

Male behaviour and territoriality in the Yellow-bellied marmot

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(With 1 plate and 8 figures in the text)

Five populations of marmots were studied in Colorado from 1962 through 1972. Males are classified by age as yearlings, two-year olds, and adults. Socially, marmots are colonial, peripheral, or transient. Each population was divided into four age-sex classes, male yearlings, female yearlings, male adults, female adults, for analysis of social behaviour. Social behaviour was amicable or agonistic. Both types of behaviour occurred between male yearlings and each of the other age-sex classes. Play-fighting characterized social behaviour among male yearlings. Agonistic behaviour characterized social interactions between male yearlings and male adults. Male yearlings avoided male adults and usually dispersed from the locality. Adult male aggression enhanced but was not necessary for dispersal of yearling males. Agonistic behaviour between males and the four age-sex classes was not related to population density.

Territorial males are conspicuous and advertise their presence by tail flagging. Many colonial males patrol their territory. Adult male social behaviour is predominantly agonistic. Mean rates of amicable and of agonistic behaviour between adult males and adult females were greater for years of male turnover than for years of male returns.

Territoriality is characterized by exclusive use of the area by the colonial male, vigorous defence against transient or peripheral males, and by a relatively fixed area. A decrease in the number of males in an area causes an increase in the size of territories. Additional males in an area causes a decrease in the size of territories. The mean size of 24 typical territories is 0.67 ha. Reduction in the number of territories in an area was associated with increased agonistic behaviour among adult males. Fights were rare and occurred when the territorial system was unstable.

The major functions of the territorial system are enhanced reproduction in a limited environment, enhanced outbreeding and enhanced fitness of colonial males.

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Introduction

The basic social organization of the Yellow-bellied marmot (*Marmota flaviventris*) consists of a male with a harem (Armitage, 1962; Downhower & Armitage, 1971). In their analysis of the polygamous mating system of the marmot, Downhower & Armitage concluded that males were most fit when their harems consisted of two to three adult females and that males, in order to have maximal fitness, should be territorial. Males were predicted to be agonistic toward other males, but amicable toward females. Previously, Armitage (1962) concluded that agonistic behaviour characterized members of a marmot population, but that territoriality did not occur in the Yellow-bellied marmot.

This paper describes the results of a long term study of five colonies of Yellow-bellied marmots. The purpose is to examine male behaviour as related to predictions based on the model of polygamous mating systems and to establish and describe the nature and function of territoriality in this species.

Methods

Study area

The populations studied are located in the East River Valley, near the Rocky Mountain Biological Laboratory, Gothic, Colorado, at an elevation of about 2900 m. Seven localities were chosen for study. Locality 6 was designated an isolated area and Locality 3 studied intermittently (Downhower & Armitage, 1971). Each locality was photographed and measurements were made between physiographic features such as boulders, trees and burrow sites. The photographs and measurements were used to construct a map of each locality. The locations of the marmot localities were reported previously (Shirer & Downhower, 1968). Subsequently, we learned that each locality has one colony of marmots so that locality refers to the place and colony to the population of animals.

Localities 1 and 2 consist of rolling grass-forb meadows located within a large bend of the East River (Plate I(a)). The burrows of Locality 1 were centred on exposed shale along the steep river bank. Burrows were developed along natural fissures in the shale. Marmots moved from the river bank out into the meadows for feeding. Old fence posts along the top of the river bank were used for sunning, lookouts, etc. The burrows of Locality 2 were under a group of cabins and old walls and building foundations. Marmots at Locality 2 could forage in the meadows which surrounded the cabins. In 1969, some of the old cabins were removed and a new cabin was built. This building activity resulted in the elimination of the marmot habitat. Those marmots that remained were used in introduction experiments. All other activities at Locality 2 were discontinued.

Locality 4 consists of a low ridge of exposed rocky rubble in one side of a large gently sloping meadow (Plate I(b)). The meadow is enclosed by aspen-spruce forest on the north and east and by willow meadows on the south and west. That part of the locality most intensively used is about 0.42 ha, but in some years animals extended their activities into the hillside meadows to the north-west and further into the meadow to the south-east which nearly quadrupled the area of use.

Locality 5 is a steep slope with a large exposure of talus. The talus is bounded by a line of aspen across midslope and by meadows on all other sides (Plate I(c)). In most years a harem occupied the talus (lower area). Above the aspen is an exposure of rocks on a steep slope. Above the rocks is a gently sloping meadow studded with large boulders. A second harem was located in this area (upper area). Between the upper and lower areas and displaced to the south is a third area (middle area). This area also is an exposure of talus, partly enclosed by shrubs, but opening into meadow upslope and across slope to the south-east. In some years a third harem occupied the middle area. The meadow lying between the lower and upper areas generally was little used except close to the areas. Sometimes yearlings or transients utilized the meadow for varying periods of time, usually brief. The total area utilized by marmots is about 3.5 ha.

Locality 7 is a steep slope with one major exposure of rocks in the large meadow (Plate I(d)). Other rocks are exposed at various places. The meadow is broken by groups of trees which effectively subdivide the meadow. However, marmots consistently occupied only the main rocky exposure. The total area of use is about 1.1 ha, but the area of intensive use is about 0.4 ha.

Trapping and observation

Marmots were trapped with wire traps manufactured by the National Live Trap Company of Tomahawk, Wisconsin. An individually numbered self-piercing size 3 strap tag was placed in each ear for permanent identification. Tags have been retained for 8 years and only two of about 460 animals are known to have lost both tags. Lost tags were replaced upon next capture. Animals were marked with various patterns of stripes and blotches with Nyanzol non-toxic fur dye for recognition during periods of observation. Marmots moult once annually and the dye mark is lost at that time. The mark usually persists until early August. Animals retagged following their moult were remarked. Because the mark persists until the following mid-summer, observation of known animals was possible before they were retrapped in the following year.

Observation of the animals' activities was made with 10×50 binoculars and a 15 to 40 power telescope from an automobile parked at least 200 m from the study area. A parked automobile did not disturb marmots and on several occasions wandering marmots walked by the vehicle. The automobile permitted not only screening of the observer from the marmots but also free movement in writing notes, etc., and freedom from distraction by biting insects so that attention could be focused on the work at hand. All social interactions were recorded in a notebook and on data sheets prepared for that purpose. At specified intervals of 10 to 30 min, the length varying among the localities depending on the ease of locating the animals, the position of each animal was marked on the map of the locality and the activity of each animal noted on the data sheet. Observation occurred primarily between 06.00–10.00 and 16.00–19.00 MST when marmots are most active (Armitage, 1962). Observation was extended later or began earlier when marmot activities of special interest were occurring. No attempt was made to observe an equal number of hours at each locality. More time was devoted to those localities where social interactions were occurring. For example, when a colony was reduced to an adult male and an adult female, little, if any, social interactions occurred and less time was spent at such a locality. By contrast, the presence of several yearlings usually was associated with numerous social interactions and more time was spent at such a locality in order to obtain more rates of social interactions. Most of the observations occurred between 10 June and 15 August each year, but in a few instances began as early as 8 May and continued until 7 October. A total of 1714 hours were spent in



observation from 1962 to 1971 inclusive. A few additional observations were obtained in 1972.

All observational data were expressed as number of social interactions per animal per unit of time. Where sample sizes permit, appropriate statistical tests were applied. Where sample sizes were too small and variances were large, statistical analysis was not carried out beyond calculation of the standard error of the mean. The large variances in rates (e.g., ranging from zero to 54/animal/1000 h, Fig. 1 male adult : male yearling amicable behaviour) among colonies and among years within colonies precluded finding many statistically significant results. In any event, statistical significance is only one of many tools in elucidating biological significance. Because of the large variances and small sample sizes, it has been necessary in some instances to develop biological significance by demonstrating patterns of association among behavioural phenomena.

Several simple experiments in which strange males were introduced into presumed territories or males were removed from their harems were conducted and will be described more fully in the appropriate sections to follow.

Types of males

Males may be classified by age or by social behaviour. Yearlings are males between one and two years of age; i.e., in their second summer of life. Yearlings are easily distinguished from other males by their small size; a yearling male weighs about half as much as an adult male. Two-year old males probably are sexually mature, but weigh about 70% of the adult weight at the beginning of their third summer (Armitage, Downhower & Svendsen, in prep.). Only one two-year old male was associated with a harem. Adult males are three years old or older, i.e., in at least their fourth summer of life.

Adult or two-year old males may be colonial, peripheral, or transient. A colonial male is one who lives with a harem of females (Armitage, 1962; Downhower & Armitage, 1971). A peripheral male is one who lives near a colony, probably has sensory contact with members of the colony, but may have no direct social contacts. Sensory contact may occur if the peripheral male can see the colonial animals, can hear alarm calls, or receive chemical stimuli. Auditory and visual interactions between peripheral males and colonial animals have been observed, but chemical communication has not been demonstrated. A transient male is one who moves through a locality, but does not stay more than a few days.

Some males live alone and are designated isolates. Isolates do not have social or sensory contact with colonial animals, but may have contact with transients.

PLATE I. (a) Localities 1 and 2 from the west, looking down on the area from the slopes of Gothic Mtn. Dispersing animals occupy the intermediate areas (I) for brief periods.

(b) Locality 4 from the south-west. This locality supports only one territorial male. The activities of the male and harem are centred on the rocky rubble (R) in one side of the meadow. Yearlings frequently use a secondary burrow system (S) at the other side of the meadow.

(c) Locality 5 from the north. This locality normally has two harems with their territorial males, one at the upper area (U) and one at the lower area (L). Rarely a third male occupies the middle area (M) which is also displaced to the south. The line of aspen (A) across the centre of the slope above the talus (T) provides a partial topographic barrier between adjacent territories. Note the large, exposed boulders (B) which serve as lookouts.

(d) Locality 7 from the north-east. Activity is concentrated on the exposed talus (T) in the centre of the meadow. Exposed boulders and logs are used as lookouts. The colonial male may extend his territory upslope beyond the screen of willows (W). Peripheral animals may occupy sites (P) beyond the screen of trees such as the large boulder in the meadow to the south. A second territory (S) rarely occurs to the west.

The social status of a male is not necessarily permanent. Of 20 transient or peripheral males trapped and marked, six subsequently became colonial in the locality where they were trapped. Of 22 isolate males, one became colonial in one of our study localities. Of 29 colonial males, one, after four years at Locality 7, was found as an isolate at Locality 6 in the next year. Two males at Locality 2 were displaced by the male from Locality 1 and both became transients. One male left Locality 4 for no apparent reason and was found a year later with a harem of females about 4 km distant.

Types of social behaviour

Social behaviour of marmots may be broadly characterized as amicable (Ewer, 1968: 186) or agonistic (Scott, 1956). Amicable behaviour occurs as a greeting (Armitage, 1962) or as mutual grooming. Agonistic behaviour is expressed as alert behaviour, flight, or chase. Alert behaviour, or more simply, alert, occurs when one animal reacts to the presence of another by a general tenseness of the body and a careful watching of the other animal. The alert animal might crouch or lie flat, with part of the body behind a rock or clump of vegetation, but the head is always held so that the marmot causing the alert is observed. If the marmot causing the alert moves on, the animal showing alert behaviour "relaxes" and continues normal activities. Alert behaviour may be followed by flight in which the alerted marmot runs away. It may run into a nearby burrow or flee through the vegetation or across the rocky slope, stopping only when losing contact with the marmot causing the flight behaviour. Flight may occur without any observable alert behaviour. In these instances the animal causing flight suddenly emerges from a burrow or high or dense vegetation or suddenly appears moving rapidly toward the location of the responder. Alert or flight may be followed by a chase in which the animal causing the agonistic response runs toward the responder. Or, the chase may occur suddenly with an absence of preliminaries. These cases occur when the dominant chaser apparently sees the subordinate animal before the subordinate animal is aware of its presence. The chase usually ends when the chaser seemingly loses sight of the chatee or the subordinate chatee flees down a burrow.

Play-fighting

General description

Play-fighting or play (Armitage, 1962) characterizes the behaviour among male yearlings (Tables I and II). Although approximately equal numbers of male and female yearlings were present in the study localities and although more yearling males emigrated and emigrated earlier from the localities, 86 % of the bouts of play-fighting had a male yearling participant. Male : male play-fights occurred three times as often as female : female play-fights (Table I).

Play-fighting has several distinct elements. One marmot may pounce on another or may attempt to grasp the other around the middle with its forelegs. Frequently the two protagonists rear up on their hind legs and rest their forefeet on the other animal's shoulder. In this position they may push one another and mouth-spar. Mouth-sparring is characterized by a jabbing of the head at the head, shoulders, or chest of the other animal while the other animal does likewise. The two may roll and tumble in a bout of wrestling. There is much flailing of legs in the air and the animal on the bottom pushes against the animal

on top. Mouth-sparring also occurs while the animal on top apparently uses its forelegs to pin the animal on the bottom. A moment later, their positions may be reversed. There seems to be some nipping, but no serious biting and evidence of inflicted pain is rare. One animal may suddenly dart away, only to return a moment later to pounce on the animal from which it ran.

TABLE I

The number of instances of play-fighting observed among yearlings. The numbers are sums for each locality for all years of observation

Locality	Male : Male	Male : Female	Female : Female	Total
1	18	30	5	53
2	42	9	0	51
4	17	23	9	49
5	16	30	13	59
7	4	8	6	18
Total	97	100	33	230

TABLE II

The number of times male yearlings and male adults were observed in social behaviours with other marmots. The numbers are summed for all localities for all years of observation.

Sex and age groups	Social behaviours								
	Greeting	Mutual Grooming	Total Amicable	Alert	Flight	Chase	Total Agonistic	Grasp	Wrestle
Male Ylg : Male Ylg	9	12	21	5	4	2	11		
Male Ylg : Female Ylg	43	20	63	8	8	9	25		
Male Ylg : Female Ad	31	13	44	13	29	44	86		
Male Ylg : Male Ad	28	0	28	19	70	60	149	7	20
Male Ad : Male Ad	0	1	1	12	11	9	32	1	3
Male Ad : Female Ad	93	12	105	34	39	26	99	34	11
Male Ad : Female Ylg	19	0	19	17	32	18	67	8	4

Ylg, yearling; Ad, adult.

Discussion

There are elements of sexual behaviour and of fighting behaviour in play-fighting. The grasp around the middle is much like that which occurs when an adult male grasps a female as part of reproductive behaviour (Armitage, 1965). Virtually all other elements of play-fighting occur in fighting among adults. The essential difference is the lack of inflicted harm between two marmots play-fighting. Also the running away and returning to the encounter is not seen in adult conflict.

What is the function of play-fighting? There seems to be no general explanation for play which applies to all species (Beach, 1945). Certainly the animals enrich their experiential world of social contacts, but Loizos (1966) argues that these experiences may be gained in other ways and that experience is not an adequate explanation of play. However,

play in marmots does provide social experience in the forms of agonistic behaviour without the attendant consequences. Patterns of aggressive behaviour of polecats first appear in the context of play (Poole, 1966) much in the same way these patterns appear in

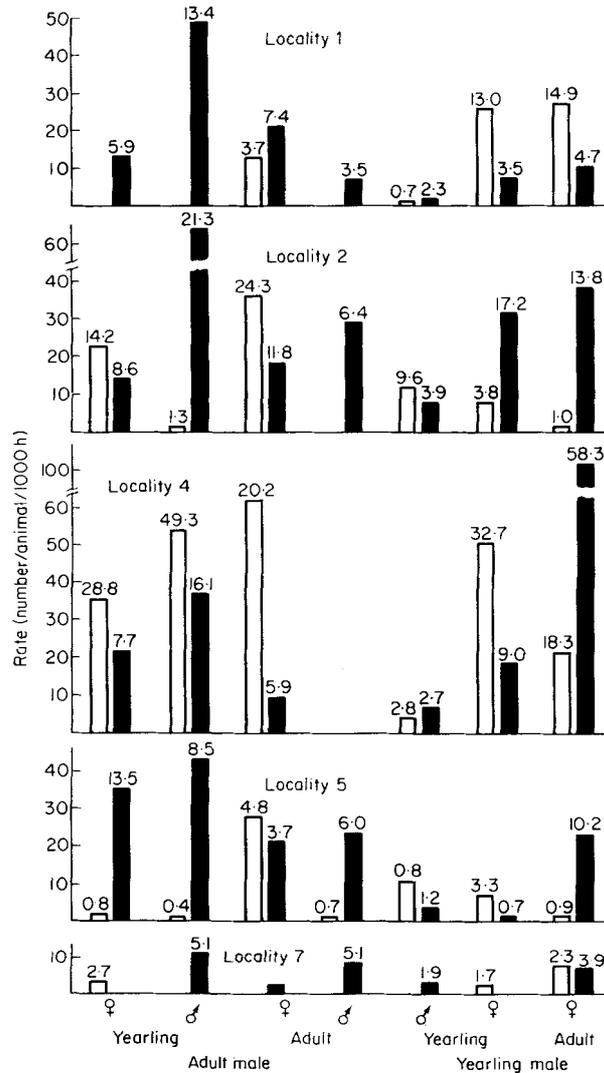


FIG. 1. The mean rates of amicable and agonistic behaviour between adult males and yearling males with each of the age-sex groupings at each of the marmot localities. The number at the top of each bar is the standard error of the mean. Means were calculated using only those years at each locality for which behavioural interactions between the listed age-sex groupings occurred. Small sample sizes precluded calculating standard errors for greeting, mutual grooming, alert, flight, and chase behaviours. □, Amicable; ■, agonistic.

marmots. As Eisenberg (1971) emphasized, some behavioural repertoires are related to phases of maturation. Perhaps play-fighting is a developmental phase in the formation of dominance-subordinance relationships. This hypothesis is consistent with the frequency

of male participation in play-fighting and accounts for the otherwise few social interactions among male yearlings (Table II, Fig. 1). Because the data are not sufficient for a clear interpretation of play-fighting, I chose to treat the phenomenon separately in the classification of social behaviour used in this report.

Behaviour of yearling males

Social behaviour

All of the social behaviours described previously occur between male yearlings and female yearlings, male adults, and female adults (Table II). Few social interactions occur among male yearlings.

Social interactions between male yearlings and female yearlings are primarily amicable (Table II, Fig. 1). Agonistic behaviour is characterized by female yearlings being alert to, fleeing from or being chased by male yearlings. In only eight instances did the male yearling have the subordinate role. By contrast, female adult agonistic behaviour occurred twice as many times as amicable behaviour and was characterized by the male yearling being alert to, fleeing from or being chased by the female adult. Agonistic behaviour was five times as frequent between yearling males and adult males as was amicable behaviour. In all instances, the yearling was subordinate to the adult.

Alert behaviour occurred much less frequently than did flight or chase behaviours in the social interactions between yearling males and adult males and females (Table II). Chases indicate the social attitude of the adults toward the yearlings. This behaviour accounted for 44% of the instances of agonistic behaviour between adults and male yearlings.

Nearly all amicable behaviour between male yearlings and male adults occurred at Locality 4 (Fig. 1) and involved one adult male and one male yearling. The behaviour of this male yearling was unique among male marmots. Whereas most male yearlings avoided adult males, he sought out the adult:

18 June 1968. Yearling ♂ 886 runs out from rocks to meadow where adult ♂ 801 is feeding. The activity appears directed as the yearling goes on a route directly to the adult and does not feed along the way. As the yearling approaches the adult, the adult flags his tail. Yearling ♂ 886 greets ♂ 801 and ♂ 801 noses around flanks of ♂ 886 who keeps low in a subordinate position and turns his back to the adult. Then the yearling runs off and ♂ 801 continues feeding. Then yearling ♂ 886 begins feeding.

Frequently the yearling presented to the adult in the manner of an adult female approaching a male during mating (Armitage, 1965). Encounters between these two males sometimes continued for 20 minutes and usually involved wrestling. These encounters account for all instances of grasping and wrestling between adult and yearling males. The adult always was dominant.

The adult male sometimes chased the yearling and nipped at him, but never with any vigour. The adult conveyed the impression that he just wanted to be left alone. Often their encounters ended with the adult male running off. The yearling male spent the entire active season within the adult male's territory, the only known instance where the centre of activity of a male adult and male yearling were virtually identical.

The male yearling seemed typical in his behaviour toward females. He tended to avoid the adult female and had three times as many agonistic interactions with her as he did

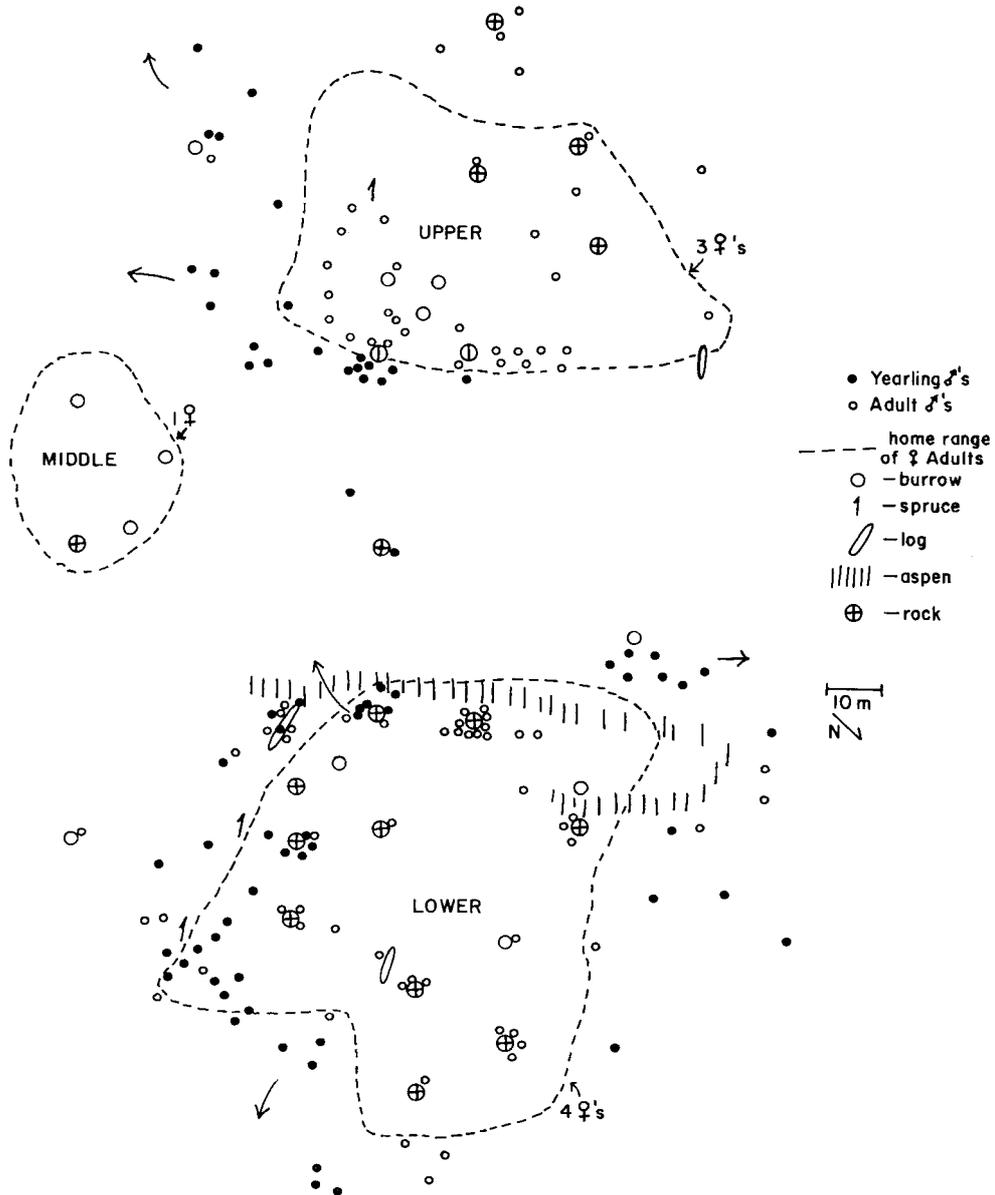


FIG. 2. Dispersion pattern of five yearling males at Locality 5 in 1965. The arrows indicate the directions the yearlings moved to avoid an adult male. The dispersion pattern of the male yearlings and the areas utilized by the adult males are shown as circles where an animal was seen during a census. Note the cluster of adult male circles around rocks or logs which served as lookouts. Two adult males were present; one was at upper and one, at lower. The home range of the adult females is the total area of all the home ranges of the number of resident females as indicated on the figure. Home ranges of individual females were less extensive.

with the adult male. His behaviour toward the female yearling was sexual. He approached and grasped her around the middle with his forelegs and attempted to mount her. The female yearling snapped at him and moved away. These interactions were typical of male : female sexual behaviour when the female was not oestrus (Armitage, 1965).

Of the other four instances of amicable behaviour between a yearling and an adult male, three occurred between colonial yearlings and transient adults. Male 886 was unique and although several interpretations of his behaviour come to mind, none can be verified. In summary, amicable behaviour between adult males and yearling males is virtually non-existent among colonial animals and, in any event, occurs only under highly peculiar circumstances.

Dispersion and dispersal

In 18 of 27 locality-years (a locality-year is one locality of marmots studied for one year), all male yearlings dispersed from their localities, usually by the end of June. Overall, 73% of 62 male yearlings dispersed during their second summer prior to 15 August. Only in one colony-year were any of the male yearlings recaptured as two-year olds. This lack of two-year old males implies late dispersal prior to hibernation or very early dispersal at the beginning of the third summer of life.

Those male yearlings that did not disperse developed one of two patterns of dispersion within the locality. Some yearlings had home ranges which only partially overlapped the adult male's home range. The per cent overlap of the area of yearling male and adult male home ranges varied from 1 to 68; the mean was 35. These home ranges tended to be toward the periphery of adult activity (Fig. 2). Occasionally, all of the male yearling home range was within the home range of the adult male, but was located at one side.

In six locality-years, more than one male yearling was colonial. The percentage overlap of home ranges of yearling males varied from 49 to 95; the mean was 75.

Eight of the nine locality years in which male yearlings remained were in some way atypical. There was a turnover in resident adult males in three locality-years. In five locality-years, there was either conflict among adult males or the male adult territorial areas were significantly larger than the typical. For example, in 1968 ♂ 355 resided at Locality 1, but was able to exclude other adult males from Locality 2. Consequently, male yearlings had intermittent contact with adult males and remained throughout the summer. Their home ranges were primarily at the outer edges of the home ranges of the females and extended into areas not otherwise utilized by the adults (Armitage, 1973). A similar situation occurred at Locality 5 in 1969. A single male occupied the entire locality whereas in most years two males were present (Fig. 2). He resided at the upper area and made excursions to the lower area. Although the yearlings fled at his approach and were sometimes chased, the adult always returned to the upper area and the yearlings persisted in the lower area (Fig. 3).

Behaviour of adult males

Individual behaviour

The most striking characteristic of adult behaviour is its conspicuousness. As a colonial male moves around a locality, he carries his tail in an arc extending above and to the rear of his body. The tail is waved back and forth in a behaviour designated flagging. Flagging

is especially characteristic of a male's behaviour when he approaches another animal. Flaggings are so easily seen that it must serve to advertise the male's presence.

Some males patrol their localities. Patrolling normally begins in the morning shortly after emergence from the burrow. The same route is followed each day, with deviations

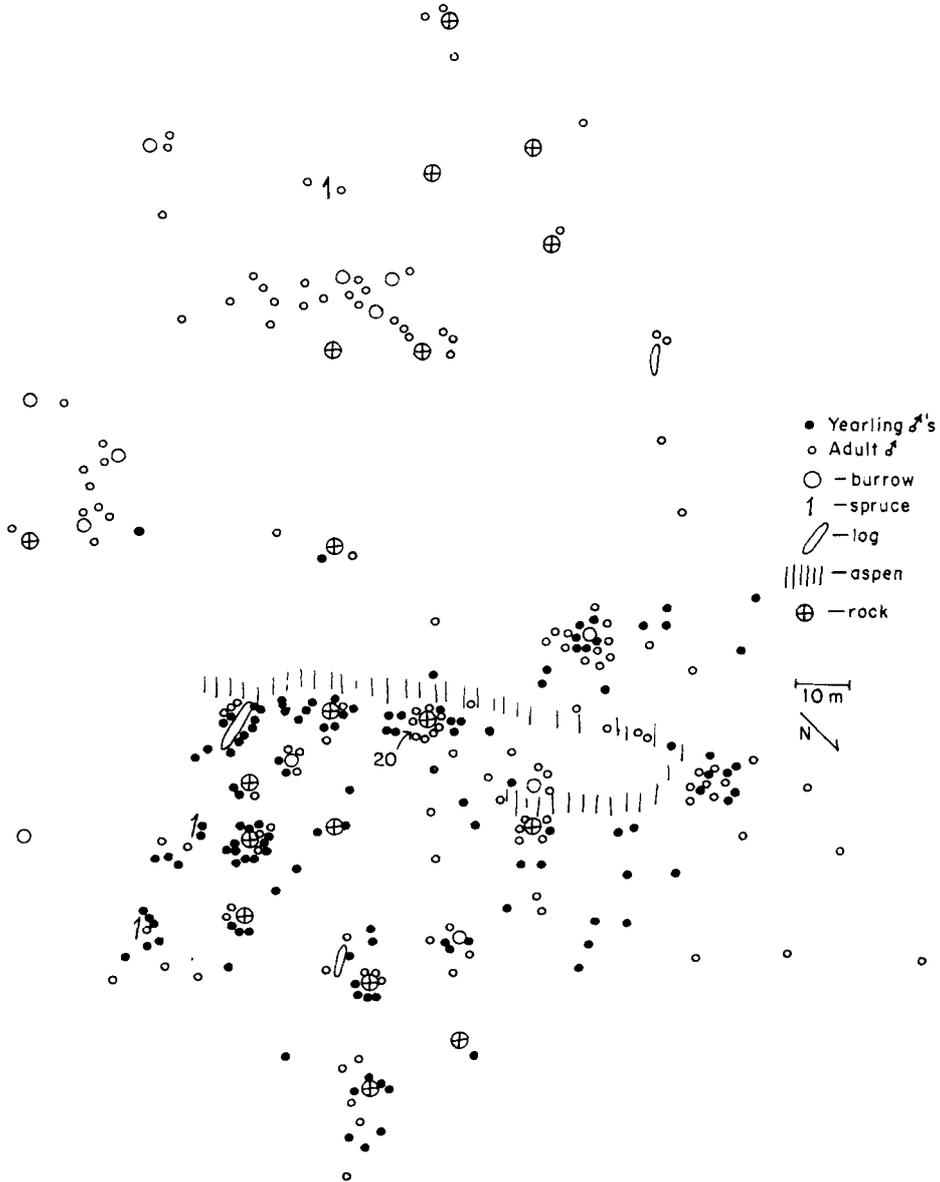


FIG. 3. Home ranges of two male yearlings and the adult male at Locality 5 in 1969. The adult male lived at the upper area (see Fig. 2). Contrast this pattern of dispersion of male yearlings with that of Fig. 2, when an adult male also lived at the lower area. Each circle represents the location of an animal during a census. The number 20 indicates an additional 20 records of male yearlings at that particular rock.

occurring when the male interacts with another animal. Along the route are boulders, logs, fenceposts or rock piles which are used as lookouts (Fig. 2). The male usually moves quickly from one lookout to the next, but may sit or lie on a lookout for several minutes and sometimes much longer. Little feeding occurs during patrolling. When the male is on a lookout, he sits or lies in an alert position. He obviously looks around and scans the area ahead of him. If he sees a harem female, he may amble over to her with flagging. A strange animal may be approached quickly, body tense, tail cocked, and body hair erect. A male may patrol until he reaches a feeding area, then complete his circuit of the locality after feeding. Some males, after a prolonged period on the lookout nearest their burrow, go directly to a feeding area and patrol somewhat later in the morning. Patrolling establishes the male's home range. Daily patrols wane as summer advances and may cease by late summer. However, the use of one or more lookouts continues until hibernation.

Not all males patrolled their entire territory. For example, ♂ 355, whose territory included Localities 1 and 2, lived at Locality 1 and went to Locality 2 only when strange males appeared. Males at the upper area of Locality 5 did little patrolling; whereas, males on the lower area of Locality 5 were among the conspicuous patrollers. All of the upper area can be readily seen by the resident male, but the lower half of the lower area cannot be seen from the line of aspen because of the steep slope (Plate I(c)). Thus patrolling seems to predominate in those localities where topography or vegetation (e.g., Locality 7, Plate I(d)) prevents the male from viewing his territory from one or two central lookouts.

A colonial male rarely departs from his normal patrolling pattern and moves far beyond his home range. One male was observed at the upper area of Locality 5 (Plate I(b)) to continue up slope, climb the cliffs, and disappear over the mountain. He returned to normal movements the next day. The function of these extended movements is unknown, but may be a carry-over from previous transient behaviour. All colonial males (except one) were born somewhere unknown other than the locality of their residence. Thus, their behaviour must have a wandering component which may be expressed by these excursions.

Social behaviour

Male social behaviour is predominantly agonistic (Table II). Only with adult females does the occurrence of amicable behaviour exceed that of agonistic behaviour. Grasp and wrestling occurred most often with adult females. These behaviours are part of the pattern of sexual behaviour of marmots (Armitage, 1965).

There was considerable variation among the colonies in the relative amounts of amicable and agonistic behaviour between adult males and adult females (Fig. 1). In colony one, agonistic behaviour exceeded amicable; in colonies two, four, and five, amicable behaviour exceeded agonistic. The few social interactions at Locality 7 were agonistic. In most colonies the agonistic response was primarily the female's; that is, the female was either alert to or fled from the male. For those chases in which the beginning of the chase was observed, half of them began when the female fled and the male gave pursuit. Of the 26 chases observed, 19 occurred at Locality 1. Most of the chases occurred in 1964 and 1965 when new males were present. Therefore, the rates of agonistic behaviour between adult males and adult females were divided into two categories: those years in which the colonial male was present the previous year (male returns) and those years in which the colonial male was new (male turnover). At Localities 1 and 5, mean rates of amicable and of agonistic behaviour were greater for male turnover than for male returns (Table III).

The pattern of these behaviours at Locality 2 is of special relevance. Male turnover occurred in 1964 and 1965 and the same male remained through 1968 and occupied Locality 1, as well. However, in 1967 and 1968 other males attempted to obtain residence at Locality 2. The rate of amicable behaviour between the females and the strange males was twice that of the rate between the females and the resident male; the rates of agonistic behaviour were 1.5 times greater with the strange male than with the resident. If the

TABLE III

Rates of social interactions (number/animal/1000 h) between adult males and adult females. The rates are means (\pm standard error of the mean) of the rates for individual years. The number of years is the number in the second set of parentheses following the rates of amicable behaviour

Social interactions	Locality 1		Locality 5	
	MR	MT	MR	MT
Amicable	8.9(\pm 2.8) (4)	19.5(\pm 7.7) (4)	9.5(\pm 2.4) (5)	19.7(\pm 3.7) (3)
Agonistic	7.5(\pm 3.1)	29.4(\pm 13.3)	5.3(\pm 3.4)	7.8(\pm 4.5)

MR, male returns; MT, male turnover.

TABLE IV

Rates of social behaviour between a resident adult female and an introduced adult male at Locality 4 in 1970. Rates are expressed as number of social interactions per 100 hours. Periods of observation coincided with the time of day of maximal activity

Date	Hours of observations	Social behaviours								
		Greeting	Mutual grooming	Total amicable	Alert	Flight	Chase	Total agonistic	Grasp	Wrestle
June 23	1.5	66		66	66			66	66	
24	1.5	92	15	107	30	15		45		
25	6.5	67		67						
27	1.5									66
28	3.5									
29	2.0									
30	1.5	67	67	134						66
July 4	2.0									50
July 7-Aug. 3	19.0	No social interactions observed								

rates with strange males are apportioned to the male turnover category, the means (no./animal/1000 h) were 44.3 (\bar{X} s.e. = 29.2) and 20.6 (\bar{X} s.e. = 14.3) for amicable and agonistic behaviour, respectively. For male returns, the respective rates were 4.5 (\bar{X} s.e. = 1.7) and 2.8 (\bar{X} s.e. = 2.2).

The above analysis implies that a strange male causes male : female conflict and that some sort of socialization process occurs after which there is greatly reduced social interactions between the male and the females of his harem. This interpretation was tested in 1970 at Locality 4. The resident female was four years old and in her fifth summer of residence at the locality. No male was present. An adult male was released on 23 June and the behaviour of the animals checked regularly thereafter (Table IV).

There were high rates of social behaviour following the introduction of the male. All amicable behaviour was initiated by the female and all agonistic behaviour was her response to the male. When the male approached the female, he usually tried to grasp her (Table V). This behaviour is typical of male reproductive behaviour (Armitage, 1965). The female often responded agonistically to the male's approach; frequently this response initiated a brief bout of wrestling. The female always was subordinate and usually broke away.

During this period, the female increased her home range by moving into areas she had never before been observed to utilize. Although these movements are interpreted as an attempt to avoid the male, she did not change to another home burrow. The male followed her into the new areas and after several days, these excursions ceased. No social interactions were observed between 4 July and 3 August when observations ceased. Both animals occupied the rocky talus together, used the same lookout rocks, and fed in the same areas.

TABLE V

Territorial size of adult colonial male Yellow-bellied marmots. A male-year is one male occupying a territory for one active season

Locality	Number of residents	Number of male-years	Size of territory (ha)		
			mean	Standard error	Range
1	1	4	0.66	0.12	0.49-1.06
	2	6	0.35	0.06	0.20-0.65
1 and 2	1	4	1.48	0.02	1.43-1.54
5 (upper)	1	5	0.55	0.08	0.28-0.76
(lower)	1	7	0.76	0.04	0.57-0.91
(entire)	1	2	1.90	—	1.81-1.98
7	1	7	0.71	0.12	0.25-1.23

Adult male : yearling female social behaviour is primarily agonistic and is characterized by avoidance of the adult male by the yearling female. No pattern was evident between those years in which there was male turnover and those years of male returns. This lack of pattern is attributed in part to the varied mortality of young (Armitage & Downhower, MS) which resulted in some years of no yearling females so that the sample size is too small for any meaningful comparison. However, the percentage of female yearlings dispersing is independent of adult male : yearling female agonistic behaviour. For example, 50 % of the yearling females dispersed from Locality 5 in 1967 when there were no observed agonistic interactions whereas 40 % of the female yearlings dispersed in 1969 when the rate was 0.05/animal/h.

The social behaviour of the adult male with male yearlings was described previously. The adult male : adult male social behaviour is entirely agonistic with a few exceptions. Wrestling and grasp among adult males occurred only at Locality 5 among two-year olds. The only observed instance of amicable behaviour (Fig. 1) was between two-year olds who lived together as yearlings. All of these behaviours occurred early in the summer and may represent manifestations of yearling male behaviour which disappear when males are fully mature.

Few adult male : adult male social interactions were observed (Table II, Fig. 1). One reason seems to be that transient males tend to avoid colonial males. Transient males usually are trapped and observed on the periphery of the colonial male's home range. The behaviour of the transient male is best described as secretive. He keeps his tail down, tends to stay in dense vegetation, and does not use lookouts. Sunning behaviours which account for 50% or more of the behaviour of colonial marmots (Travis & Armitage, 1972) are not seen. The animal acts "uneasy" and takes flight quickly at the appearance of the colonial male.

If a transient male stays for several days and uses a burrow within the male's home range, the colonial male modifies his normal patrolling behaviour and focuses his activities on the area and burrow where the transient is active. The following behaviour at Locality 5 illustrates the different behavioural patterns of the transient and colonial males (see Plate I(c) for locations of aspen, etc.):

16 June 1963. Colonial ♂ 63 moving upslope. Transient ♂ 74 runs along the log, through the aspen and finally seen on big rock 30 m upslope between lower and upper areas. Then ♂ 63 seen running along the log to the aspen and along the edge of the aspen and turns down slope to the burrow used by ♂ 74. ♂ 63 sniffs around the rocks, then sits by the burrow and stares upslope.

Several days later ♂ 63 was still visiting the burrow, examining the area around it, sitting up and looking around, and climbing on a lookout and lying there and facing the burrow. However, ♂ 74 had departed. This behaviour by ♂ 63 was not observed again.

Only one encounter was observed between a peripheral male and a colonial male. Although the colonial male ran toward the feeding peripheral male, the peripheral male did not flee. After a brief period of alert behaviour, the two males parted with no clear pattern of dominance established.

Encounters between colonial males were especially rare because the populations were distant from one another. One encounter was observed at Locality 7. Both males flagged their tails, but there was no other evidence of conflict. Neither attempted to chase the other; the "invading" male ran slowly towards his resident locality while the resident male followed several metres behind. By contrast, a colonial male sometimes went well beyond his normal home range after a strange male:

13 June 1972. ♂ 5 entering meadow by the road where another animal who acts like a male is active. ♂ 5 chases other animal around the tree, then out into the road as ♂ 5 chased the other animal 30 m up the road. Then ♂ 5 returned to the tree with vigorous tail flagging. Five minutes later ♂ 5 starts back up the road where the other animal lies in ready-alert. Animal flees and ♂ 5 chases. Chase is long and vigorous, going through the willows, back across the road and into the willows on the other side.

Social behaviour and population density

Mean rates of social interactions between yearling males or adult males and the four age-sex categories varied among localities (Fig. 1). The generally high standard errors indicate much variation among years within localities.

One possible explanation for the variability in the rates of social interactions is that they are a function of population density. There is no *a priori* reason for assuming that

the density of any particular age-sex category can be used as the measure of a relationship between rates of social behaviour and population density, for example, agonistic behaviour between adults and male yearlings could be a function of the number of male yearlings, or the number of adults, or the total number of adults and male yearlings.

The possible effect of density was tested by plotting the rates of amicable behaviour, agonistic behaviour, and total social interactions (amicable+agonistic) between yearling males and each of the other age-sex categories against the number of yearling males, the number in the other age-sex category, and the number of yearling males plus the number in the other age-sex category. For adult males, rates were plotted against the number in the other age-sex category and the number of adult males plus the number in the other age-sex category. Plots were not made using the number of adult males as a measure of density because in 32 of 47 colony-years, only one male was present.

A total of 42 plots were made using the various combinations of age-sex categories as measures of density. The relationships were tested by Olmstead & Tukey's corner test for association (Sokal & Rohlf, 1969: 538).

Amicable behaviour between yearling males and yearlings females was negatively related to the number of male yearlings ($P=0.1$) and the total number of yearlings ($P=0.1$). Total social interactions were negatively related to the number of male yearlings ($0.1 > P > 0.05$) and the number of female yearlings ($P=0.1$).

There were no relationships in the social behaviour among male yearlings or between male yearlings and male adults (all $P > 0.1$).

Amicable behaviour between yearling males and adult females was negatively related to the number of male yearlings ($0.1 > P > 0.05$). All other rates were independent of measures of density ($P > 0.1$).

Although amicable behaviour between adult females and adult males evidenced some tendency to be higher at lower densities of adult females, the relationship was not statistically significant ($P > 0.1$). There was no significant relationship between agonistic behaviour or total social interactions and measures of population density ($P > 0.1$).

Introduction and removal experiments

The encounters described thus far plus all others in which a colonial male reacted to a strange male indicated a vigorous defence of the locality by the colonial male or, at the least, the exclusive use of the locality or part of a locality by a male. If these encounters could be interpreted as territorial behaviour, then the pattern should be modified by removing resident colonial males.

In 1969, ♂ 402 was removed from Locality 2. A transient ♂ 767, first trapped at Locality 1, then moved into Locality 2. In 1972, ♂ 16 was removed from Locality 4 for several days and a two-year old male moved in.

In 1967, three adult males resided at Locality 5. By June 17, male yearlings had dispersed to peripheral areas (Fig. 4). The male on the lower area was removed on 17 June, and the male yearlings moved into the area (Fig. 5). After two weeks, the adult males extended their activities into the lower area and the yearling males shifted their activity toward the periphery of the males' ranges (Fig. 6). No encounters were observed between ♂ 494 and ♂ 418. Both males maintained residence in their previous areas (Fig. 4), but extended their movements into the lower area. The time of their visits did not overlap, but usually

were at least 30 minutes apart. There was some overlap in home ranges (Fig. 6). Three of the four male yearlings remained throughout the summer, only the second time in 11 years male yearlings were resident for that length of time. In 1968, a further adjustment

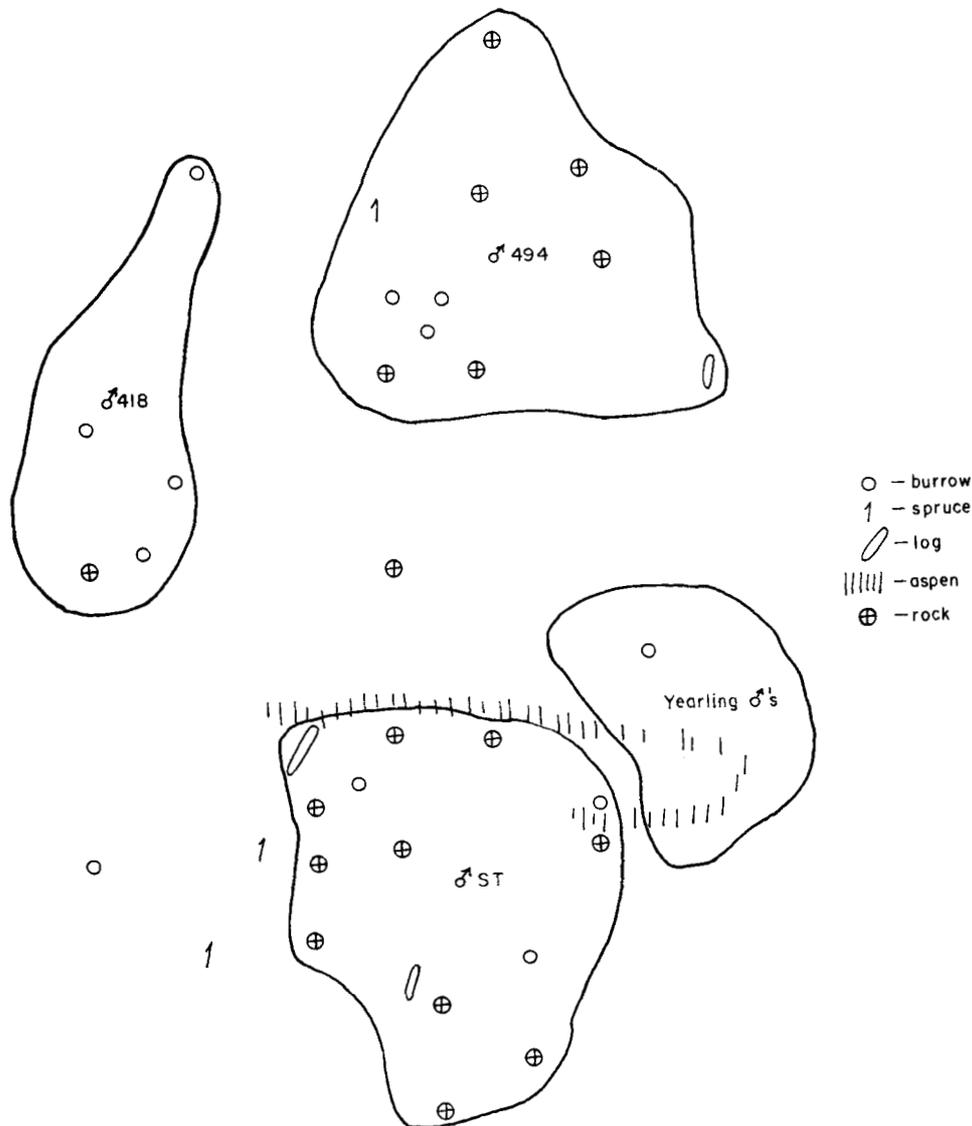


FIG. 4. The territories of three adult males and the home range of four yearling males at Locality 5 in June 1967. The territories and home ranges are outlined with the solid lines.

occurred in the movements of the adult males. ♂ 494 was limited to the upper area and ♂ 418 occupied the entire lower slope plus the middle area where he resided in 1966 and 1967.

Nine yearling males were introduced into localities where a colonial male resided. All yearlings subsequently emigrated. Three two-year old males and three three-year old males

were similarly introduced. All emigrated, usually within two to three days. The behaviour of the introduced male is typified by ♂ 402. He was resident at Locality 2 and introduced into Locality 7. There he fled at the approach of the resident male and entered a burrow.

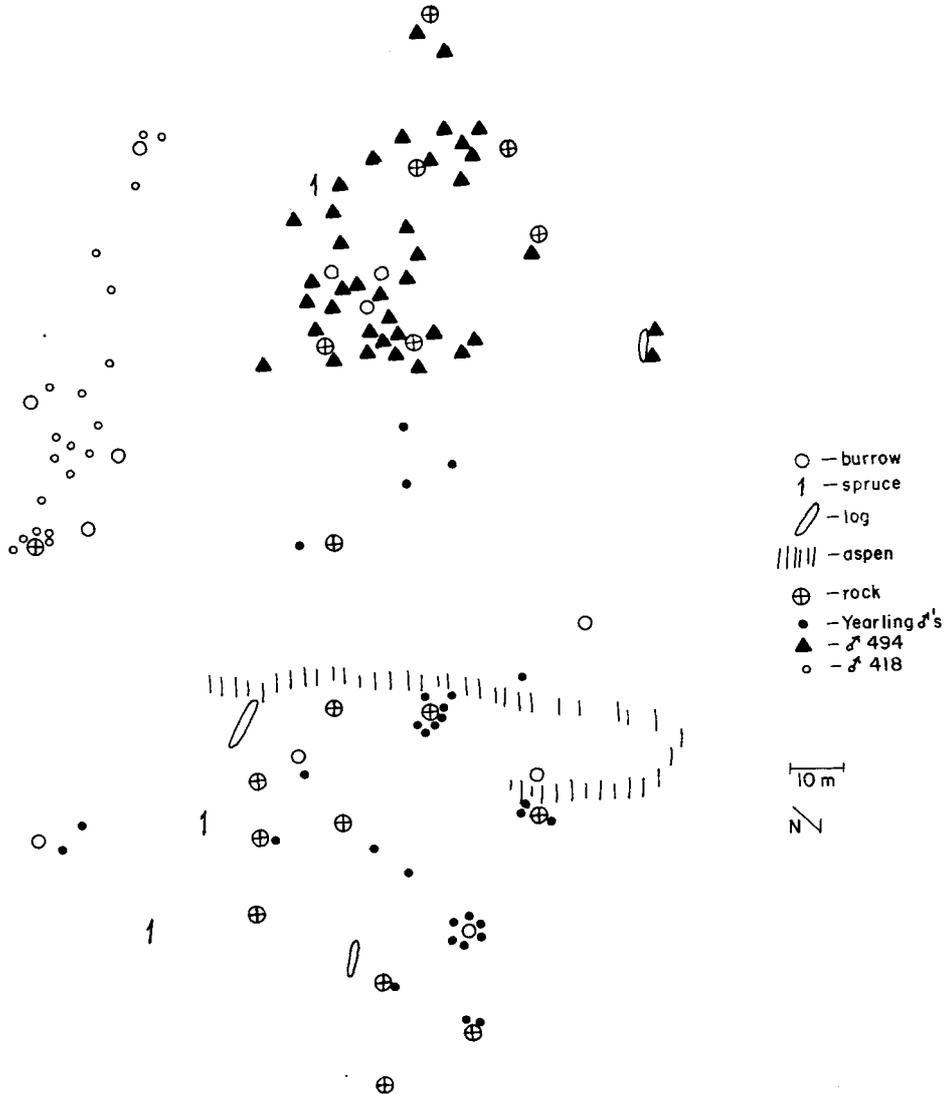


FIG. 5. The dispersion of the remaining two adult males and of four yearling males in the two weeks following removal of ♂ ST on 17 June 1967, from the lower area. Each circle or triangle represents the location of an animal during a census.

He soon disappeared and reappeared two weeks later at Locality 5. Here his behaviour was quite different as he apparently tried to establish residence:

6 July 1969. Vigorous tail flagging at upper area. ♂ 402 retreats with tail flagging as ♂ 418 approaches.

7 July 1969. ♂ 402 becomes alert and darts off as ♂ 418 approaches. Seven minutes later ♂ 402 again retreats. Both males with tail high, hairs erected, both running. Ninety minutes later ♂ 402 flees into a burrow as ♂ 418 approached. Ten minutes later as ♂ 418 remained near burrow where ♂ 402 entered, ♂ 402 emerges and runs uphill. ♂ 418 chases and catches him about 12 m upslope. Vigorous fighting in form of

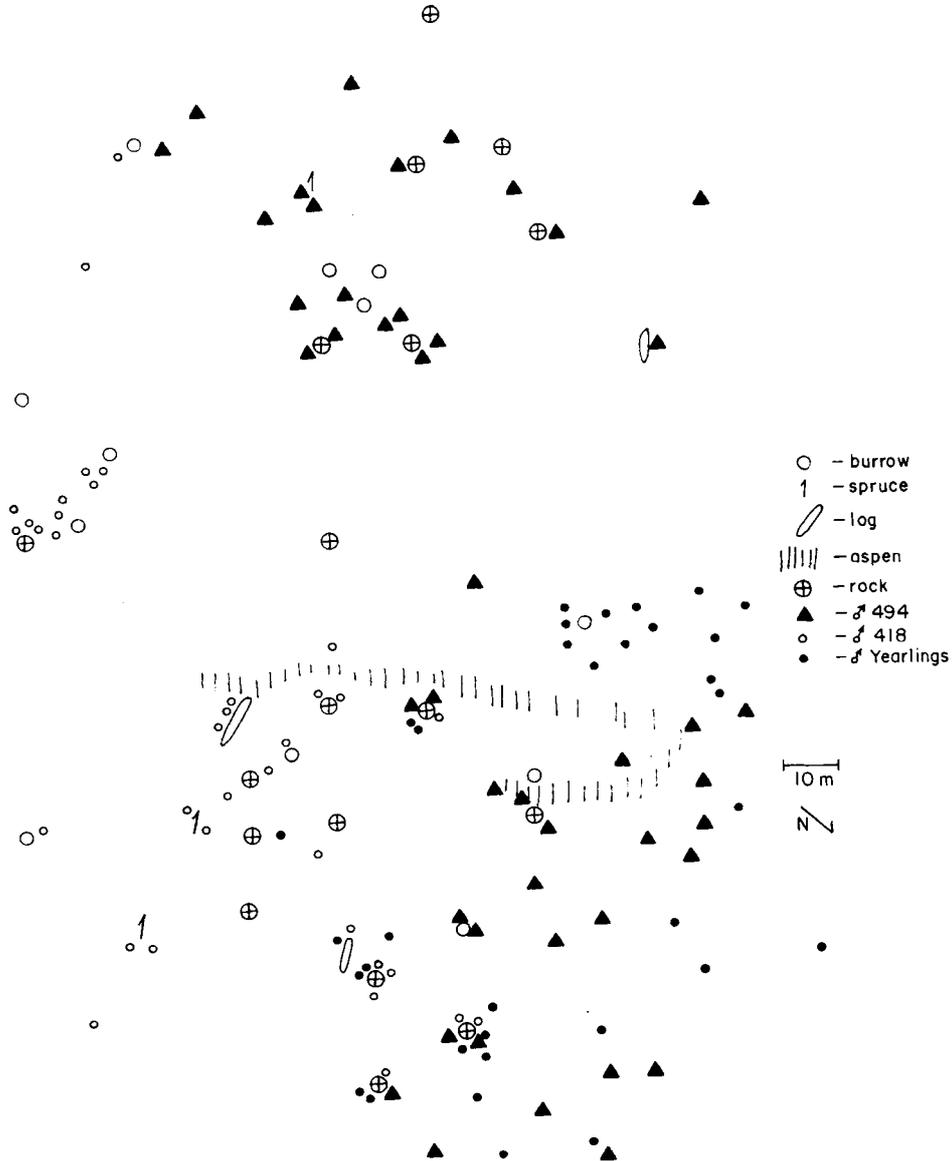


FIG. 6. The territories of the adult males and the dispersion pattern of the yearling males after 1 July 1967. The adult males have extended their territories into the lower area and the male yearlings have moved toward the periphery of the area (contrast with Figs 4 and 5). Each circle or triangle represents the location of an animal during a census. Note that the home ranges of the adult males overlap only slightly.

chasing and wrestling as they come back down the hill. Tail flagging and mouth-sparring. They stand on rear legs and push with forelegs. They appear to grasp with their jaws, the head, jaws or shoulder of the other, wrestle and tumble for three minutes and roll down through the bushes and now downslope from the burrow about 10 m. ♂ 402 breaks away and ♂ 418 pursues. Both males out of sight after a total of eight minutes for the encounter.

Following the encounter, ♂ 402 was not seen. He must have remained in the vicinity because he became resident at the upper area of Locality 5 in 1970.

Size of territories

Overall, size of territories varied from 0.20 to 1.98 ha (Table V). In order to establish a basis for examining the causes of such a wide variation in the size of territories, those years in which one male was present at a locality, or two males at Locality 5, were considered typical. These typical conditions occurred at the localities in 24 male-years. The mean size of these 24 territories was 0.67 (\bar{X} s.e. = 0.05) ha. The individual locality means ranged from 0.55 to 0.76 ha. Territory size of individual males ranged from 0.28 to 1.23 ha, about a four-fold difference. This range of size of typical territories was less than the overall range.

All territories exceeding one hectare occurred when the number of resident males was reduced below the typical number (Table V, Locality 1 and 2; Locality 5, entire).

The subdivision of a locality into more territories results in a reduction of mean territory size. For example, mean territory size at Locality 1 when two males were present was one-half the mean territory size when one male was present (Table V). In 1966 when there were three males at Locality 5, the third male was restricted to the middle area with a small territory of 0.18 ha. The second male at Locality 7 in 1971 was restricted to the northwestern side (Plate I(c)) in a territory of 0.22 ha. A territory of about 0.2 ha appears to be minimal. An area smaller than that would likely not have the combination of burrow sites, sunning and lookout sites, and low vegetation feeding areas associated with marmot behaviour (Travis & Armitage, 1972).

The subdivision of a locality into more than one territory does not produce much overlap in adjacent territories. At Locality 1 in 1962, only 1.7% of the territories overlapped; there was no overlap in 1963 and 1964; although in 1964 one male made one excursion into the territory of the adjacent male.

Stability of territories

Because marmots typically inhabit talus slopes in meadows which are separated by forest (Plate I), one might expect a territory to be co-extensive with the habitat. This situation apparently prevails at Locality 4 where one male and one or two females reside (Armitage & Downhower, MS). For nine of ten years at Locality 7, there was one territory centred on the main talus (Plate I(d)). The second harem in 1971 was on the north-west edge of the area and did not cause any modification of the typical male territory at this locality.

However, territories did wax and wane at the other localities. In 1962 through 1964, three territories existed at Localities 1 and 2. The territories were separated by topographic features; a ravine separated the two territories at Locality 1 and the territory at Locality 2

was separated from those at Locality 1 by a distance of 500 m. These territories were stable even though there was a complete turnover of males in 1964. Despite their close proximity, only one male : male interaction was observed among the territorial males and that occurred between the two males at Locality 1 in 1964 when both were newly resident.

From 1965 through 1968, ♂ 355 occupied both locations. He resided at Locality 1 and went to Locality 2 primarily when other adult males appeared there. No agonistic behaviour between males occurred at Locality 1 during these four years, but occurred in three of the four years at Locality 2. Four different males at different times spent up to a month in and around Locality 2 during the four years. In the same four years, only one transient entered Locality 1 and he remained only two or three days. Usually when ♂ 355 journeyed to Locality 2, the invading male retreated into the nearby hills. After ♂ 355 returned to Locality 1, the invading male returned to Locality 2. Two of the males were chased by ♂ 355 and eventually departed from the area. A third, who was a two-year old, departed without any observed agonistic behaviour. The fourth, however, contested ♂ 355 and several encounters occurred, of which the following is the most complete example of their behaviour:

16 June 1968. ♂ 402 by the upper cabin and ♂ 355 comes up past the wall. Both flagging and moving about. Much circling, first one advances then the other. Each rubs head alongside bricks, etc., in the yard. ♂ 355 returns to the wall and ♂ 402 follows and marks bricks at the wall, then retreats to the cabin as ♂ 355 follows. More circling and flagging. Each appears to turn to expose the anal region to the other. ♂ 355 starts down bank past wall and ♂ 402 follows. Suddenly ♂ 402 jumps on ♂ 355 and vigorous wrestling follows. They appear to lock jaws. ♂ 402 seemed dominant, then ♂ 355. ♂ 402 broke off and ran and ♂ 355 followed. ♂ 402 entered burrow under cabin porch and ♂ 355 remains at entrance, jumping and moving around and rubs side of head on boards above burrow entrance, then lies stretched out on porch, then moves off. Encounter lasted about ten minutes.

Although ♂ 402 could not establish residence at Locality 2, he remained in the area and was trapped there in 1969.

At Locality 5, territories were at the upper and lower areas from 1962 through 1965. The territories varied somewhat from year to year, but were essentially like those in Fig. 2. The line of aspen across the middle of the slope seemed to be a dividing line. The lower male rarely went upslope and the upper male rarely moved downslope. Although six different males occupied these two areas in the four years, no agonistic encounter between these colonial males was observed. Some encounters occurred with transient males, who soon departed.

In 1966, a third male was resident at the middle area (Fig. 4). No agonistic interactions among males were observed. In 1967, the lower male was removed with the subsequent change in male activity described previously (Figs 5 and 6). In 1969, ♂ 418 resided in the lower area, but patrolled the entire locality. He successfully prevented ♂ 402 from occupying the upper area. However, in the spring of 1970, ♂ 402 was at the upper area. In mid June, ♂ 418 died; by mid July ♂ 402 was regularly patrolling the area just below the aspen. A new two-year old male became active in July in the lower part of the lower area (Fig. 7).

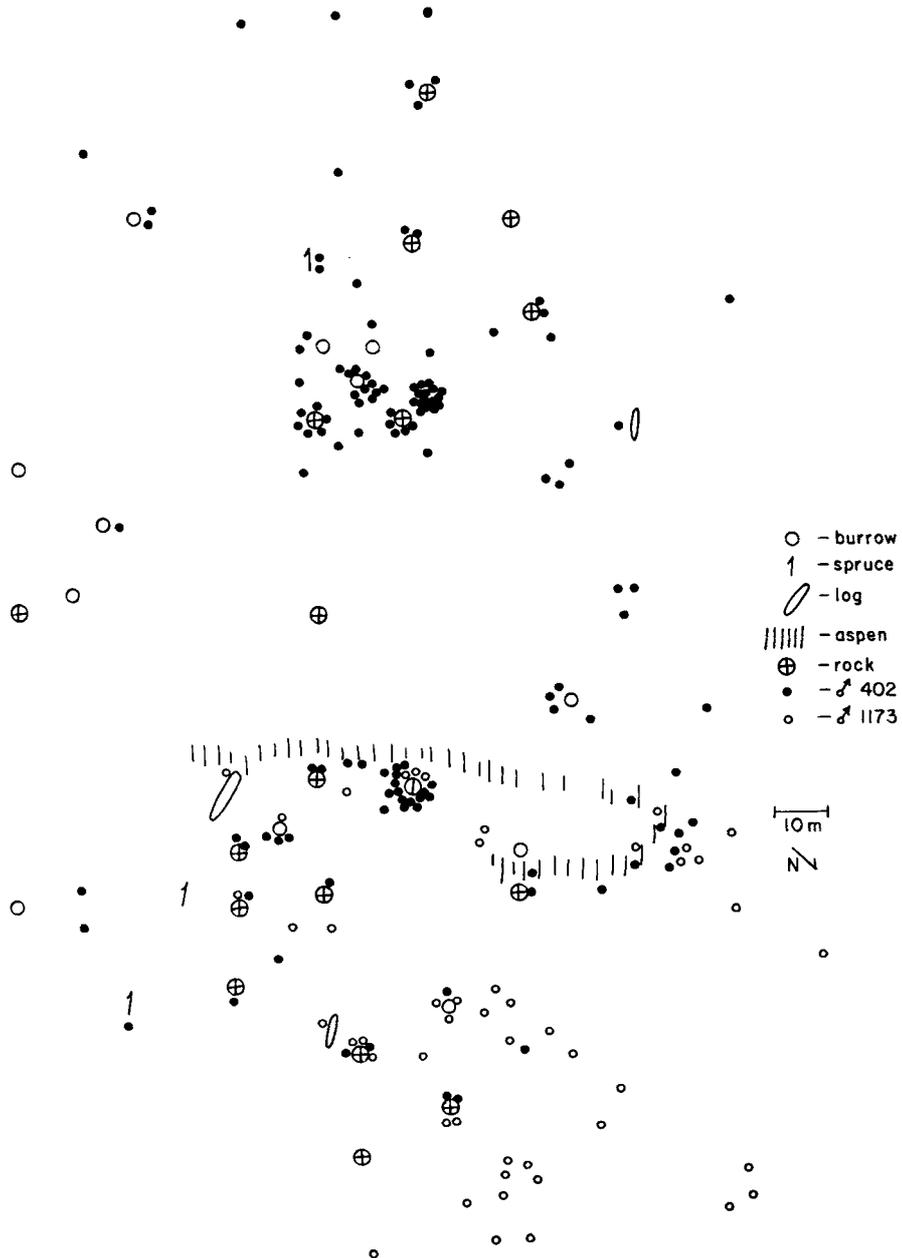


FIG. 7. The dispersion patterns of two colonial males at Locality 5 in 1970. Note the wide distribution of activity of ♂ 402 in the lower area and the more restricted activity of ♂ 1173. Each circle represents the location of an animal during a census.

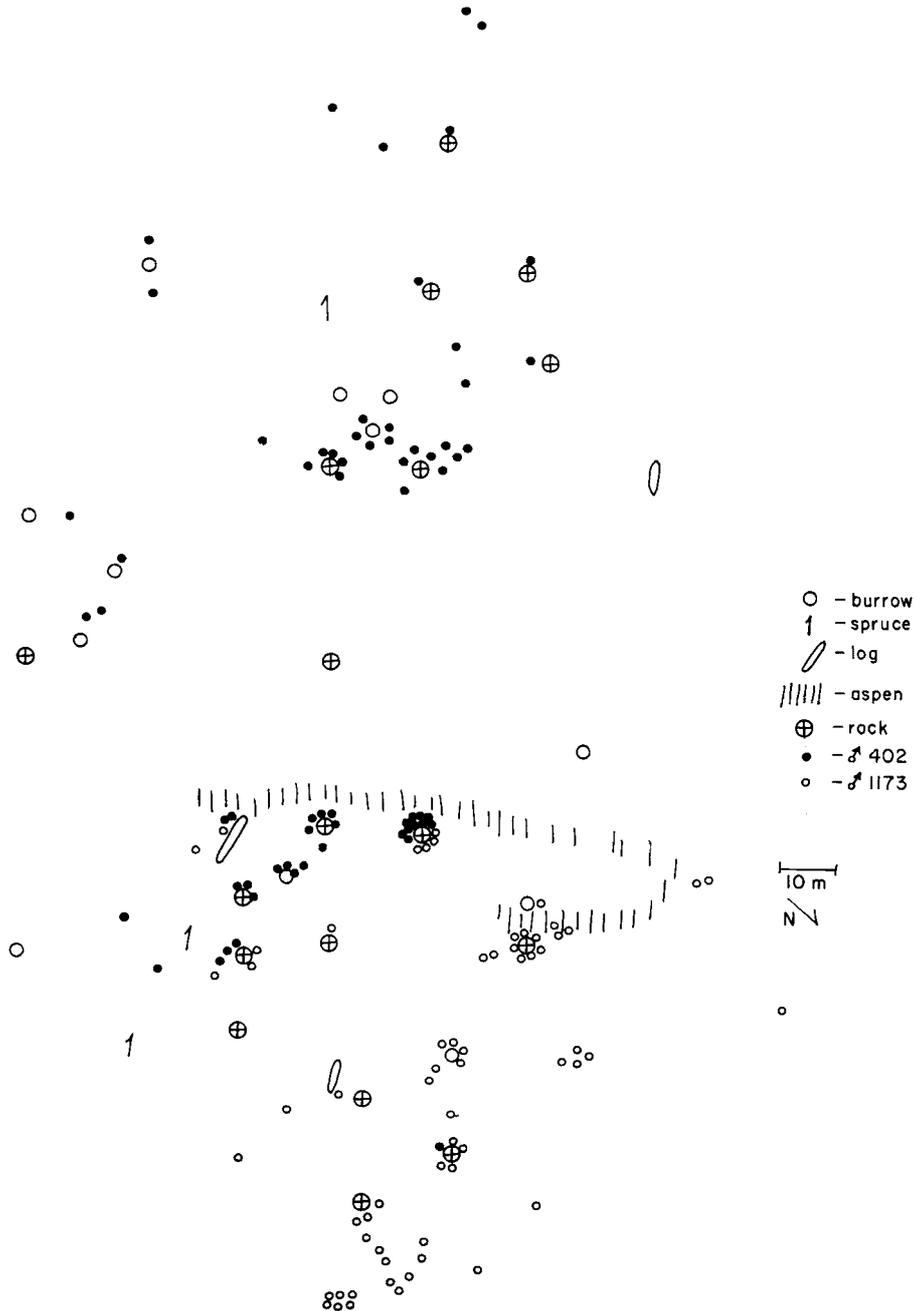


FIG. 8. The dispersion patterns of two colonial males at Locality 5 in 1971. Note that ♂ 402 was limited to the area just below the aspen and along the south side of the lower area (compare with Fig. 7). By contrast with 1970, ♂ 1173 had more activity toward the centre of the lower area. Only rarely did he venture into that part of the lower area frequented by ♂ 402 even though ♂ 402 resided at the upper area. Each circle represents the location of an animal during a census.

Both males had numerous amicable and agonistic behaviours with the resident females on the lower area as both males were "turnover" males or strange males to the females. There were no encounters between the males. Whenever ♂ 402 appeared at the upper edge of the lower area, ♂ 1173 would move off downslope, sometimes at a run, but ♂ 402 never pursued. Their territories overlapped by 31.8%. In 1971, the pattern of use was regularized. Although ♂ 402 continued to visit the lower area, his movements were restricted to the upper south side (Fig. 8), whereas ♂ 1173 occupied the remainder of the area, but again retreated downslope when ♂ 402 appeared. The overlap of territories was reduced to 9.7%. In 1972, the locality again had essentially an upper and a lower territory. However, ♂ 402 still continued his visits to the lower area, but new ♂ 5 did not flee. Their encounters consisted mainly of lying or sitting and watching each other and some tail flagging. However, a new element in their behaviour was observed:

21 June 1972. ♂ 5 at big rock, ♂ 402 appears at flat rock 15 m distant. ♂ 402 vigorously grooms—sits on haunches and grooms chest, wipes forefeet over head and mouth and onto chest. Then he moves north 15 m to fallen log. Then ♂ 5 goes through same grooming movements as ♂ 402 moves upslope into aspen. ♂ 5 flags after ♂ 402. ♂ 402 has disappeared.

This behaviour was observed several times and seems to be an example of displacement activity (Marler & Hamilton, 1966: 185; Tinbergen, 1964) as the grooming occurred in a conflict situation and was the only situation in which intensive grooming occurred. Normal grooming occurs shortly after emergence in the morning or during a period of sunning on a lookout, and is much more leisurely.

Discussion

Yearling male behaviour

The male yearling normally emigrates from his colony of birth during his second summer of life. Agonistic behaviour between the adults and yearlings enhances dispersal as male yearlings were observed leaving a locality immediately after being chased. However, agonistic behaviour is not sufficient to cause dispersal. High rates of agonistic behaviour occurred at Locality 2 in 1968 and 50% of the male yearlings remained (Armitage, 1973). By contrast, the rate at Locality 2 in 1967 was half of that of 1968 and all three yearling males emigrated by 18 June. Therefore, the continual presence of the adult male is necessary to cause yearling male dispersal. This conclusion is supported by the failure of all yearlings to become residents when introduced into a locality with a resident male, by normal patterns of their dispersion, and by the patterns of movement following removal of an adult resident male. Also, the continual presence of yearling males at Locality 2 and the lower area of Locality 5 when adult males resided elsewhere, the lack of any significant relationships between agonistic behaviour of male yearlings and measures of density, and the residency of male yearlings in years of adult male turnover also support this interpretation. In conclusion, dispersal is a natural consequence of the male yearlings' avoidance of the adult male and does not require overt aggression by the adult male, although such agonistic behaviour may enhance or quicken dispersal. A basic pattern of avoidance of a resident male is part of the social experience of most if not all male marmots.

Territoriality in marmots and other ground squirrels

A territory is a defended area (Noble, 1939) or the defended part of a home range (Burt, 1943). However, acts of defence may not always be evident. Thus, a territory additionally is characterized as a fixed area which is used exclusively by the possessor (Brown & Orians, 1970). The behaviour of adult, colonial, male marmots meets all three criteria as evidenced by the non-overlapping of home ranges of adult males, defence by the resident male of his home area against strange males, failure of any introduced males to become resident, by modification of home ranges of resident males when nearby males are removed, by quick invasion of a locality by new males when adult males are removed, and by social behaviour among males being almost entirely agonistic.

By contrast, male yearlings do not establish territories. This conclusion is supported by the lack of agonistic behaviour among male yearlings, overlapping home ranges, and association together in play-fighting.

Previously, Armitage (1962) concluded that although agonistic behaviour characterized members of a marmot population, territoriality did not occur in the yellow-bellied marmot. Armitage also suggested that territoriality had not been demonstrated in *M. marmota* (Bopp, 1954, 1955, 1956). Subsequently, Bronson (1964) described agonistic behaviour in *M. monax* as being characterized by interactions among nearest neighbours, but not leading to territoriality. Thus, early evidence seemed to favour an absence of territoriality in *Marmota*.

However, I clearly was wrong. I studied an isolated population and observed only one social interaction between adult males in four years. In the present study, a similar situation occurred at Locality 4 where no social interactions between adult males were observed.

The harem as the basic social structure is widespread among rodents (see Eisenberg, 1966; Ewer, 1968, for reviews). Within the ground-dwelling Sciuridae, there is a range of social structure from the solitary to the highly complex. *M. monax* (Bronson, 1964), *Citellus lateralis* (Gordon, 1936) and *Eutamias* spp. (Broadbooks, 1970; Sheppard, 1972) are essentially solitary. Both sexes of *C. lateralis* and *Eutamias* may defend territories centering on the burrow. Colony members of *Citellus armatus* (Balph & Stokes, 1963), *C. mexicanus* (Edwards, 1946), *C. townsendi* (Alcorn, 1940), *C. beecheyi* (Linsdale, 1946) and *C. richardsonii* (Yeaton, 1972) defend their burrow area and its immediate environs. Members of these colonies live essentially as individuals. *M. flaviventris* forms a social unit consisting of a territorial male and his harem. Females do not form territories (Armitage, 1962). The most complex social organization occurs in *Cynomys ludovicianus* (King, 1955). The Black-tailed prairie dog coterie is behaviourally identical to the marmot harem except that an additional adult male may be present. Coterie are closely grouped into wards. All members of the coterie actively defend the territory, but the male is the most vigorous in defence. The colony of marmots at Locality 5 when three harems (= coterie) occurred was organizationally similar to a prairie dog ward, except that marmot harems were not closely packed.

Territory size and stability

The concept of territory as a fixed area must be more precisely described as both size and stability of Yellow-bellied marmot territories vary.

Within a locality, some of this variation results from the method of measuring territory size. The size is determined by observing where a male went in a locality. For example, ♂ 873 at Locality 7 had a territory of 0.26 ha in 1970 which was nearly doubled to 0.51 ha in 1971. In 1971, several peripheral and transient males were present and ♂ 873 went into areas used by these other males. In 1970, additional males were not present. Probably the male's territory was identical in both years, but in 1970 there was no cause for the male to move through all parts of the territory. The territory actually measured is co-extensive with the home range of the male, but the true territory is likely to be larger as the perceptual field of the male is larger than the field through which he moves. There is no way of knowing the true size of a male's territory, but it is likely to be as large as the largest home range measured during his years of residency. I have followed the more conservative method of measuring territory as the area actually used by the male. In reality the territory sizes reported in Table V are minimal.

Territory size also is influenced by the presence of nearby males. When the male was removed from the lower area of Locality 5 in 1967, ♂ 418 increased his territory from 0.18 to 0.71 ha and ♂ 494 increased his territory from 0.28 to 1.25 ha (Figs 4 and 6). The realignment of territories by these males in 1968 resulted in a decrease in the territory of ♂ 494 to 0.82 ha as he was limited to the upper area, and an increase in the territory of ♂ 418 to 1.45 ha as he took over all of the lower area plus the middle area (Plate I(c)). When only one male lived at Locality 5, the size of the territory was greatly increased (Table V, Locality 5: entire).

Territory size and stability are not determined by topographic features, although topography by determining the location of burrows, etc., must play some role. But the enlargement of territories at Localities 5 and 1 occurred across what appeared in some years to be topographic separations between males.

Why does the variation in the territory size, such as that observed at Localities 1, 2, and 5, occur? There seems to be two factors. One is male vigour. There is a large range of behavioural profiles in adult males; colonial males are more aggressive than non-colonial males (Svendsen & Armitage, 1973). The males who occupy extensive territories may be among the more aggressive (♂ 402 so tested in 1972 at seven years of age). There may also be a chance factor. When there are no males in a locality, the locality will be populated by the first males to arrive on the scene. If several arrive at about the same time, the locality may be partitioned among them. This partitioning apparently occurred at Locality 1 in 1964 and at Locality 5 in 1966. The two new males at Locality 5 in 1966 were both known as peripheral males in 1965 and could easily have moved into the colonial areas about the same time. If neither male is sufficiently vigorous to claim the entire area, the number of territories in the locality may be temporarily increased.

The number of territories also may be determined by the distribution of females. At Locality 5, each male was associated with at least one female and the male territories developed around the activity centres of the females. No male occupied the middle area at Locality 5 until a female resided there. After her death no male resided there and male visitations occurred only when females were active there temporarily. Thus, the presence of females has some effect on the territory of the male. If, on the other hand, one male arrives at a locality before other males, he may establish his presence and the attendant signals produce avoidance patterns in late arrivals. However, these large territories, though defended, have more strife than normal and are unstable from one year to the next.

Male behaviour and territoriality

The fundamental basis for territorial behaviour in the Yellow-bellied marmot is the lack of amicable behaviour among adult males. In other words, adult male behaviour is basically agonistic. This agonistic behaviour is expressed chiefly as avoidance of one male by another and is well developed in yearlings. Because the territorial male is conspicuous in his activities, he is easily seen by other males who come into the area. Smell may also be important. The burrow of a male has such a strong, characteristic odour, that the presence of the male is easily determined by the human observer. Marmots have anal glands which may be extruded by an animal when it is handled. The display between two males in which the tail is erected and the hindquarters pointed toward the antagonist is consistent with a role for odour in male behaviour. The male sits on many lookouts, etc., and could leave scent markings. Invader males have been observed to sniff rocks, etc., when entering a male's territory. Males have been seen to rub their heads on rocks, etc., in the same manner described for the use of cheek glands to deposit scent marks by captive *M. marmota* (Koenig, 1957). Therefore, it is likely that scent and scent marking plays some role in territorial behaviour in *M. flaviventris*. The result of visual conspicuousness and scent marking is that male marmots signal their presence and usually are avoided by other males. If the signals are not sufficient to exclude another male, then chases and, ultimately, fights occur.

Fights are rare and those observed occurred when the territorial system was unstable, in the sense that a single male was attempting to defend an area traditionally occupied by two or three males. Territorial stability is maintained when a locality is filled; that is, when a minimal number of males are present to saturate the environment with signals. Such saturation occurs when no matter what route a transient male follows into the locality, he receives persistent signals that the area is inhabited. Such stable situations occurred at Localities 1, 2, and 5 (Figs 4 and 5). Males on adjoining territories are not in conflict because signals are present. However, once signals cease or are discontinuous, new males may invade a locality or adjoining males may attempt to enlarge their territories. A male tends to maintain the same territory in subsequent years (e.g., ♂ 355, Localities 1 and 2; ♂ 402, Figs 7 and 8).

Some authors (e.g., Lorenz, 1966) regard aggression to be spontaneous; that is, there is aggressive appetitive behaviour. Others (e.g., Scott, 1958) emphasize the importance of external stimuli in eliciting aggression. The best evidence favouring aggressive appetitive behaviour stems from laboratory studies (Hinde, 1969), but Manning (1972: 81) points out that the best studies are with animals selectively bred for their aggressiveness. This problem is difficult to study in the field because of lack of control or knowledge of the probable state of motivation. Patrolling of a territory is consistent with the interpretation of an aggressive appetitive behaviour (Hinde, 1969), although Marler & Hamilton (1966) suggest that patrolling may result from a more general appetitive behaviour.

Patrolling is not universal in territorial *M. flaviventris*. It occurs most conspicuously where males cannot see all of their territory from one lookout. Because visual stimuli play a predominant role in marmot behaviour, patrolling is an activity which enables a male to detect possible intruders. The most obvious modification of a male's normal activity pattern is the presence of a strange male. Clearly, a strange male does elicit aggressive behaviour by a territorial male. But the presence of a nearby territorial male does not elicit aggressive behaviour except when the nearby male is forming his territory from part

of an unusually large territory. There are ample opportunities to seek fights, but adjacent males avoid fights. When the two males at Locality 5 were extending their territories in the area from which a resident was removed, they avoided one another. A male marmot expresses aggression only when his perceived territory is invaded. There is no evidence that a male attempts to extend his territory at the expense of another male. If males seek fights, they have ample opportunity which they by-pass. Perhaps the consistent presence of adjacent territorial males habituates each to the other and reduces aggressive appetitive behaviour below the threshold for expression.

Another interpretation is that because fighting may be harmful to the male and to the social stability of the population, selection has reduced aggression to those instances in which the social stability is threatened (i.e., the presence of an invading male). Thus, aggression need not be inevitable, but may be considered an adaptive component of the social system.

Behavioural profiles derived from factor analysis of behavioural data obtained from mirror-image stimulation revealed three general types of males, sociable, aggressive, and avoiders (Svendsen & Armitage, 1973). There was no evidence of aggressive appetitive behaviour in these encounters; the degree of aggressiveness was consistent with the male's social behaviour. Thus, the most aggressive males were territorial and the avoiders were isolates. These results support the hypothesis that aggressiveness depends, in part, on the social context in which the animal lives. The full range of behavioural profiles is present in young males who have been active above ground for a month (Svendsen, 1973). This range of behavioural variability could easily result from early experience (Scott, 1958) and does not require genetic determination. However, much is yet to be learned about the expression of aggressive behaviour in natural populations and the factors which determine this expression.

Territoriality and the model of polygamous mating

The model of polygamous mating systems based on studies of Yellow-bellied marmots predicted that males should be agonistic toward other males, should be territorial and should readily accept or attract females; i.e., male : female social behaviour should be amicable (Downhower & Armitage, 1971).

The first two predictions are supported by the results of this study. However, social behaviour between males and females often is agonistic (Table II, Fig. 1). More than two-thirds of this agonistic behaviour was avoidance of the male by the female or a rebuff of sexual advances of the male by the female. Half of the chases of females by males occurred when the female fled and the male pursued. "Grasp and wrestle" are associated with sexual behaviours and females not in oestrus can either avoid the male or engage in conflict with him. In these encounters, the male asserts his dominance. The entire sequence occurred when the strange male was introduced to the resident female (Table IV) and when male turnover occurred (Table III). Sex and aggression are closely related; brain areas controlling these behaviours overlap and many elements are shared in common between the two control systems (Ploog, 1971). I have no evidence that a male has excluded a female from joining his harem or has caused a female to emigrate. If male : female behaviour is sexual-aggressive, the recorded agonistic behaviour may be part of the sexual-aggressive system rather than agonistic in the male : male sense. If so,

the prediction of male : female behaviour based on the model of polygamous mating is essentially correct, though requiring modification because of the nature of sexual-aggressive behaviour.

Functions of marmot territoriality

Territoriality in marmots has three major functions. First, reproduction is enhanced. Marmot habitat is highly restricted (Svendsen, 1973) in the high mountain environment. The polygamous system permits maximal numbers of females to be associated with a minimum number of males, thus maximizing the potential production of young. Associated with this numerical advantage is the social stability provided by the male. Competition for females and possible disruption of reproduction is reduced. In those years of male turnover, the production of young is markedly lower than in years of male return (Armitage & Downhower, MS). The mean length of residency of a colonial male is 2.4 years. Thus, on the average, social stability occurs in two years out of three and provides an optimal social environment for reproduction.

Secondly, the system enhances outbreeding. Because a male rarely becomes resident in the colony of his birth, the probability of father-daughter, brother-sister, or mother-son matings is very low. The maximum probabilities for such matings can be calculated from residency and life expectancy data (Armitage & Downhower, MS).

The probability of a male becoming resident in the colony of his birth is 0.04 (the probability that a colonial male was born in that colony) times 0.15 (the probability that a male would live to be three years of age) which equals 0.006 or about six males in a thousand. The probability of an adult female living three years is 0.4. Thus the probability of a mother-son mating is 0.4 times 0.006 which is 0.0024 or about 24 matings in 10,000. The probability of a female living to two years of age is 0.37 and the probability of her becoming resident in her colony of birth is 0.21. The product of these probabilities is 0.08. Thus the probability of a brother-sister mating is 0.08 times 0.006 or 0.00048; that is about five matings in 10,000. In reality these matings must be more rare. The only known male to become resident in his colony of birth was five years old at the time; the adult females of his year of birth had died and none of the female young of the year of his birth were recruited into the population.

Father-daughter matings have a higher probability. For these to occur, a male must be resident for three years and one of his daughters must become resident in his harem. The probability of such a mating is the probability of a two-year old female becoming resident in the colony of her birth (0.08) times the probability of a male being resident for three years (0.25) which is 0.02, or about two matings in a hundred. However, only about one-third of the two-year old females breed at that age, thus the real probability decreases. Only about six litters in every thousand litters produced by two-year old females are likely to result from daughter-father matings. The probabilities become increasingly lower for three-year old females, etc.

Third, the system enhances the fitness of colonial males. Downhower & Armitage (1971) showed that the fitness of a male (as measured by reproductive success) was the sum of the fitness of the females with whom he mated and that maximum fitness occurred when harems had two to three females. Thus, a territorial male with a harem has a greater probability of making a genetic contribution to the next generation than isolate, peripheral, or transient males.

Summary

Male behaviour and territoriality were studied in five populations of marmots in the East River Valley, near the Rocky Mountain Biological Laboratory, Gothic, Colorado, at an elevation of 2900 m, from 1962 through 1972.

Males may be classified according to age as yearlings, marmots in their second summer of life; two-year olds, in their third summer; and adults, animals three years old or older. Socially, marmots may be categorized as colonial, peripheral, or transient. A colonial male lives with a harem of females, a peripheral male lives near a colony, and a transient male moves through a locality, remaining only a few days near a colony.

Social behaviour was classified broadly as amicable or agonistic. Both types of behaviour occurred between male yearlings and female yearlings, male adults, and female adults. Social behaviour among male yearlings was characterized as play-fighting. Play-fighting has elements of adult sexual and of adult fighting behaviour. However, play-fighting cannot be classified in traditional behavioural categories and may be a developmental pattern in establishing adult modes of behaviour.

Social interactions between yearling males and yearling females were primarily amicable. When agonistic interactions occurred, the female usually had the subordinate role. Social interactions between yearling males and adult females were agonistic twice as many times as amicable. The yearling male was subordinate. Social behaviour between yearling males and adult males was nearly always agonistic. The yearling was always subordinate. Amicable behaviour between yearling males and adult males occurred only under unusual circumstances.

Most male yearlings dispersed from their parent colonies during their yearling summer. Male yearlings disperse because of the continued presence of an adult male. Agonistic behaviour between an adult male and yearling males is not necessary to cause yearling male dispersal, but supplements the natural avoidance patterns of the yearling males.

The behaviour of adult males is characterized by its conspicuousness. Flagging of the tail advertizes the male's presence. Some males patrol their territory. Patrolling is evident at those localities where topography or vegetation prevent the male from viewing his territory from one or two central lookouts.

Adult male social behaviour is predominantly agonistic. Only with adult females does the occurrence of amicable behaviour exceed that of agonistic behaviour. There was considerable variation among the colonies in the relative amounts of amicable and agonistic behaviour between adult males and adult females. Mean rates of amicable and of agonistic behaviour between adult males and adult females were greater for years of male turnover than for years of male returns.

Rates of social behaviour between male adults or male yearlings and the four age-sex categories showed little relationship to measures of population density.

A colonial male vigorously defends his territory from strange males. The removal of a territorial male results in nearby males increasing their home range to occupy all or part of the vacant territory, or in a new male occupying the territory. All males introduced into established territories dispersed.

The mean size of 24 typical territories is 0.67 ha. Territories may be larger when the number of males is reduced, or may be smaller when the number of territories at a locality is increased. Territories are co-extensive with the habitat at smaller localities. At the larger localities, the number of territories depends on the vigour of the males and the

availability of males to replace deceased territorial males. Reduction in the number of territories resulted in an increase in agonistic behaviour among adult males. Fights are rare and occurred when the territorial system was unstable. There was no evidence of aggressive appetitive behaviour. Fighting occurs only when social stability is threatened.

The major functions of the territorial system are enhanced reproduction in a limited environment, enhanced out-breeding, and enhanced fitness of colonial males.

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