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Scent-marking in the yellow-bellied marmot (*Marmota flaviventris*)

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Cheek-marking in yellow-bellied marmots (*Marmota flaviventris*) was studied by observations of cheek-marking in two colonies from 10 June to 6 August, 1996 and by experimental studies of responses to olfactory secretions from the perioral gland. The rate of cheek-marking declined significantly as the season progressed. Most cheek-marking occurred within 3 m of the main burrow system and was primarily associated with sitting or lying and short locomotory bouts around the main burrow area. Cheek-marking rates of individuals differed significantly and adults appeared to mark more than yearlings. In the experiment, marmots cheek-marked stakes with perioral secretions significantly more than stakes without secretions. However, they marked unfamiliar and familiar smells equally. Marmots investigated strange secretions longer than familiar secretions and familiar secretions longer than the blank treatment. Functionally, cheek-marking is a multipurpose activity. It provides cues for young of the year to learn the safe areas in the home range, imparts familiarity with the burrow area, communicates burrow occupancy, and functions in territorial defense.

KEY WORDS: *Marmota flaviventris*, behavior, olfactory communication, cheek-marking, territoriality.

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INTRODUCTION

Olfaction is a valuable way in which many mammals assess their social environment (Eisenberg & Kleiman 1972). In sciurids, "Greeting" behavior, sniffing of the oral angle of another individual, is an important cohesive behavior (Barash 1989). Deposition of scent from the oral angle by cheek-marking, which occurs in marmots and spermophiles, but not in prairie dogs (Halpin 1984), may further reinforce group cohesion as well as impart additional information to other individuals. Proposed explanations for sciurid scent marking include self-grooming (Halloran & Beckoff 1995), information about breeding status (Hébert & Prescott 1983), familiarity with the burrow (Taulman 1990), territory defense (Bel et al. 1995, Lenti Boero 1995, Blumstein & Henderson 1996), dominance (Hébert & Barrette 1989), and self-reassurance (Armitage 1976, Meier 1991); however, the function of scent-marking is still unresolved.

Oral glands may facilitate species, group, sexual, or individual identity. Columbian ground squirrels distinguish between the oral secretions of neighboring and strange males (Harris & Murie 1982) and group member discrimination occurs via familiarity with substrate-borne chemical cues (Hare 1994). Golden marmots distinguish between both male and female scent and unfamiliar and familiar individuals (Blumstein & Henderson 1996). Group identification may also be possible through the sharing of individual odors within a group (Halpin 1985). This sharing may create a "scent pool" facilitated by greeting behaviors and other social interactions such as mutual grooming (Steiner 1975).

Familiarity with the burrow system may be maintained through scent deposition by orienting individuals within the home range (Johnson 1973, Ferron 1983). Saturation of the area with scent may also impart greater familiarity with neighbors and may, in turn, reduce the possible costs of aggression (Harris & Murie 1982). Imparting of "home" scent on outlying refuge burrows that would be occupied in the event of a predator attack could also be highly important not only for locating the burrow but also for reassurance (Taulman 1990). The young of the year may also use familiar scents to find their way back to the burrow in the same way as rat pups find their way back to their nest using olfactory cues (Gregory & Pfaff 1971). In addition to finding their way back to the nest when they are first emerging, they may also identify areas with familiar scent deposits as safe areas with strange scent or no scent as beyond the home range (Bel et al. 1995).

Territory and burrow defense may also be facilitated by cheek-marking (Murie & Harris 1984, Meier 1991). In golden marmots (*Marmota caudata aurea*) cheek-marking occurs more frequently in adults than in subadults and cheek-marking declines throughout the season as a function of territory size (Blumstein & Henderson 1996). In the hoary marmot, cheek-marking of the territory is more costly than normal foraging, thus marking of the territory may impart some benefit, possibly by reducing invasions by competitors (Taulman 1990). Territorial male *M. vancouverensis* (Heard 1977) *M. bobak, M. caudata* and *M. baibacina* (Shubin & Spivakova) cheek-mark more than other age-sex classes. Female *M. vancouverensis* occasionally scent-marked in their areas of exclusive use (Heard 1977). Male and female *M. marmota* deposited scent with equal frequency; scent deposition was

concentrated near the boundaries of family home ranges and near the main burrows (LENTI BOERO 1995). Cheek-marking seems to function in territorial defense in many species but only a few species have been examined. The function of scent-marking may depend on the social system of the species.

Cheek-marking may also function to establish and maintain dominance (ARMITAGE 1976, HÉBERT & BARRETTE 1989). Self-reassurance is probably linked to dominance and is difficult to identify on its own. In woodchucks dominant individuals sometimes scent-marked after agonistic encounters (HÉBERT & PRESCOTT 1983) and dominance or subordinance could be predicted prior to the introduction of unfamiliar individuals because future subordinates cheek-mark secretions of future dominants more than future dominants cheek-mark the secretions of future subordinates (HÉBERT & BARRETTE 1989). It is likely that cheek-marking is important to dominance status but little evidence is available.

This paper describes cheek-marking by yellow-bellied marmots (*Marmota flaviventris*) with the objective of determining its functions by observations of the time, place, and behavioral context of cheek-marking in addition to an experiment using the perioral secretions from individuals of the same group and of different groups.

METHODS

Observations of two colonies of yellow-bellied marmots were conducted in the Upper East River Valley, Gunnison County, Colorado, USA from 6 June through 6 August, 1996.

Marmots from both colonies were trapped, sexed, and weighed each week. Individuals were marked with a non-toxic fur dye for visual identification and first-caught animals received a uniquely numbered Monel metal tag in each ear for permanent identification. Samples of perioral glandular secretions were taken by rubbing cotton pads over the oral region. The samples were dated, labeled, and stored in ziplock freezer bags for later use in the olfactory experiment.

Study populations

Marmots live in colonies organized into kin groups of closely-related females and an attached male (ARMITAGE 1991). These colonies are grouped on patchy habitat and individual groups are territorial (ARMITAGE 1991).

River Colony is spatially divided into three separate but adjoining flat-topped areas with burrow systems on each area. The population was composed of two distantly related matrilines and one unrelated 4-year-old male. One matriline consisted of two 7-year-old sisters (both showed nipple development but neither weaned litters). The other matriline consisted of a 6-year-old mother, her 4-year-old daughter (both of whom weaned litters), two male yearlings and two female yearlings.

At Marmot Meadow a rocky talus on the northern side of the meadow provides a site for sitting and lying as well as for home burrows. A small burrow system is also present on the southern side of the meadow. The population consisted of three 2-year-old sisters all of whom weaned litters.

Behavioral observation

Marmot obsrvations were conducted in the morning (06:30-10:30) and afternoon (16:00-19:30) on most days because marmots exhibit a biomodal activity pattern with highest

activity levels during these times (Armitage et al. 1996). Continuous scan sampling was used to detect scent-marking bouts, which included (1) cheek-rubbing, tilting of head either to right or left and rubbing the perioral gland across a substratum (Blumstein & Henderson 1996) and (2) chin-rubbing, rubbing of the chin across a substratum. Intensity of the bout was measured by the number of times the perioral gland and/or the chin was rubbed against the substratum. The sequence of behaviors prior to and after a scent-marking bout were also noted to establish the context in which scent-marking occurred. Behaviors were considered part of a scent-marking sequence if they occurred within five acts before or after a scent-marking bout (Ouellet & Ferron 1988). The level of dominance of each individual was calculated for each colony to provide additional information about individual interactions. Greeting behavior, sniffing of the perioral gland, was used to determine dominance, assuming subordinate individuals initiate greeting behavior more than dominant individuals. Although agonistic interactions are more informative, they were rare. Dominance was calculated by tallying the number of greetings an individual initiated and individuals were ranked from low to high numbers of initiations.

Chin-rubbing suggests the presence of exocrine glands (Koenig 1957), but glands have been described only on the cheeks and at the angulur oris (Rausch & Bridgens 1989). Given the uncertainity that chin-rubbing deposits scent, only cheek-marking was used in the following analyses. Seasonal rates of cheek-marking for 10-day blocks were calculated by counting the number of cheek-marking bouts that were observed per block in each colony divided by the number of hours observed divided by the number of marmots present to obtain a colony rate. The rates for each colony were then combined.

Detailed maps depicting individual rocks, roots, and vegetation as well as photographs with grid marks were used to establish the precise location of each cheek-marking bout. In addition to data on the location of cheek-marking, the locations of each active marmot were recorded every 10 min as a pair of grid coordinates, in order to provide a spatial framework of where scent-marking occurred. The number of times a location was recorded for each animal was used as an index of activity.

Locational data were used to determine the amount of time spent in areas in which cheek-marking occurred and to calculate space-use overlap between individuals (Armitage 1996). The space-use overlap at River Colony was used to establish areas shared by group members (members of the same matriline) and non-group members (members of distantly-related or unrelated matrilines). Once separate categories of group and non-group were established, areas of scent deposition for each group were examined to determine if cheek-marking was more likely in areas where space-use overlapped with a non-group member or a group member.

The number of precise places each individual marked were tallied. The percentage of those substrates marked by an individual that were marked by another individual were then calculated in order to identify the influence of individual smells on other individuals. The places young cheek-marked were compared to adult cheek-marking to establish the influence of adult cheek-marking on young cheek-marking.

The number of cheek-marking bouts was tabulated for each individual and adjusted for the amount of time active above ground by dividing the number of bouts by the index of activity. Mean number of adjusted cheek-marking bouts was calculated for adult females, the adult male, yearling females, and yearling males at River Colony and for adult females and young at Marmot Meadow.

Olfactory experiment

At the beginning of each trial, three 50 cm tall, clean, wood stakes were placed 50 cm apart in front of a burrow entrance or a common perching rock of a marked marmot. Perioral secretions obtained during trapping were checked for pungency. Cotton pads were usually used within two weeks of collection. In each trial one cotton pad contained secretions from a group member, one pad contained secretions from a non-group member (always an unrelat-

ed individual from a location distant from the experimental location), and one pad was blank. Cotton pads were randomly assigned to each stake and stapled to the stakes 40 cm above the ground.

An interaction began when a marmot was within 5 cm of the stakes. Data were taken on (1) the time of discovery, (2) which stakes were approached, (3) how much time was spent at each stake, (4) which, if any, stakes were scent-marked, (5) how long they were marked, and (6) how many times they were marked. Only the first marmot to interact with the stakes was recorded to avoid any complications due to additional scent deposits. Because several marmots lived in each colony and spent time in the same areas, it was not possible to control which individuals interacted with stakes during each trial.

Because marmots often did not respond to all of the cotton pads, there were many zero values; so the data were plus one transformed. A general linear mode (GLM) ANOVA was used to test the responses to treatments. Cheek-marking on the stakes was analyzed by looking only at trials in which cheek-marking occurred. If the same individual was included in this category more than once, a single trial for that individual was randomly picked. The intensity of cheek-marking was then summed for each category (group, non-group, control) and tested, using Chi-square, against the null hypothesis that there was no difference in cheek-marking among treatments.

RESULTS

Observation

In 140 hr of observation on two social groups, 254 cheek-marking bouts were observed. One adult male, 7 adult females, 2 yearling females, 3 yearling males, and about 12 young were observed cheek-marking. Cheek-marking occurred primarily on the vertical and horizontal surfaces of rocks; a few cheek-marking bouts occurred on fence posts or exposed tree roots; none occurred on soil.

Because marmots were often out of sight within five behaviors before or after a cheek-marking bout, only those behaviors occurring within closs proximity to the cheek-marking substrate were considered for the analysis. Cheek-marking was associated with aggressive encounters (chasing), social encounters (greeting), vigilance, sitting and lying (often alert), moving short distances around the burrow area (locomotion < 3 m), digging, and foraging. Cheek-marking occurred with the highest frequency immediately following movement around the burrow area and sitting or lying on commonly used rocks (Fig. 1). Although aggression between members of distantly-related matrilines was observed only 15 times, vigorous cheek-marking occurred after 73.3% of those encounters. In 60.0% of those encounters only the aggressor marked.

Season influenced the rate of cheek-marking by adult females (Fig. 2). As the season progressed the rate of cheek-marking declined significantly. Similar seasonal decline was reported for *M. monax* (Hébert & Prescott 1983), *M. olympus* (Barash 1989), and *M. marmota* (Bel et al. 1995). Adult males and yearlings were not tested due to low sample size.

The amount of cheek-marking differed significantly among individual adult females at both Marmot Meadow (Chi-square test: $\chi^2 = 11.1$, $P < 0.025$, df = 3) and River Colony (Chi-square test: $\chi^2 = 26.6$; $P < 0.001$, df = 2). At River Colony adults were observed cheek-marking more than yearlings and at Marmot Meadow adult females cheek-marked at a much higher rate than the young (Table 1). For a brief period during the summer a yearling male attempted to invade Marmot Meadow

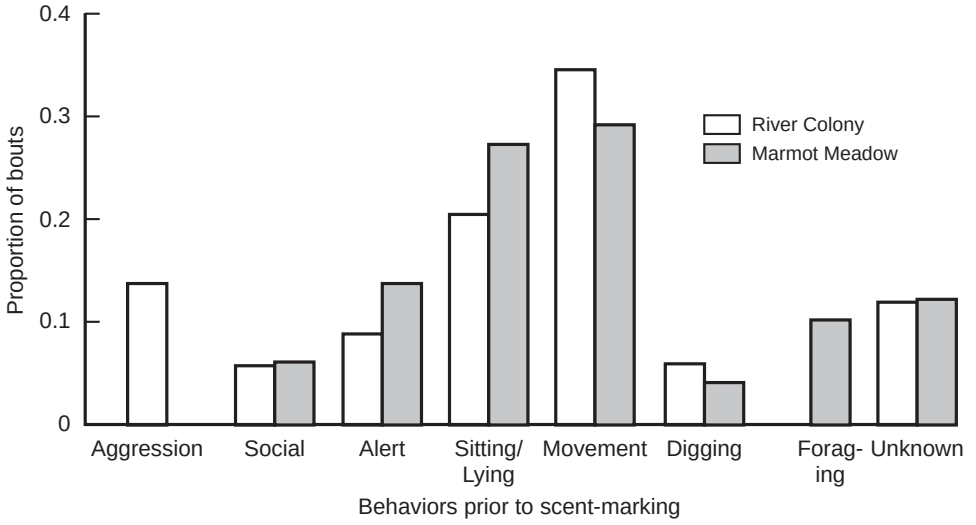

Fig. 1. — Proportion of scent-marking associated with behaviors occurring prior to scent-marking bouts for seven adult females from two populations of yellow-bellied marmots. Number of scent-marking bouts were tallied and divided by the total number of scent-marking bouts (River n = 40, Marmot Meadow n = 87).

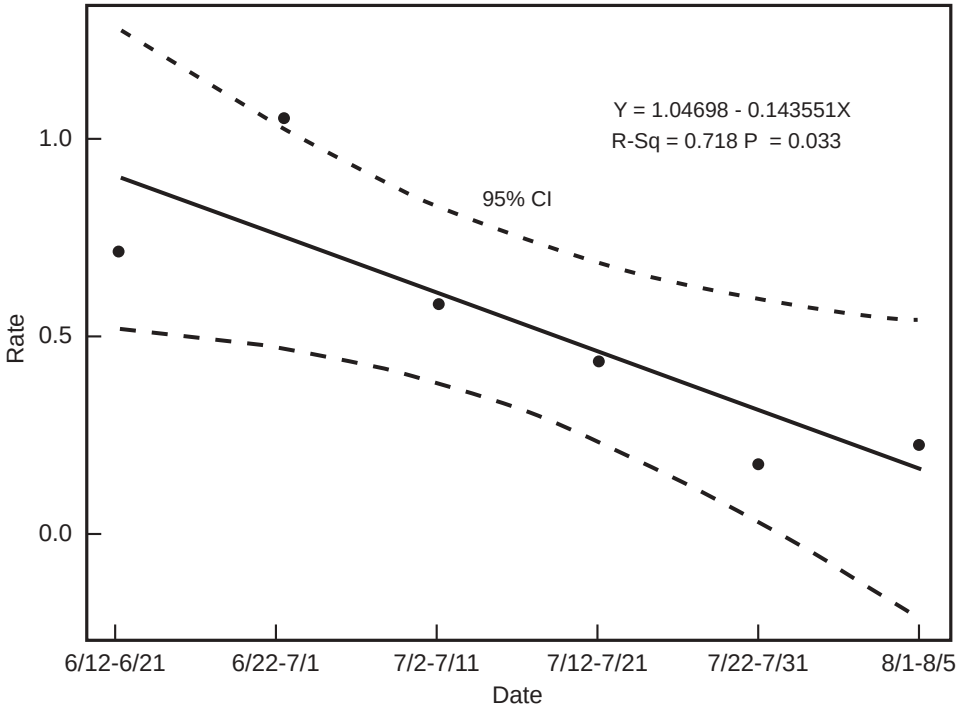

Fig. 2. — Regression of the rate of scent marking versus time for seven adult females from two populations of yellow-bellied marmots.

where no adult male was observed. He was observed to cheek-mark at a much higher rate than the females, marking a total of 17 times while the three females present at the time marked only 3, 3, and 0 times.

Although the substrate available for cheek-marking differed between the two sites, there was little difference in the number of places used for cheek-marking (River, 1-12 places; Marmot Meadow: 5-15 places). Marmots in both colonies also spent about the same amount of time in areas in which they cheek-marked (Two sample t-test: $t_4 = 1.20$, NS). Adult females spent an average of 27.1% (± 4.03, n = 7) of their time in areas where cheek-marking occurred.

Determination of the specific places individuals marked allows the analysis of how scent deposits affect where other marmots mark (Table 2). Adult female 2009 was present on the rocky outcrop of Marmot Meadow early in the season when her two sisters were present on the other side of the meadow. Prior to emergence of young the two sisters moved to the rocky outcrop. After this move female 2009 marked 100% and 75% of the rocks her sisters marked and she marked 47 times while her sisters marked 33 and 12 times. Female 2009 initiated the fewest greetings and female 2019 initiated the most greetings but females 2007 and 2009 were too close for clear determination of dominance rank. However, 2009 appeared to be dominant for the following reasons: (1) her two sisters moved to a separate burrow

Table 1.

Average number of cheek-marking bouts per individual at each location for various age/sex categories at River Colony and Marmot Meadow. Number of bouts was adjusted for the amount of time active above ground. The standard error for the adult male could not be calculated because only one adult male was observed. Individual rates and standard error could not be obtained for young because they were often difficult to individually identify. Because young were difficult to observe at River, they were not included.

Location	Class	$\bar{x}$ ± SE	n
River Colony	Adult male	0.39	1
River Colony	Adult females	0.19 ± 0.14	4
River Colony	Yearling males	0.04 ± 0.02	2
River Colony	Yearling females	0.09 ± 0.01	2
Marmot Meadow	Adult females	0.26 ± 0.19	3
Marmot Meadow	Young	0.003	11

Table 2.

Percentage of rocks marked by individuals that were marked by another individual at Marmot Meadow. Individuals 2007, 2009, and 2019 are adult sisters and individual 2041 was an invading male yearling that was observed on three separate occasions.

Individual	Number of rocks marked	Percentage of rocks marked by:				
		2007	2009	2019	2041	Any marmot
2007	5	—	100	60	20	100
2009	15	33	—	40	33	60
2019	8	38	75	—	38	88
2041	7	14	71	43	—	86

system during gestation and lactation possibly to avoid stress during this critical period, (2) she participated in the fewest greetings, and (3) she marked more of the intruding male's rocks than her sisters marked. At River Colony one individual was out of sight most of the time and skews the analysis so she will be ignored. There was conflict between two cousins living in different social groups, adult females 279 and 1399. Female 279 was invading the territory of female 1399; 100% of the rocks marked by 279 were then marked by 1399 even though only about 9.3% of their space use overlapped.

The number of rocks marked by pups was much fewer than by the adults. In 60 cheek-marking bouts by 12 young, only 6 rocks were marked. All marked rocks were within 3 m of the main burrow and were marked by at least one adult (67% of the rocks were marked by at least two adults) (Fig. 3).

Experiment

Time spent investigating the stakes differed significantly among the three treatments (GLM: $F_{2,2,19,23} = 4.96$, $P < 0.02$). Stakes with non-group scent were investigated more than stakes with group scent, which in turn were investigated more than the control stakes (Fig. 4a).

In nine trials marmots cheek-marked. The differences in the intensity of cheek-marking between the treatments were significant (Chi-square test: $\chi^2 = 7.3$; $P < 0.05$, df = 2), indicating that marmots are much more likely to cheek-mark if perioral secretions are present (Fig. 4b).

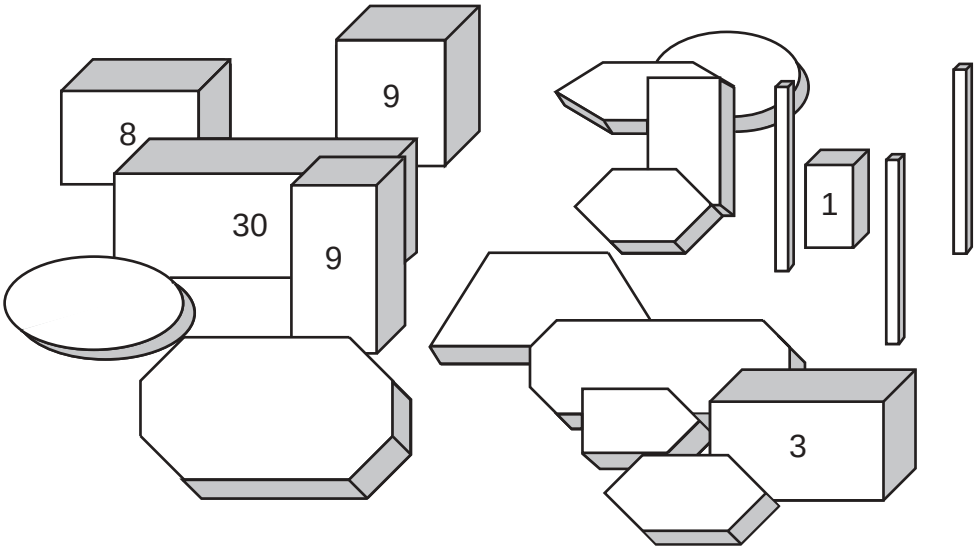

Fig. 3. — Diagramatic representation of rocks and stakes at the main burrow system at Marmot Meadow. Numbers indicate the number of scent-marking bouts performed by pups on individual rocks. Note that not all available rocks are used for scent marking. The experimental stakes were located near the rock with one scent-marking bout.

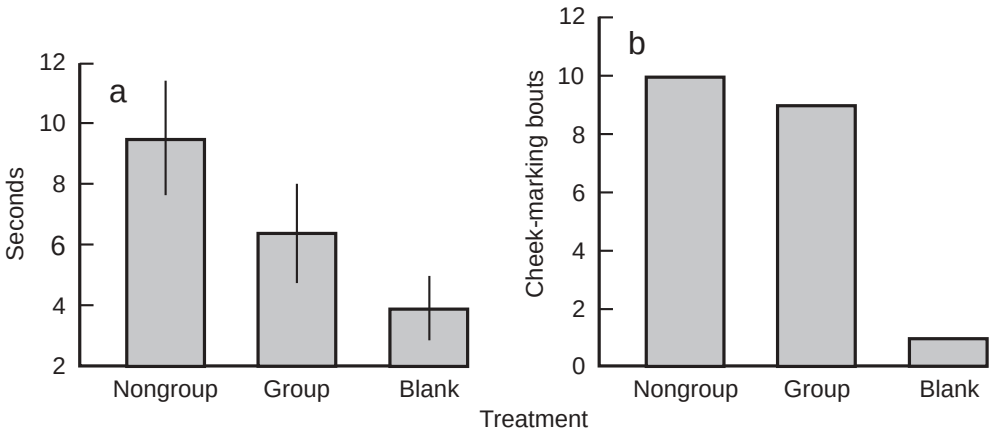

Fig. 4. — (a) The mean (± SE) number of seconds seven adult female marmots investigated perioral secretions of non-group members, group members, and a blank. All three treatments were presented to the marmots simultaneously. (b) Total number of times marmots rubbed the perioral gland against the stakes in each group. Six adult females cheek-marked the stakes. Only one trial for each individual was randomly chosen.

DISCUSSION

Response to the experiment

Stakes containing scent were examined longer than the control treatment, which indicates that the marmots responded to the secretions and could distinguish cotton pads containing secretions from blank cotton pads. Unfamiliar smells were investigated more than familiar smells, which supports the hypothesis of territoriality. When only cheek-marking on the treatments was considered, however, unfamiliar and familiar smells received equal numbers of cheek-marks, which indicates that any odor from a marmot may elicit cheek-marking and supports the hypothesis of familiarity and group smells as well as territoriality.

Function of cheek-marking behavior

Several less complex functions of scent-marking have been described in other species of sciurids. Communication of reproductive state was described in several species including the woodchuck (*Marmota monax*) but typically it has been described in addition to other motivated factors (Ouellet & Ferron 1988). In the yellow-bellied marmot, however, cheek-marking continued throughout the active season beyond mating and gestation and was performed by adults, yearlings, and juveniles, indicating that scent deposits communicate more than or other than reproductive status. In Abert squirrels (*Sciurus aberti*) cheek-marking behaviors function as a form of self-grooming to remove food residue and the deposition of scent is a by-product of this activity (Halloran & Bekoff 1995). Cheek-marking in the yellow-bellied marmot, however, was primarily associated with sitting or lying and short locomotory bouts and rarely after food-related behavior or grooming. More com-

plex aspects such as orientation within the home range, territoriality, and social structure may better explain the functions of cheek-marking.

Orientation

Cheek-marking may function to impart a familiar smell to outlying burrows used for refuge from attack and to maintain familiarity with the main burrow system (TAULMAN 1990). This hypothesis predicts that cheek-marking should occur primarily around burrow entrances. The prediction is confirmed for *M. bobak, M. caudata, M. baibacina* (SHUBIN & SPIVAKOVA 1993), and M. *flaviventris* and is supported by high frequencies of marking at the main burrow in *M. marmota* (LENTI BOERO 1995). Cheek-marking should also occur at equal rates in males and females as well as among individuals of the same sex because they presumably are at the same level of risk. The comparison between males and females in this study is difficult because there was only a single adult male. Although he marked at one of the highest rates, he did not mark statistically more than the females. Individuals, however, marked at different rates, which indicates other factors influence cheek-marking.

Saturation of the main burrow with scent deposits could help young of the year identify safe areas and orient within the home range (BEL et al. 1995). When young yellow-bellied marmots first emerged, they intently sniffed the burrow area and intense sniffing bouts were commonly observed over the main burrow system for the rest of the season. A young wandered around the main burrow area at Marmot Meadow until it encountered an experimental stake on which the smell of a strange individual was attached whereupon the young promptly ran into a burrow. The young seem to respond to the scent deposits of adults because the only rocks that young cheek-marked were previously marked by adults. Although young appear to detect scent deposits, cheek-marking may have additional functions because nonreproductive females and yearlings cheek-mark as well.

Territory defense

Cheek-marking may communicate burrow occupancy and function in territorial defense (OUELLET & FERRON 1988, MEIER 1991, BEL et al. 1995, LENTI BOERO 1995, BLUMSTEIN & HENDERSON 1996). Marking deters potential intruders by preventing them from entering a territory or causing their withdrawal (GOSLING 1982). The presence of scent may further embolden group members and intimidate non-group members (GOSLING 1982, TAULMAN 1990). Marking of these defended areas may minimize the costs of aggressive encounters (GOSLING 1982). The yellow-bellied marmots investigated the secretions of strange individuals more than the secretions of familiar individuals during the experiment, which indicates that intruders may be detected by group members and that intruders could identify the presence of other marmots in a territory. The marmots also concentrated cheek-marking bouts near or on the main burrow system. However, when conflict between members of different matrilines occurred, cheek-marking occurred in the area where space-use overlapped and possibly served to inhibit further penetration of the territory by the intruder. The golden marmot (*M. caudata aurea*) also cheek-marked at the highest densities near the core of the territory (BLUMSTEIN & HEN-

DERSON 1996) and *M. marmota* marked intensively in the home burrow area (LENTI BOERO 1995). This localized deposition of scent and the ability to distinguish secretions from strange and familiar individuals indicate that cheek-marking could transmit cues that communicate burrow occupancy and that these cues could play a role in territorial defense.

Social group structure

Cheek-marking may play a large role in the social system of yellow-bellied marmots by communicating individual presence in the group and maintaining familiarity with other individuals. Marmots cheek-mark in areas where cheek-marking previously occurred and they cheek-mark at equal rates on stakes with strange and familiar smells, indicating that cheek-marking may be elicited by the presence of scent. Sniffing of the perioral gland during greeting further supports that these secretions may play a role in familiarity between individuals.

Cheek-marking may further function to establish and maintain dominance (BARASH 1989, HÉBERT & BARRETTE 1989) or it may serve as a means of reassurance for subordinate or stressed individuals (ARMITAGE 1976, WALRO et al. 1983, MEIER 1991). The fact that aggressors in agonistic interactions usually cheek-mark and receivers often do not indicates that reassurance is an unlikely function of cheek-marking. Dominance, on the other hand, is supported by aggressor marking in agonistic encounters as well as the high cheek-marking rate by the dominant female at Marmot Meadow. In addition, significant variation between individual cheek-marking rates indicates that social factors are likely to be involved because different individuals experience different social pressures. These social factors may be important aspects of cheek-marking function, but they are difficult to test and support in the yellow-bellied marmot where dominance is difficult to distinguish.

CONCLUSION

Because yellow-bellied marmots cheek-mark primarily in the central burrow area, several functions are likely. Saturation of the home burrow system with scent may be advantageous to the emerging young as they begin to learn the burrow system, helping them to orient and decreasing conflicts with neighboring marmots in the social group. Scent deposits in this location can also help exclude intruders and decrease conflict. For those intruders who attempt to stay, the scent may embolden group members and help expel the intruders. Lastly, the communication of presence, familiarity with other individuals, and social organization may be maintained through the use of cheek-marking.

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REFERENCES

ARMITAGE K.B. 1976. Cheek-marking by yellow-bellied marmots. *Journal of Mammalogy* 57: 583-584.

ARMITAGE K.B. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and Systematics* 22: 379-407.

ARMITAGE K.B. 1996. Resource sharing and kinship in yellow-bellied marmots, pp. 129-134. In: Le Berre M. et al., Edits. Biodiversity in marmots. *Lyon/Moscow: International Marmot Network*.

ARMITAGE K.B., SALSBURY C.M., BARTHELMESS E.L., GRAY R.C. & KOVACH A. 1996. Population time budget for the yellow-bellied marmot. *Ethology Ecology & Evolution* 8: 67-95.

BARASH D.P. 1989. Marmots social behavior and ecology. *Stanford: Stanford University Press*.

BEL M.C., PORTERET C. & COULON J. 1995. Scent deposition by cheek rubbing in the alpine marmot (*Marmota marmota*) in the French Alps. *Canadian Journal of Zoology* 73: 2065-2071.

BLUMSTEIN D.T. & HENDERSON S.J. 1996. Cheek-rubbing in golden marmots (*Marmota caudata aurea*). *Journal of Zoology, London* 238: 113-123.

EISENBERBG J.F. & KLEIMAN D.G. 1972. Olfactory communication in mammals. *Annual Review of Ecology and Systematics* 3: 1-32.

FERRON J. 1983. Scent marking by cheek rubbing in the northern flying squirrel (*Glaucomys sabrinus*). *Canadian Journal of Zoology* 61: 2377-2380.

GOSLING L.M. 1982. A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie* 60: 89-118.

GREGORY E.H. & PFAFF D.W. 1971. Development of olfactory-guided behavior in infant rats. *Physiology and Behavior* 6: 573-576.

HALLORAN M.E. & BEKOFF M. 1995. Cheek rubbing as grooming by Abert squirrels. *Animal Behaviour* 50: 987-993.

HALPIN Z.T. 1984. The role of olfactory communication in the social systems of ground-dwelling sciurids, pp. 201-225. In: Murie J.O. & Michener G.R., Edits. The biology of ground-dwelling squirrels. *Lincoln: University of Nebraska Press*.

HALPIN Z.T. 1985. The rodents III: suborder Sciuromorpha, pp. 458-479. In: Brown R.G. & Macdonald D.W., Edits. Social odours in mammals. *Oxford: Clarendon Press*.

HARE J.F. 1994. Group member discrimination by Columbian ground squirrels via familiarity with substrate-borne chemical cues. *Animal Behaviour* 47: 803-813.

HARRIS M. & MURIE J.O. 1982. Responses to oral gland scents from different males in Columbian ground squirrels. *Animal Behaviour* 30: 140-148.

HEARD D.C. 1977. The behaviour of Vancouver Island marmots *Marmota vancouverensis. M.S. Thesis, Vancouver: University of British Columbia*.

HÉBERT P. & BARRETTE C. 1989. Experimental demonstration that scent marking can predict dominance in the woodchuck, *Marmota monax. Canadian Journal of Zoology* 67: 575-578.

HÉBERT P. & PRESCOTT J. 1983. Étude de marquage olfactif chez la marmotte commune (*Marmota monax*) en captivité. *Canadian Journal of Zoology* 61: 1720-1725.

JOHNSON R.P. 1973. Scent marking in mammals. *Animal Behaviour* 21: 521-535.

KOENIG L. 1957. Beobtungen über Reviermarkierung sowie Droh-, Kampf-, und Abwehrverhalten des Murmeltieres (*Marmota marmota* L.). *Zeitschrift für Tierpsychologie* 14: 510-521.

LENTI BOERO D. 1995. Scent-deposition behaviour in alpine marmots (*Marmota marmota* L.): its role in territorial defence and social communication. *Ethology* 100: 26-38.

MEIER P.T. 1991. Response of adult woodchucks (*Marmota monax*) to oral-gland scents. *Journal of Mammalogy* 72: 622-623.

MURIE J.O. & HARRIS M.A. 1984. The history of individuals in a population of Columbian ground squirrels: source, settlement, and site attachment, pp. 353-373. In: Murie J.O. & Michener G.R., Edits. The biology of ground-dwelling squirrels. *Lincoln: University of Nebraska Press*.

OUELLET J.P. & FERRON J. 1988. Scent-marking behavior by woodchucks (*Marmota monax*). *Journal of Mammalogy* 69: 365-368.

RAUSCH R.L. & BRIDGENS J.G. 1989. Structure and function of sudoriferous facial glands in Nearctic marmots, *Marmota* spp. (Rodentia: Sciuridae). *Zoologischer Anzeiger* 223: 265-282.

SHUBIN V.I. & SPIVOKOVA L.V. 1993. Cutaneous glands and scent marking of marmots (*Marmota*, Sciuridae). *Selevinia* 1: 69-80.

STEINER A.L. 1975. "Greeting" behavior in some sciuridae, from an ontogenetic, evolutionary and socio-behavioral perspective. *Le Naturaliste Canadien* 102: 737-751.

TAULMAN J.F. 1990. Observations on scent-marking in hoary marmots, *Marmota caligata*. *Canadian Field-Naturalist* 104: 479-482.

WALRO J.M., MEIER P.T. & SVENDSEN G.E. 1983. Anatomy and histology of the scent glands associated with the oral angle in woodchucks. *Journal of Mammalogy* 64: 701-703.