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Cheek-rubbing in golden marmots (*Marmota caudata aurea)*

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(With 2 figures in the text)

We studied the function of cheek-rubbing in golden marmots (*Marmota caudata aurea*) by combining observations of the external morphology of the orbital gland, observational studies of marmots cheek-rubbing, and experimental studies of marmots' responses to olfactory secretions from the orbital gland. Adult males had larger eyepatches—areas without hair above the orbital gland—than adult females. Both sexes produced sufficient glandular exudate to pool on the surface of the skin or fur above the orbital gland. Adult males cheek-rubbed more than adult females throughout the summer active season, but both males and females generally cheek-rubbed within 10 m of a main burrow. Adult males responded more vigorously to the smells of non-group members of both sexes than to group members of either sex. Adult females responded more vigorously to the smell of non-group females than to non-group males or group members of either sex. Our results are consistent with the hypothesis that marmot cheek-rubbing functions to mark defended areas, possibly to minimize costs of aggressive interactions.

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Introduction

Olfactory communication in sciurid rodents has received considerable attention. Prairie dogs, ground squirrels, and marmots have all been reported presumably to scent-mark objects by rubbing parts of their heads (hereafter cheek-rubbing) on a variety of objects (reviewed in Halpin, 1984, 1985). To understand better the function of cheek-rubbing, a combination of observational and experimental approaches must be applied (Ralls, 1971; Halpin, 1984). Among the sciurids, olfactory communication in marmots seems the least well studied (Barash, 1989). In this paper, we report the results of a series of observations and experiments designed to study possible functions of cheek-rubbing in golden marmots (*Marmota caudata aurea*), an Old World sciurid rodent.

All studied species in the genus *Marmota* possess two facial glands; a perioral gland (often called an 'oral angle' gland—e.g. Ouellet & Ferron, 1988), and a facial gland found between the eye and the ear—hereafter called an 'orbital' gland (Rausch & Bridgens, 1989). As Rausch & Bridgens (1989) pointed out, studies of New World marmots focused on the functions of perioral glandular secretions and rubbing, while studies on Old World marmots focused on orbital gland secretions and rubbing.

Golden marmots cheek-rub by tilting their head to the left or right and rubbing the orbital region of their forehead across a substratum [similar to Koenig's (1957: 512) figures 3 and 4]. Cheek-rubbing was both obvious and unambiguous. Golden marmots have been observed to cheek-rub naturally bare ground, stones, boulders, and possible bushes. In contrast to some congeners (*M. olympus*—Barash, 1989; *M. monax*—Ouellet & Feron, 1988), but similar to others (*M. broweri*—Rausch & Rausch, 1971; *M. marmota*—Koenig, 1957), golden marmots appeared only to rub their orbital gland across objects.

There have been at least five non-mutually exclusive hypothesized functions of cheek-rubbing in the genus *Marmota*. Cheek-rubbing and associated olfactory secretions may be used to: 1) recognize individuals (Taulman, 1990); 2) self-reassure residents (Armitage, 1976; Taulman, 1990; Meier, 1991); 3) communicate breeding status (Hébert & Prescott, 1983); 4) signal dominance (Armitage, 1976; Barash, 1989; Hébert & Barrette, 1989; Taulman, 1990); and 5) identify territories or burrows (Rausch & Rausch, 1971; Zimina, 1978; Ouellet & Ferron, 1988; Meier, 1991). Unfortunately, these functions are not mutually-exclusive (Ralls, 1971). For instance, cheek-rubbing may deposit secretions that mark defended area and work by individually identifying the residents. In the following sections we report the results of observations of the external surface of the orbital gland, observations of marmots naturally cheek-rubbing, and the results of an experiment to clarify the function of cheek-rubbing.

Materials and methods

We studied olfactory communication in golden marmots at Dhee Sar (36° 81′ N, 74° 95′ E, elevation 4130 m) in Pakistan's Khunjerab National Park between 3 May and 5 September 1993. Golden marmots are large (3–5 kg) Old World sciurids found in the Karakoram mountains of Central Asia (Roberts, 1977). At Dhee Sar, marmots were active between late April and mid-to-late September. Breeding occurred immediately before, or just after, emergence from the hibernaculum (Blumstein & Arnold, unpubl. data). Details of the study site were reported elsewhere (Blumstein, 1992, 1994).

Marmots were trapped in Tomahawk live-traps set in burrow entrances. Once trapped, a marmot was transferred to a canvas handling bag in which it was: sexed, weighed and measured, aged, permanently marked with ear tags, and temporarily marked on the back with Nyanzol fur dye.

The orbital gland

Immediately following trapping, we noted the status and size of the marmot's orbital glands. Orbital glands are located above the marmot's cheek whiskers, between the eye and ear; similar to those found in other species (see Fig. 3 in Koenig, 1957). We classified both the right and left orbital gland according to its surface moisture (dry, moist), and according to whether it was hair covered or not (bald, hairy). We refer to bald spots as 'eyepatches'. The maximum length and width of each eyepatch—when present—was measured with a dial calliper to the nearest mm and these measurements were used to compare the approximate area of each eyepatch. To study the seasonal changes in the orbital gland, we compared orbital gland measurements between adult males and females and summarize orbital gland measurements by month.

Observations of cheek-rubbing

Marmots were observed between 05:00 and 09:30 h on most mornings and we recorded all occurrences of cheek-rubbing (Martin & Bateson, 1986) in 17 marmot social groups. Because all groups were not equally visible, only those cheek-rubbings conducted in 8 highly visible social groups containing 2 or more marmots (mode = 5, range = 3 – 7) are reported.

We report and analyse data on the number of bouts of cheek-rubbing and define a bout as the occurrence of one or more individual cheek-rubs conducted on the same object. In addition to who cheek-rubbed, the distance between the cheek-rubbing marmot and the nearest main burrow was estimated either on a marked grid, with reference to known points on the ground, or by using the length of the marmot as a reference. Finally, the relationship between eyepatch area and rate of cheek-rubbing was plotted.

Olfactory experiment

To determine whether orbital secretions could influence the behaviour of another marmot, we conducted an experiment. Specifically, we tested the hypothesis that marmots could not distinguish the orbital secretions from: 1) adult males from the same social group (group males); 2) adult females from the same social group (group females); 3) adult males from a different social group (non-group males); 4) adult females from a different social group (non-group females).

Orbital gland secretions were collected by rubbing a fresh cotton ball just removed from a sealed plastic bag around the orbital gland (*sensu* Meier, 1991) of trapped marmots. Generally, 4 cotton balls were collected per marmot, but occasionally a few more were collected if a marmot was particularly 'pungent'. Cotton balls were immediately transferred into a resealable plastic bag ('ziploc' brand), and bags were kept in a cool stone hut until use. We assumed that cotton balls that were obviously pungent to us also were detectable to marmots. Thus, only pungent cotton balls were used in the following experiment. Throughout, cotton balls were always handled with clean forceps.

The experiment involved simultaneously placing 2 cotton balls—a treatment and a control—on 2 different pre-established metal stakes located 1 m from the entrance of the main marmot burrow (see Blumstein, 1994 for a distinction between main and escape burrows). Cotton balls were fixed to the metal stakes with uncoated steel wire. The 2 stakes were opposite each other; the first stake was placed a randomly selected compass direction from the burrow. Cotton balls were 20 cm above ground (Meier, 1991), and the stakes were 22 cm high. One of the 4 types of olfactory secretions, the 'treatment', was randomly selected and randomly assigned to a main burrow. Marmots 'discovered' the cotton balls by chance. The control cotton ball was an unused cotton ball. Metal stakes with 'dummy' cotton balls fixed to them were placed outside main burrows at least 2 weeks before the first experiment and marmots appeared to habituate to the experimental apparatus quickly. Experimental treatment and control cotton balls were placed on the stakes before the marmots first emerged from their burrows (before 05:15 h).

We quantified marmots' responses to both the treatment and the control stimuli; observing marmots from hides with 15–45 × spotting scopes. The following definitions will be used in the remainder of the paper. We define an *exposure* as any time a marmot's nose was estimated to be within 1 m of a cotton ball. When a marmot approached a cotton ball to within 10 cm, we scored a *contact*. Contacts were unambiguous and marmots always appeared to sniff the cotton balls. A trial began when a marmot walked to within 1 m of the treatment or the control cotton ball, and ended when the marmot moved to >1 m from the cotton balls. Observations of marmots interacting with the cotton balls were recorded on a microcassette recorder and later decoded with a stopwatch so that we were able to record both events and durations of behaviours.

To study marmots' responses to the cotton balls, we recorded the following variables for both treatment and control cotton balls: 1) the number of contacts; and 2) the duration (in seconds) of contacts. Because marmots often did not respond to the presence of either cotton ball, we had many zero values. To maintain our balanced experimental design, we transformed all data by adding 1 to each observed value. Then we calculated the response to the treatment using Bateson's suggested technique to calculate 'response ratios' (Bateson, 1990: 151):

$$R = E/(E + C) \tag{1}$$

where R = the response to the treatment, E = the observed response to the experimental stimulus, and C = the observed response to the control stimulus. We used these response ratio values in the following analyses.

We also recorded the number of cheek-rubs per exposure. These values were transformed by adding 1 to the raw scores. Because it was not always possible to determine whether a marmot was cheek-rubbing in response to either a treatment or control stimulus, we did not calculate response ratios to test for significant differences.

Since total exposure time could influence responsiveness, we checked to see whether total exposure time was varied by stimulus category and whether significantly different exposure times were correlated with dependent variables.

Statistical analyses

Eyepatch statistics were calculated using the individual as the unit of analysis, thus no individual appears more than once in the data set. Observational summaries were calculated using social group averages and non-parametric statistics. Experimental results were tested with non-parametric statistics. These are very conservative ways to summarize results but since an individual's cheek-rubbing behaviour may not be independent of the behaviour of its group-mates, and since experimental results did not meet the distributional assumptions of parametric tests, the analyses were appropriate. Because we chose to conduct extremely conservative statistical tests, we interpret P-values between 0·05 and 0·1 as moderately significant, and P-values less than 0·05 as significant. All statistical tests were computed using StatView 4.0 (Abacus Concepts, 1992).

Results

The orbital gland

We measured eyepatches on 78 adult marmots—33 females, 45 males. Overall, more males had eyepatches than females (31·6% of the males versus 24·2% of the females), and for those individuals which had eyepatches, male marmots had larger eyepatches than females (Table I). Interestingly, some marmots of both sexes without eyepatches produced glandular secretions that pooled on the surface of their skin or fur. Moreover, not all marmots with eyepatches produced enough glandular secretions to pool on the surface (Table II). Anecdotal observations suggested that marmots with both 'dry' and 'moist' orbital glands produced a pungent smell. Marmots with

TABLE I

*Monthly average (± S.D., **n** with eyepatches/**n** examined) eyepatch size of adult male and female marmots. Calculations are for those marmots which had eyepatches. Note: some marmots had an eyepatch on one side of its head but not on the other. The average area reflects the 0 mm² area on one side of the head. While some marmots were captured multiple times during the study, each marmot contributes only one randomly selected data point to these summary statistics. Males had larger eyepatches than females (Mann-Whitney U = 1·0, tied **P** = 0·0433)*

	Female			Male		
	x̄ (mm²)	S.D.	*n*/*n*	x̄ (mm²)	S.D.	*n*/*n*
May	0	0	0/7	144·6	110·6	2/5
June	62·7	37·1	4/6	254·8	171·6	2/5
July	198·1	167·7	3/14	313·6	115·1	9/28
August	134·2	0	1/6	223·6	0	1/7

moisture above their orbital glands produced a smell that was more pungent (to us) than marmots without moisture; we were unable to detect differences between the odours of males or females.

Observations of cheek-rubbing

In 699 h of observation on eight marmot social groups we observed 41 different marmots cheek-rubbing: 18 adult males, 13 adult females, four subadult males, and six subadult females. Because only half the groups had subadults, and analyses were based on group means, subadult mean values are reported, but not tested for significance.

Adult males cheek-rubbed more than adult females (Mann-Whitney $U = 16{\cdot}0$, tied $P = 0{\cdot}0821$, $n = 8$ marmot groups), and appeared to cheek-rub more than subadults (no significance test run). Season did not significantly influence the rate of cheek-rubbing (Table III). There were weak and not significant trends for adult males and adult females to cheek-rub slightly less as the season progressed (male Spearman $\rho = -0{\cdot}4$, tied $P = 0{\cdot}4884$; female Spearman $\rho = -0{\cdot}4$, tied $P = 0{\cdot}4884$), and for subadults to cheek-rub slightly more (subadult male Spearman $\rho = 0{\cdot}4$, tied $P = 0{\cdot}4884$; subadult female Spearman $\rho = 0{\cdot}6$, tied $P = 0{\cdot}2987$). In all cases, cheek-rubbing rates dropped off in August. Adult males did not cheek-rub at significantly different distances from the nearest marmot main burrow than adult females (Mann-Whitney $U = 28$, tied $P = 0{\cdot}6742$, $n = 8$ marmot groups) and 72·5% of all adult cheek-rubs were within 10 m of a main burrow.

TABLE II

*Proportions (**n**) of adult marmots that produced enough glandular secretions to pool on the surface of their fur ('hairy'), or the skin above their orbital gland ('bald')*

	Female (*n* = 33)	Male (*n* = 45)
Hairy	0·42 (14)	0·33 (15)
Bald	0·15 (5)	0·20 (9)
Total Greasy	0·57 (19)	0·53 (24)

TABLE III

Average (± S.D.) number of bouts of cheek-rubbing observed in adult and subadult marmots, the monthly rate of cheek-rubbing (#CR/h), and the relative frequency with which cheek-rubbing was observed within 10 m of a marmot's main burrow. Means were calculated from the average of each marmot group's mean value and significance tests were run on the group mean values (significance values reported in text). Because only half the marmot groups had subadults, we conducted significance tests only on adult marmots

	Adult		Subadult	
	Female	Male	Female	Male
x̄ (± S.D.)	0·016 (0·010)	0·035 (0·022)	0·014 (0·010)	0·009 (0·010)
Monthly rates: CR/h (± S.D.)				
May	0·019 (0·016)	0·042 (0·044)	0·010 (0·020)	0 (0)
June	0·018 (0·016)	0·036 (0·029)	0·004 (0·008)	0·012 (0·011)
July	0·024 (0·024)	0·045 (0·038)	0·016 (0·025)	0·015 (0·011)
August	0·008 (0·010)	0·025 (0·026)	0·011 (0·008)	0·006 (0·012)
⩽ 10 m	0·72 (0·13)	0·73 (0·19)	0·74 (0·25)	0·87 (0·22)

When each sex is examined singly, female and male monthly average eyepatch areas and cheek-rubbing rates appeared not to be correlated (female Spearman $\rho = 0{\cdot}2$, $P = 0{\cdot}7290$, $n = 4$ monthly means; male Spearman $\rho = 0{\cdot}4$, $P = 0{\cdot}4884$, $n = 4$ monthly means). When sexes are combined, there appeared to be a positive, yet spurious, relationship between eyepatch area and cheek-rubbing rate (Fig. 1). This relationship was an artefact of males having larger eyepatchs and cheek-rubbing more than females.

In addition to these quantitative measurements of cheek-rubbing, we also recorded *ad libitum* observations. These observations suggested that cheek-rubbing often followed an agonistic encounter and seemed to occur when an adult marmot moved from one social group to another.

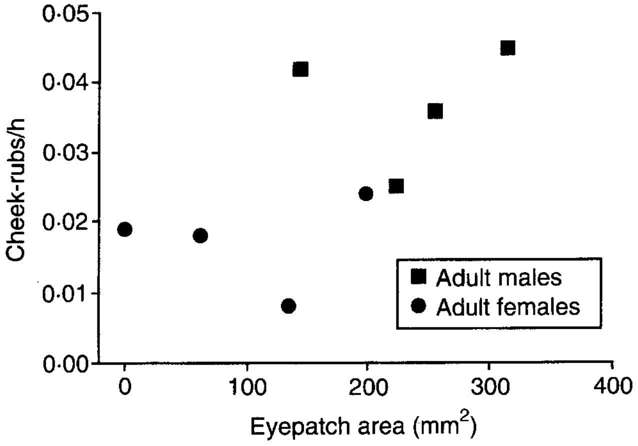

FIG. 1. The relationship between eyepatch area (mm^2) and rate of cheek-rubbing (cheek-rubs/h). Eyepatch area based on monthly mean values of adult males ($n = 45$) and adult females ($n = 33$). Cheek-rubs per observation hour based on the monthly mean numbers of cheek-rubs observed in eight different marmot social groups.

Much, but not all, of this latter form of cheek-rubbing occurred around the main burrows of the group with the new marmot. At least some residents responded by following the new marmot around and cheek-rubbing in its wake.

Olfactory experiment

Between 9 June and 2 September 1993 a total of 13 different adult marmots (seven males, six females) received all four treatments. Because some marmots received the same treatment several times, we randomly selected a single observation for subsequent analysis.

Marmots responded to the experiment by contacting the stakes with cotton balls, and cheek-rubbing either on or around the stakes (Fig. 2). Cheek-rubbing in response to an experiment was rare and did not differ significantly according to the four treatment secretions (non-group female, non-group male, group female, group male—Fig. 2). Overall, there was a highly significant treatment effect on the number of contacts and the duration of the contacts (Fig. 2). There were sex differences in the response to the treatments although all were not highly significant. Males responded both by contacting non-group members more than group members and by spending more time contacting non-group members than group members. Females contacted group members and non-group members similarly but spent significantly more time contacting non-group females than non-group males and significantly more time contacting non-group females than group males.

Overall, total exposure time did not appear to differ significantly by treatment (Friedman tied $P = 0{\cdot}4459$, $n = 12$ marmots), and females were exposed for similar amounts of time to the different treatments (Friedman tied $P = 0{\cdot}5939$, $n = 5$ females). Males appeared to be exposed for different amounts of time to the different treatments, spending slightly more time exposed to group female stimuli than other stimuli (Friedman tied $P = 0{\cdot}0660$, $n = 7$ males). However, there was no relationship between the duration of exposure and number of contacts (Spearman Rank Correlation, ρ corrected for ties $= 0{\cdot}624$, $P = 0{\cdot}1266$), total time contacted (Spearman Rank Correlation, ρ corrected for ties $= 0{\cdot}624$, $P = 0{\cdot}1266$), or cheek-rubs per exposure (Spearman Rank Correlation, ρ corrected for ties $= 0$, $P = 1$). Thus we conclude that differential responsiveness to the experimental treatments did not bias our results.

Discussion

This is the first study to combine observations of the external morphology of the orbital gland, observational studies of marmots cheek-rubbing, and experimental studies of marmots' responses to olfactory secretions to study the functions of cheek-rubbing in a marmot species. A fundamental problem in studying the function of cheek-rubbing and olfactory secretions is that secretions may have different functions at different times of the year or to members of different age/sex classes. Additionally, golden marmots cheek-rub infrequently, making it difficult to collect sufficient information to evaluate alternative hypotheses. What follows is an attempt to understand the function of cheek-rubbing in golden marmots.

Individual recognition

Marmots may cheek-rub to identify their presence to conspecifics (Taulman, 1990). The aseasonality of golden marmot cheek-rubbing is consistent with the individual recognition hypothesis and contrasts results reported for other species by Koenig (1957), Hébert & Prescott

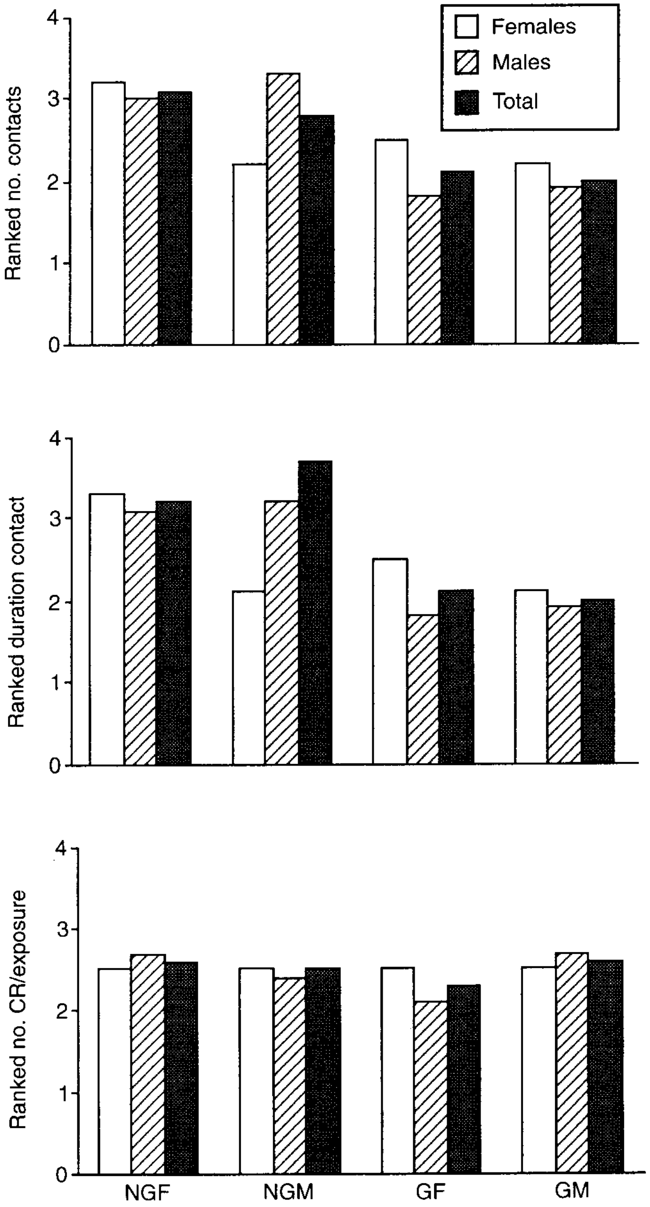

FIG. 2. Responses of 13 adult marmots (6 females, 7 males) to the four olfactory treatments, odours of: non-group females (NGF), non-group males (NGM), group males (GM), and group females (GF). Ranked number of contacts and ranked duration of contacts were calculated by comparing the response to a treatment stimulus and a simultaneously presented control stimulus. Equation 1 illustrates the calculation of these 'response ratios'. The dependent variable, number of cheek-rubs per exposure, was ranked by comparing each individual's responses to the four different experimental treatments (Siegel & Castellan, 1988: 174–183).

(1983), and Barash (1989: 104–105) who found that cheek-rubbing was most intense during the reproductive season. We have no explanation for this disparity; cheek-rubbing was infrequent even in the beginning of May—golden marmot's reproductive season. The response of marmots to experimental odours neither fully supports nor refutes the individual recognition hypothesis: marmots may recognize group-members by their odour and therefore not respond to group-member odours. That females responded more to non-group females than to non-group males suggests that females may be able to distinguish the sex of potential signallers from their olfactory secretions. Yet mechanisms other than individual recognition may account for aseasonal marking and differential responses to olfactory secretions. Marmots could identify their presence and/or residence status (e.g. group member or non-group member) by scent-matching (Gosling, 1990; Gosling & McKay, 1990). Whether marmots individually recognize conspecifics, or scent-match, a non-group marmot detecting a cheek-rubbed spot may avoid potentially dangerous encounters with group members.

Self-reassurance

Cheek-rubbing appeared not to reassure individuals engaged in an aggressive encounter (Ewer, 1968; 117). We never saw marmots smell themselves while engaged in an aggressive interaction; perhaps because the orbital gland was located in a position that did not facilitate self-sniffing. We did see marmots cheek-rub during prolonged aggressive interactions, and saw individuals apparently increase their rate of cheek-rubbing following movement to a new social group. To determine properly whether this increase in cheek-rubbing reassured individuals or was a form of status signalling (Gosling, 1990), we would need a more focused definition, and a more sensitive measurement of 'reassurance'.

Communication of breeding status

The aseasonality of golden marmot cheek-rubbing is not consistent with the hypothesis that cheek-rubbing communicates breeding status (Hébert & Prescott, 1983). To test the breeding status hypothesis properly, facial secretions from animals in different breeding conditions must be exposed to test subjects and their responses scored.

Communication of dominance status

Dominance relations between individuals within and among social groups was unknown for we had no independent measure of dominance. Yet the pattern of golden marmot cheek-rubbing was not consistent with a dominance signalling hypothesis. More than a single individual in a group simultaneously had an eyepatch and/or secreted fluid from their orbital gland. Thus, the mere ability to produce an odoriferous secretion was probably not restricted to potentially dominant individuals. Furthermore, that marmots were consistently less responsive to odours from group members suggests that within-group dominance relationships may have not been communicated by the secretions.

Territory identification

Scent-marking may be a way to identify defended areas which minimizes the costs of aggressive interaction (Gosling, 1982). Our data are consistent with the territory identification hypothesis. Adults have more developed orbital glands and cheek-rub more than subadults. Cheek-rubbing occurs throughout the active season. The observed decline in cheek-rubbing rate in August parallels a decrease in home-range size (Blumstein, unpubl. data). Cheek-rubbing seems to occur in the core of the marmots' home ranges—around their main burrows. Other evidence suggests that it is mainly this core area that is defended from other marmots (Blumstein, unpubl. data). Finally, adult marmots respond more intensively to the smells of non-group members than to group members. The sex difference between male and female responsiveness to the smells of non-group males and non-group females is interesting. In 1993, a female moved from a social group that had another adult female to a social group that had no adult female. Male residents in the new group responded by aggressively chasing the new female whenever she approached a main burrow. Future analyses of the reactions of residents to dispersing marmots will better quantify male and female responses to non-group members of both sexes.

Our data provisionally support the hypothesis that cheek-rubbing by golden marmots functions to indicate occupancy of an area. Both group members and intruding marmots could potentially benefit from territorial marking. Group members would benefit if such marking deterred intruders, while intruders would benefit if they could identify a resident and avoid escalating a potentially dangerous fight (Gosling, 1990). Because marmots were less responsive to odours from group members than to odours from non-group members, we infer that odours did not communicate within-group dominance relationships. Whether marmot orbital secretions are used for individual recognition, signal breeding status, or 'reassure' residents requires further study.

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