek	72—216	72—198	72—198	72—180*
Mean size of home range:				
East of hot creek	461	336	368	306
West of hot creek	136	110	115	119
Mean of all home ranges	232	178	200	180

*If the two ♀'s that wandered between B21 and an area 150 yards north-east of the colony are included, the range is 72—1082 feet; the mean west of the hot creek is 438 feet; the mean of all home ranges is 405 feet.

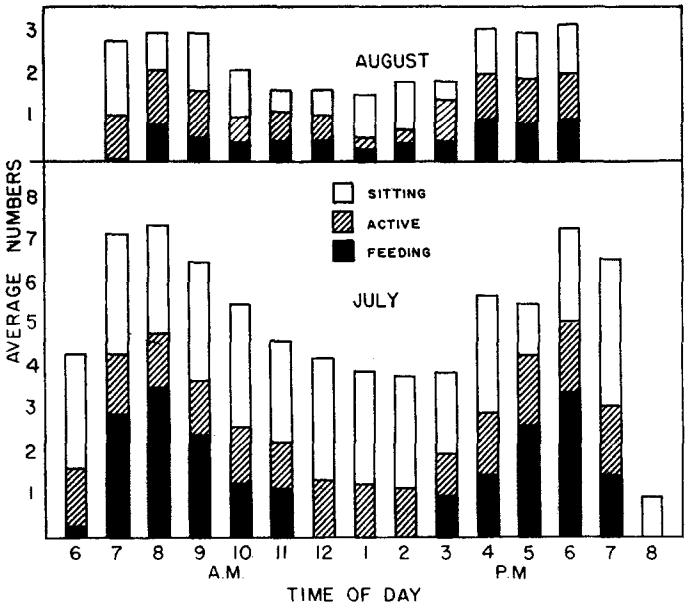

Fig. 4. The pattern of daily activity of adults for July and August for 1956, 1957, and 1961. The activity data for 1955 were not recorded in the three categories of sitting, active and feeding. Total activity for 1955 shows the same pattern as the above. Active refers to any activity; e.g. running, playing, other than feeding and sitting.

immediately after emergence, one could speculate that intestinal physiology served as the stimulus for emergence. About the first 15-30 minutes after emergence were spent grooming and sunning. Gradually the animals dispersed to the feeding areas; by 8.00 a.m. this activity reached a peak that lasted for about two hours. The remainder of the day was spent in activities such as sunning and digging, or was spent in the burrow with occasional forays for feeding. From about 10.00 a.m. until about 4.00 p.m. there was a marked reduction in overall activity. There was a second peak of activity concerned mainly with feeding from 4.00 p.m. until sunset. During the last hour of light the animals returned to their burrows. Usually they sat near the burrow entrance for a short time before entering the burrow. All the animals entered their burrows by 15-30 minutes after sunset. This general picture was highly modified by such things as alarm calls, thunderstorms, interactions with other members of the colony, etc.

The general pattern changed somewhat in August. The peak of activity was later in the morning and the late afternoon activity reached a peak earlier and the level was sustained over a longer period of time. This shift in activity may have resulted from the decreased day length of August and/or colder temperatures in the early morning hours. The total mount of activity also was lower, primarily because many adults hibernated.

There is some further indication that the general pattern of activity was modified by air-temperature (Table III). Although the data are scanty, there appears to be a general drop in activity when the air-temperature exceeds 20°C.

Feeding

Typically the animals lay down and crawled through the beds of clover while feeding. Thus a clover patch soon came to have a large number of "crawlways" winding and criss-crossing through it. Usually an animal raised its head while chewing. Sometimes an animal sat up from time to time. Animals feeding at the south flat sat up more frequently than animals feeding on the west side of the hot creek near the centre of the colony (Table IV). The behaviour of ♀634 varied with the area in which she was feeding. When she fed at the southeast border, she sat up frequently; she never was observed to sit up when feeding near the centre of the colony. Feeding in the last hour before sunset was predominantly near the home-burrow.

Table IV. Number of Times an Adult Marmot Sat Up While Feeding. Data from 10 Observations of Three or More Adults from Each Area.

	Range	Mean
Centre of colony	0-2·2/min.	0·8/min.
South flat feeding area	3·5-6/min.	5·1/min.

Locomotion

There were two basic patterns of locomotion which differed in the way the tail was carried. Adults going to the feeding grounds usually held the tail up in a half moon and waved it from side to side. When reacting to an alarm signal, the tail was held down or pointed directly

Table III. The Per Cent. of the Adult Population Active at Various Temperatures for Selected Hours of the Day in July of 1955 and 1956.

The number of observations is given in brackets prior to the range. Where no range is given, only one observation was made.

Temperature C°.	Time							
	9:00		10:00		11:00		17:00	18:00
	Range	Av.	Range	Av.	Range	Av.	Av.	Av.
14	(2) 88—100	94						
18	(5) 55—100	77					100	100
19			(3) 68—100	80		88	100	100
20	(2) 55—66	60		77		45		
21				67	(2) 11—55	27		
22			(4) 37—67	50		62		
23			(2) 37—55	46	(3) 22—62	35	33	67
24			(3) 25—56	40				
25				18	(2) 12—31	21		
26				68				
27						25		
28						31		

posteriorly. Each of these patterns was associated with dominance-submissiveness relationships. A dominant animal held the tail up, cocked in the "half-moon" position whereas a submissive animal always held her tail low. Either position of the tail was associated with a slow walk or with a rapid, bounding run, a gallop in which the hind feet are set before the fore-legs (Munch, 1958; Müller-Using, 1954).

Those animals living in the centre of the colony usually moved from the home-burrow to the feeding ground or to an auxiliary burrow en route to the feeding ground in one move. However, an animal living on the east side of the colony usually moved much more cautiously when going to the south flat feeding area. For example, ♀634 once spent 17 minutes moving from B1 to B50 and stopped and looked around thirty-eight times, sitting up seven of these. During the same time ♀524 went from B13 to near B33 in two minutes. Thus ♀524 moved at the rate of about 72 feet per minute while ♀634 was moving at the rate of about 25 feet per minute. However, ♀524 did not always move as slowly as indicated by this example; she often moved at about the rate of 60 feet per minute, but always stopped more frequently. When moving at this more rapid rate, the bounding motion was used. After each stop, she pumped her tail up and down once as she started forward again. This tail pumping was quite characteristic but has no known significance. It may be considered an intention movement.

Sunning

Early in the morning when the air was cool, the animals orientated their bodies broadside towards the sun. However, during the late morning or afternoon, the marmots lay lengthwise toward the sun. During the hot part of the day sunning was restricted and animals were more likely to lie in the shade of a boulder or log pile.

Sitting Up

This position was nearly always used whenever a marmot was looking around in response to an alarm, or while at a feeding ground, or while en route to or from a feeding ground. This position was not used when a marmot was exploring its immediate surroundings, but only when the marmot was observing a distant object or scanning the landscape. *Citellus armatus* (author's observation) and prairie dogs (King, 1955) sit up in much the same circumstances as do marmots.

Grooming

Grooming was likely to occur at any time during the day, but was most frequent shortly after the period of emergence during the morning and prior to feeding. There were only five observations of adults grooming other adults during the four years of study. In each case the grooming was associated with agonistic behaviour in which the dominant animal groomed the submissive animal.

Nest Building

Digging and the collecting and carrying of grass were infrequent. There were four new burrows (9, 59, 60, 61) added on the east side of the hot creek during the course of the study. Several animals participated in the digging. Digging was done with the forelegs, the dirt being thrown between the hind legs. Dirt that piled up at the entrance of a burrow was pushed away by the animal lying down and shoving the loose dirt with its chest and forelegs.

Marmots lay down to gather grass. They tore some loose with the mouth and positioned the grass in the mouth with their forelegs, repeating these steps until the mouth was full. Usually only one trip was made to the burrow. Of 26 observations of gathering of grass by adults during the period of study, 14 of these were in August about the time of hibernation.

Social Interactions

Play

Activity designated as play was frequent among the young, but was seen to occur between adults only in 1955. Several times adults played with young. When the animals were identified, a female was playing with one or more members of her own litter.

Communication

Communication is used in the same sense as it is used by Scott (1958: p. 189); i.e., the maintenance of contact between members of a group. Marmots employ sight and hearing for the main part, with some use of smell and touch.

The basic sound was a shrill whistle which is a high cry originating in the vocal cords (R. & D. Müller-Using, 1955; Munch, 1958). This sound alerted other members of the colony who frequently responded by sitting up and looking around. The alarm call seemed to be the same basic note, but given higher and sharper. When this higher call was given, marmots reacted by running to a burrow.

Frequently young marmots at play made a sound resembling a shriek. This was occasionally given by a submissive adult when she was approached by a dominant male adult. A fourth call, a growl, was heard only from animals in their burrows.

The alarm call was elicited by moose, deer, horses, bears, fishermen, sandhill cranes, ravens, blackbirds, swallows, marsh hawks, a great blue heron and a coyote. Frequently animals causing the alarm call were at a distance from the colony; e.g., across the river. Usually not all the marmots reacted to an alarm call, but only those on the side of the colony from which the "intruder" was observed.

The reaction to birds was varied. Ospreys flying along the river near the colony did not elicit an alarm call. The reactions of marmots to other birds occurred as the result of a sudden movement or sudden appearance of the bird in question. There was no indication that the marmots were reacting to a particular shape moving in a particular direction as described for gallinaceous birds (Tinbergen, 1951: pp. 31 and 77).

Marmots reacted to coyote calls, the bark of a cow elk, and the clanging of a trap closing. Only the coyote call elicited a major response.

No particular animal acted as a sentinel. There always were some animals active and the alarm was given by whichever animal first reacted to the stimulus. Sometimes the stimulus did not produce an alarm call in some of the animals.

The author considers the main function of the whistle of the marmot to be an alert or alarm call. However, German workers studying *M. marmota* have interpteted the call as an acoustical territory marker (Bopp, 1955a, 1958; Munch, 1958). However, Müller-Using (1955) emphasizes the warning nature of the call and points out that the call may function incidentally as an acoustical territory marker. As will be discussed later, the author does not think that territorial behaviour occurs in *M. flaviventris*. The whistle may be used in agonistic behaviour, but nearly always the animal being chased was the one that whistled.

Several times a particular individual was observed whistling long after any other animal in the colony was alerted. Such an individual also appeared to be highly nervous. Perhaps the basic stimulus for the call of the marmot is an internal uneasiness. Any such sound produced as a result of the uneasiness would be heard by other near-by animals. A prime cause of uneasiness would be an intruder such as a predator. Thus natural selection would establish alert and alarm calls from the vocal utterance of internal distress. Uneasiness might also result when another marmot entered the home range of an individual. The same call might be given and might appear to be a territorial marker.

Another means of communication seemed to involve several stimuli, but primarily olfactory. This was designated the "greeting". It was most commonly seen between young or between an adult and a young. The two animals approached each other head on, with tails arched and appeared to sniff at each other's cheeks (Fig. 5).

Fig. 5. Two young showing the "greeting position". Note especially the manner in which the tails are held and that the animals appear to be sniffing each other's cheeks. Drawing sketched from a colour transparency.

Usually there was little if any contact. There was no mouth contact as described by King (1955) for prairie dogs. A similar pattern has been described for *M. marmota* (Müller-Using, 1955; Munch, 1958).

Sometimes only one animal was active in a "greeting". Frequently the active animal remained several feet away from the animal that was "greeted". Often the "greeter" appeared to sniff the "greeted". Usually this ended when the "greeter" (a young) ran away from the "greeted" (an adult). This pattern might also be one of dominance-submissiveness as it is similar to the "ready alert" described below.

Agonistic Behaviour

Agonistic behaviour refers to conflict between two individuals (Scott, 1956). Its use is preferred to the term "aggressive" behaviour as the latter recently is used in a more restricted sense as a "tendency to initiate a vigorous fight" (King & Gurney, 1954: p. 326). Agonistic behaviour is broader in its implications and enables one to encompass a large amount of interaction between individuals in one category of behaviour. Aggressive behaviour, then, is one aspect of agonistic behaviour.

One position frequently used by adults in conflict was similar to the "greeting" except the bodies were held lower and more curved and the tails were held lower. This position was designated the "ready alert" as it often was followed by one adult chasing the other. Frequently a chase occurred only after the submissive animal began to run.

There is some indication that mounting or attempting to mount may be associated with dominance. The two adults that were observed attempting to mount other adults were clearly dominant to other adults in their areas.

Most relationships were complex. For example, in 1955, ♀1287 with her litter and a larger female, dominant to ♀1287, occupied B30, each using a different set of entrances. But ♀1287 was not completely submissive as she chased other adults, except the male from B21. Once, after being chased by the larger female of B30, ♀1287 retaliated by biting her from behind, then fled to her burrow.

On the east side of the hot creek in 1955, ♀524 was clearly dominant to all other marmots, and the yearling was submissive to all other adults even at her own burrow. The remaining two females tended to be dominant at their home burrows, with the exception that they were both submissive to ♀524.

♀524 occupied burrow systems 13 and 14. In 1955, she frequented the area from B16 to B9. But in 1956 she sometimes went north to B16, but usually she went via B13, along the hot creek and crossed over and fed near B32 and B33. Female 634 now occupied B1. She always went south or east of B1, never went north and never crossed the hot creek. There was no observed contact between ♀634 and ♀524. The latter was aggressive to yearlings and young but did not come into contact with other adults prior to late August. At the start of the period of observation in 1956 there were two adults at B3. Only one, ♀693, persisted throughout the summer. This animal was clearly submissive to ♀634. During part of the summer ♀693 frequented the area around B1 and never abandoned going there. But ♀693 avoided contact with ♀634, even entering the burrow at B1 when ♀634 approached. Thus dominance or submissiveness was not necessarily associated with a topographic area, but was always associated with interactions between animals.

In 1957, ♀693 had essentially the same home range as she had in 1956. ♀634 moved to B14 and spent much of her time feeding in the north flat feeding area where she never went in 1956. ♀524 was not present. ♀622 now ranged to the south. She was clearly dominant to ♀693 and probably was dominant to ♀634. In general, ♀634 tended to avoid ♀622 who had complete freedom of movement. The relationship between these two animals illustrates the subtle nature of aggressive-submissive actions postulated by Colias (1944: p. 83), "It is possible that aggressiveness in a more subtle form may be expressed simply by independence of action, and its opposite, submissive behaviour, merely by avoidance of another animal".

Some animals tended to be submissive wherever they were in the colony. The reaction of ♀693 to young marmots typifies this behaviour. In 1957, she had a litter of young at B13 that appeared above ground about three weeks later than the other young in the colony. By this time the older young were wandering widely. Whenever one approached B13, it was vigorously chased by ♀693. But when ♀693 went into an area where she was extending her home range, she reacted quite differently to young marmots and elements of her basic submissiveness appeared:

10.29 a.m. 8th July, 1957. Young chased by ♀693 at B13. 10.35 a.m. ♀693 went from B13 to hot creek and crossed over. A young (from B21) was at B32 and ♀693 lay down on the bank while the young sat and watched her. She then moved past the young, at first holding her body low, tail down in slinking fashion. Then ran south. The young ran to B32 (Fig. 6 a-e).

Agonistic behaviour may lead to territorial behaviour. Burt (1943: p. 351) has specified territory as "the protected part of the home range" and Carpenter (1958: p. 228) has emphasized that territoriality is a "behavioural system which is expressed in a spatial-temporal frame of reference". The agonistic behaviour of marmots did not have a spatial reference nor was it territorial in the sense that it is in prairie dogs where all members of a coterie defend the area that they inhabit against members of adjoining coteries (King, 1955). Bopp (1954, 1955b, 1956) writes of family and of colony territories in *M. marmota* but uses the word territory to mean home range. There was no defence against other individuals in the colony. Munch (1958) reports one incident of agonistic behaviour, but does not present any data for territorial behaviour. Therefore, one must conclude that agonistic behaviour with its attendant dominance-submissiveness relationships be-

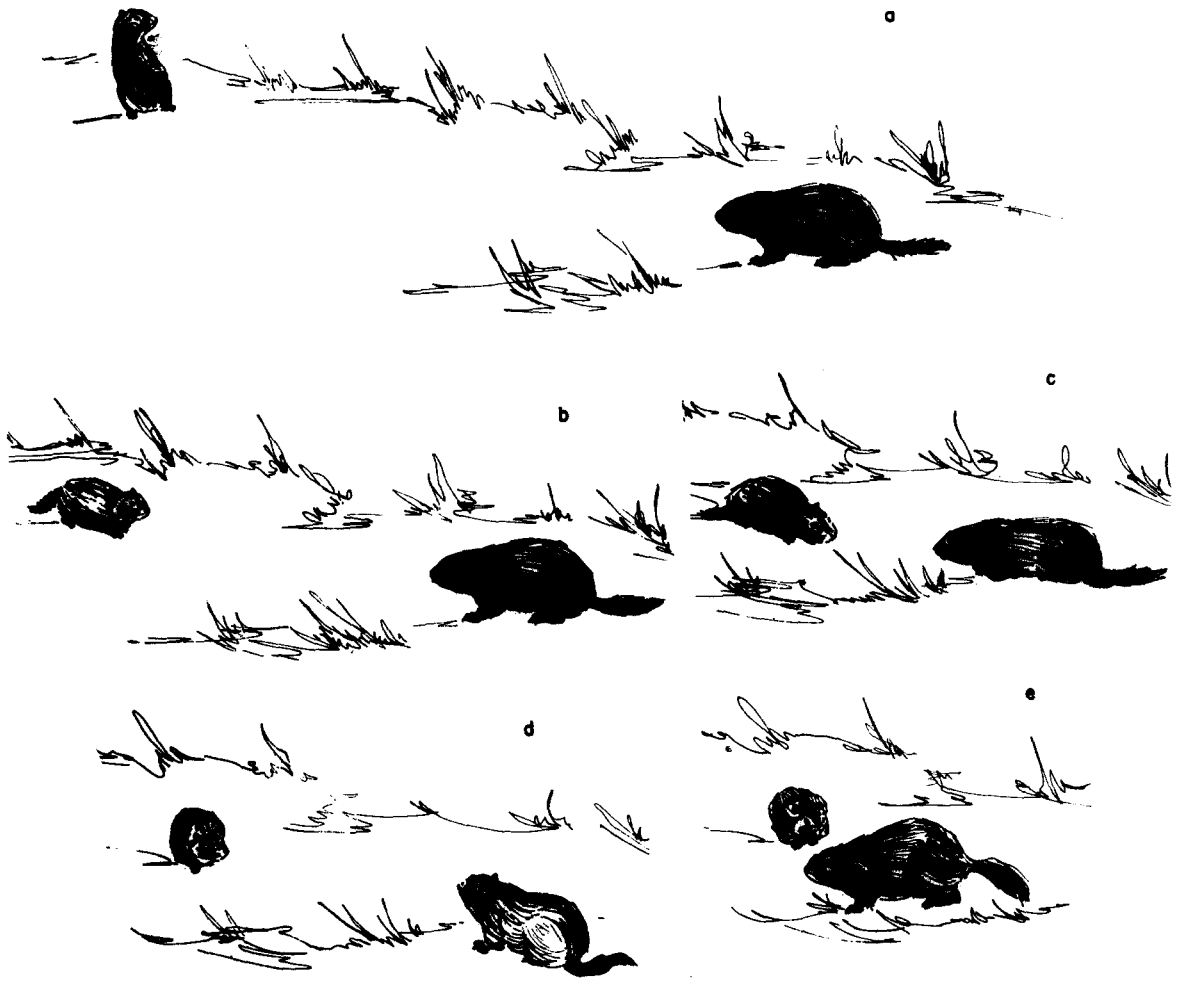

Fig. 6. (*a*) Female 693, on her way to B32, stops as a young from B21 sits up and looks at her. (*b*) The young approaches the adult, both animals have tail down. (*c*) The modified greeting occurs. The young is the "greeter" as it extends its head toward the adult. The adult crouches lower in submissive position. (*d*) The young backs off and the adult assumes a more dominant position with her head up. (*e*) The adult moves past the young, but the tail of the adult remains low as she continues to display elements of submissive behaviour. The above sequence of activity took place in an area where ♀693 was extending her home range. Near her home-burrow she would have reacted to the young by actively chasing it. The drawings were sketched from a series of colour transparencies.

tween individuals is characteristic of marmots and that territorial behaviour, *sensu strictu*, does not occur.

Agonistic behaviour may be a characteristic feature of sciurid behaviour. Gordon (1936) reported chases and churring in *Sciurus fremonti* and *S. douglasii* and he observed some semblance of chase order in *Citellus lateralis* and *Eutamias quadrivittatus*. Layne (1954: p. 259) reported that the red squirrel, *Tamiasciurus hudsonicus* does ". . . not normally establish exclusive property rights over specific areas within the home range, and that territorial behaviour is usually restricted to a small area immediately surrounding a feeding station or particular den site". . . . Many instances of scolding, chasing, and lunging at another animal were reported, indicating a general pattern of agonistic behaviour. Yerger (1953) observed chasing in the chipmunk in central

New York. The peak of chasing occurred in the autumn and was associated with a high population. Much of the behaviour seemed to be agonistic, some of which was territorial. The author has observed agonistic behaviour in *C. armatus* in which the patterns of activity appeared to resemble the territorial behaviour of the prairie dog (King, 1955).

Hibernation

Some adults hibernated during the first two weeks of August. Females that had littered and the young did not hibernate prior to the last week of August when observations were discontinued.

The most characteristic change in behaviour was breakdown in patterns of home range. During August, 1956, females 634, 524, and 693 all extended their home ranges across the hot creek where they never had been previously.

A second striking change in behaviour was in the level of activity. Alert calls and conflicts were less numerous (Table V) than earlier in the season. It was often possible to approach within a few feet of animals that earlier would not allow the observer to approach within several yards.

The third characteristic change in behaviour was an increased wandering whereby some adults traversed great areas of the colony and in some cases left the colony. Anthony (1923) postulated that seeking hibernation sites might be the cause of such wandering.

Discussion

The patterns of agonistic behaviour indicate that the adults which make up a colony of marmots must be aggressive enough to obtain a place, but at the same time some adults must be submissive enough to stay out of the way of or appease a more aggressive animal. Such a relationship implies that some animals may not have the behavioural (and underlying physiological) characteristics that will enable them to persist in the colony. Perhaps, then, agonistic behaviour has a role in the population dynamics of the marmot.

Such a role is evident from the data on sex ratios. As only one adult male is present in the colony, this means that, in effect, half of the young are lost to the population because of their sex. In addition, harassed adults and yearlings often emigrate.

Table V. The Number of Chases and Alert Calls per Observation Hour.

Mean date of emergence of young, 19th June. Hibernation began in the 7th week in 1961 and in the 8th week in all other years. Yearlings are included with the adults.

	Adult:Adult				Adult:Young				Alert Calls	
Time	1955	1956	1957	1961	1955	1956	1957	1961	1957	1961
Pre-emergence of young			·60	·57					0	·31
Post-emergence of young:										
1-2 weeks	1·25		·36	·38	·25		·21	·03	·27	1·25
3-4 weeks	·30		·10	·27	·30		·03	·12	·37	·75
5-6 weeks	·35	·30	0	·08	·28	·09	·08	·11	·08	·37
7th week	·50	·26	·11	·07	·25	0	·22	·21	·11	·50
8th week	0	0	0	·10	·50	·05	·28	·20	·28	·25
9th week	·11	0	0	0	·11	0	0	0	0	·20
Mean	·38		·17	·24	·28		·12	·11		
Mean/Adult	·022		·012	·018						
Mean/Individual (includes young and adults)					·0057		·0030	·0050		

Agonistic behaviour was directed particularly toward yearlings. Although yearlings formed 21 per cent. of the adult population over the four summers, they were involved in 52 per cent. of the chases. For the four years, of a total of 12 yearling present when observations began, four remained at the close of observations. Three of these were in 1961 when the adult population was the lowest.

However, agonistic behaviour is not directly related to population density. The rate of contact between adults was only slightly higher in 1955 than in 1961 (Table V), although there were twice as many adults in 1955. Although there were more adults in 1957, the rate of contact was lower than in 1961. In 1955 the contacts were scattered through the population, but in 1961, ♀636 was involved in 32 per cent. of all the contacts. This female had a marked effect as an individual as she caused two adults to leave the colony and caused other adults to have large home ranges in order to avoid her.

Agonistic behaviour may also act on the young. The number of adult:young chases/hour was greatest in 1955, although the rate of chases/hour/total population was only slightly higher than in 1961 (Table V). But in 1955 the young wandered over a greater distance within the colony and half the young emigrated during the summer (thus reducing the rate of contacts) whereas not more than one-third emigrated in any of the other years.

In summary, agonistic behaviour may function to reduce the number of marmots in a colony when the population density is high, because the number of contacts between animals is increased and emigration by members of all age groups results. Or similar results may occur because of the high level of agonistic behaviour of one or two individuals.

Evidence of predation on marmots is scarce. Wolves (Fryxell, 1926) and coyotes and various raptors have been described as predators (Borrell & Ellis, 1934; Couch, 1930; Craighead, 1951), but weasels probably are not predators on marmots (Quick, 1951). The author found marmot hair in one of twenty-one sets of coyote scats collected in the vicinity of the colony. It seems reasonable that coyotes capture some of the marmots, especially young, that leave the colony. Most of the animals taken in this manner might be marmots that would die anyway for a lack of a proper place in which to live. Because of a lack of evidence that predation is an important factor in the population dynamics of the yellow-bellied marmot, it is postulated that agonistic behaviour is the main factor that limits the numbers of marmots in a colony. However, data are not available on other aspects of population dynamics, such as reproduction, mortality, and indirect physiological effects of agonistic behaviour.

In conclusion, there seem to be two advantages to the social organization of *M. flaviventris*. First, agonistic behaviour aids in regulation of the population on the colony site; secondly, social facilitation through alarm calls, presence of reproductive mates, etc., increases the probability of survival of the resident population. These advantages of social organization seem to be contradictory in that the first limits the number of animals and the second prevents the reduction of animals and also acts to increase their numbers. These opposing functions can be interpreted as a homeostatic mechanism for maintaining a near optimum number of animals on a colony site. The second function assures that there will be a sufficient number of animals to maintain the species; the first assures that overpopulation with its potential mal-effects will not occur.

Summary

The social behaviour of a colony of yellow-bellied marmots was studied from June 18th to August 30th, 1955; July 12th to August 24th, 1956; June 10th to August 23rd, 1957; and June 14th to August 21st, 1961. The colony is located along a river terrace near the south entrance of Yellowstone National Park on the east side of the Snake River slightly south of the junction of the Lewis and Snake Rivers.

The home-burrow is where the young are reared, where an animal normally spends the night, and where an animal goes when an alarm call is given. Auxiliary burrows are used temporarily as a place of refuge. The burrows are connected by a trail system that directs the movements of the animals. The distribution of adults and litters indicated a preference for burrows in the central part of the colony.

Patterns of home range were of three types, those with no overlap, those with slight overlap and those with major overlap. Animals which utilized the same home range frequently avoided one another. The shape of the home range depended primarily on the nearness of the feeding area. Agonistic behaviour modified both size and shape of home ranges. Some home ranges were larger when the population was more dense

or when agonistic behaviour was more frequent. Patterns of home range tended to change during the first two weeks of August when some animals hibernated. Changes in home range from year to year were correlated with changes in the individuals occupying home-burrows.

The animals emerged from their burrows at about sunrise. There was a morning peak of activity followed by a midday low with a subsequent second peak of activity in the late afternoon. All the animals entered their burrows by 30 minutes after sunset.

Communication between marmots involved the senses of sight, smell, touch, and, most importantly, hearing. The alarm call was given in response to any kind of intrusion into the life of the colony. No particular animal acted as a sentinel. Olfactory communication consisted of the "greeting" in which two animals sniffed each other's cheeks.

One or two animals were dominant. Several tended to be submissive to all with which they had contact. Females with young may be aggressive in the vicinity of their home-burrows toward other animals, but may be submissive in other parts of the colony. Other relationships seem best characterized by a kind of neutrality in which each of the two animals avoids the other. Dominance is characterized by independence of action, tail flagging and grooming. Submissiveness is characterized by avoidance of other animals, slinking posture with tail down and submission to being groomed. Territorial behaviour does not seem to occur in the yellow-bellied marmot.

Hibernation began in the second week of August. Conflicts and alert calls were less numerous and activity in general greatly decreased. Increased wandering was shown by some adults.

It is postulated that agonistic behaviour is one of the factors that limits the number of marmots on a colony site.

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Accepted for publication 30th October, 1961