

Master Thesis

Hannah Cross

Female yellow-bellied marmots  
(*Marmota flaviventris*)  
do not display the  
Dear Enemy Phenomenon in  
response to female anal  
gland secretions



**Telemark University College**

Faculty of Arts and Sciences

## Master of Environmental Health

Female yellow-bellied marmots (*Marmota flaviventris*) do not display the Dear Enemy Phenomenon in response to female anal gland secretions



Hannah Cross

Telemark University College 2012  
Faculty of Arts and Sciences  
Department of Environmental and Health Studies  
Hallvard Eikas plass  
N-3800 Bø

<http://www.hit.no>

This dissertation represents 60 credits (ECTS).

© Rights under the law on intellectual property: Hannah Cross

Printed by the copycenter in Bø

Photo front/illustration: Hannah Cross

## **Preface**

This masters thesis is part of the Master degree program at the Department of Environmental and Health Studies at Telemark University College in Bø, Norway. I plan to publish my paper in the journal *Ethology* and so I have written my paper in this style.

I would like to thank my supervisor Frank Rosell for the help I received, through time, knowledge and patience and Daniel Blumstein for his help both out in the field and in the processing of the data. I would like to thank The Rocky Mountain Biological Laboratory marmot field crew of 2009 and Susan Jojola for their help in the field. I would also like to thank Veronica Tinnesand for her reassurance and encouragement!

Lastly I would like to thank my parents for their interest in my work, which even brought them to visit me at RMBL, and their encouragement and enthusiasm which is very much appreciated.

Bø i Telemark, 13 March 2012-03-13

Hannah Cross

**Female yellow-bellied marmots (*Marmota flaviventris*) do not display the Dear Enemy Phenomenon in response to female anal gland secretions**

Hannah Cross

**Abstract**

The dear enemy phenomenon (DEP) is a form of neighbour – stranger discrimination in which resident territorial individuals respond less agonistically to intrusions by known neighbouring conspecifics than they do to stranger conspecifics. I tested philopatric female yellow-bellied marmot (*Marmota flaviventris*) for the presence of DEP. As males treat females impartially I focused on the responses of the dominant adult female of a territory. I hypothesised that dominant females discriminate between the Anal Gland Secretion (AGS) from female neighbors and strangers, and predicted that they would respond more agonistically (as reflected by the duration of both sniffing and physical behavior) towards AGS from strangers than neighbors. Additionally, I also hypothesized that female yellow-bellied marmots will respond differently to kin and non-kin female neighbors, and predicted a lower agonistic response to related individuals. Direct observations of resident marmot responses to the olfactory trials showed that marmots spent significantly longer durations sniffing the AGS of both neighbours and strangers than a neutral scent free control. However, there was no significant difference in the sniffing response duration towards AGS from a neighbour or a stranger. In addition, kinship was not found to influence the responses of residents to neighbours or strangers. I conclude that although female yellow-bellied marmots detect AGS they do not seemingly discriminate between neighbours and strangers via AGS scent marks, and that they may not exhibit territorial behaviour but this needs further study

**Key Words:** *Anal gland secretion, dear enemy phenomenon, kinship, Marmota flaviventris, marmots, scent marking.*

## Introduction

A territory is an area or part of a home range defended by a group or an individual (Davies & Houston 1984; Maher & Lott 1995). Territoriality occurs when the benefits gained from exclusive access to limited resources, such as food sources and nest sites, exceed the costs of defence (Brown 1964). Territory defence costs can include time incurred, risk of predation due to announcement of presence via olfaction or vocalisation, and injury from physical encounters (Bradbury & Vehrencamp 1998). Once territorial boundaries have been established a territorial neighbour may pose less of a threat, enabling reduced aggression between neighbours. This has been called the *dear enemy phenomenon* (DEP) as well as the *familiarity hypothesis* (Randall et al. 2002, Briefer et al. 2008, Booksmythe et al. 2010, Zenuto 2010). Mammals reported to show DEP include badgers (*Meles meles*) (Palphramand & White 2007), kangaroo rats (*Dipodomys sp.*) (Murdock & Randall 2001) and root voles (*Microtus oeconomus*) (Rosell et al. 2008).

The presence or not of DEP tends to depend on the type of territory being defended; it has been frequently found to occur in multi-purpose breeding territories but not in feeding territories (Temeles 1994). The stability of both the group and the territory may be a key driver for the presence of DEP since the benefits of DEP accumulate when neighbours are stable. Indeed, in some species with limited territorial stability, males, females, or both sexes do not respond differently to neighbours versus strangers (Bee 2003, Lachish & Goldizen 2004).

Gland secretions and DEP has been studied in the Columbian ground squirrel (*Urocitellus columbianus*) (Harris & Murie 1982, Raynaud & Dobson 2011), woodchucks (*Marmota monax*) (Meier 1991) and Eurasian beaver (*Castor fiber*) (Rosell & Bjørkøyli 2002). In many species the anal/anogenital gland (AGS) is important for chemical communication (Sun & Müller-Schwarze 1999). The constituents of AGS can code for sex, age, social status and kinship (Sun & Müller-Schwarze 1999, Rosell & Bjørkøyli 2002, Zhang et al. 2003, Yuan et al. 2004, Rosell et al. 2011). AGS in the yellow mongoose (*Cynictis penicillata*) and other

herpestids function as long lasting marks (Le Roux et al. 2008). Rosell & Bjørkøyli (2002) found that Eurasian beavers displayed the DEP when presented with AGS from a neighbour and a stranger, however to my knowledge no other studies have focused specifically on AGS in relation to DEP in other free ranging rodents.

In addition to neighbour familiarity, kinship may also influence response to an olfactory signal (Hurst & Benyon 2010). Kinship discrimination of unfamiliar kin, and not just learning the cues of familiar individual kin during rearing, implies that individuals can recognise genetic similarity – either to self or to other known kin (Hurst & Benyon 2010). This has been demonstrated in: coyote (*Canis latrans*) (Tegt 2004), Columbian ground squirrels (Raynaud & Dobson 2011), root voles (Rosell et al. 2008), beaver (*Castor canadensis*) (Sun & Müller-Schwarze 1999) and ring-tailed lemur (*Lemur catta*) (Hurst & Benyon 2010). However, only Raynaud and Dobson (2011) have considered kinship between related females when investigating DEP, yet in philopatric societies, neighbours may often be close kin and therefore may pose less of a threat than unrelated strangers (Ferkin 1988). Genetic relatedness therefore needs to be taken into account when determining the presence of DEP to prevent any confusion as to whether individuals are distinguishing kin from non-kin or neighbours from strangers (Rosell et al. 2008).

Yellow-bellied marmots (*Marmota flaviventris*) are diurnal semi-fossorial sciurid rodents (Frase & Hoffmann 1980, Blumstein 2007) active for four to five months annually (Armitage 2003). Marmots dig numerous burrows within their 0.13 to 1.02 ha home ranges that serve as refuges (Armitage 1975) and typically occupy ‘multipurpose/breeding’ home ranges. Marmots mate just before or just after emerging from hibernation, pups are born a month after emergence (Armitage & Downhower 1974), and are weaned at 25-35 days (Nee 1969, Armitage 1981). Marmots are a harem-polygamous social species and form matrilineal groups, where philopatric females may share burrows and have extensive home-range overlap with female kin (Armitage 1991). About 50% of females are philopatric (Armitage 1991; 1999), reaching

breeding maturity at two years old (Blumstein & Armitage 1999). Males occasionally control more than one matriline (Armitage et al. 2011) and therefore it is expected that some neighbours are related by sharing a father. Resident adult females should respond aggressively toward intrusions by strange females, because their reproductive success is increased by ensuring their daughters survive and eventually reproduce. Armitage et al. (2011) found that survival of daughters is higher for recruits than dispersers. Additionally, access to foraging areas is strongly influenced by kinship; only closely related ( $r \geq 0.25$ ) adult females share foraging patches (Frase & Armitage 1984). Adult females exhibit a peak in scent-marking during the gestation and lactation periods (May and June), when they are their most territorial and scent marking rates decrease throughout the season (July – September) (Armitage 1999, Cross 2012).

Yellow-bellied marmots have three anal papillae that may be protruded from the anus (Rausch & Bridgens 1989). Anal glands exude AGS; a fatty secretion with a strong odour (Lassen & Ingdal 2008). To date most scent related behavioural studies in marmots have focused on facial rubbing behaviour (Armitage 1976, Brady & Armitage 1999, Olsen and Blumstein 2010, Jojola 2011) and no behavioural studies have focused on AGS. Therefore, the function of AGS in marmots is still unknown (Armitage 1975, Rausch & Bridgens 1989, Lassen & Ingdal 2008).

In this study I investigate the use of AGS as an olfactory cue to aid assessment of the threat imposed by intruding female yellow-bellied marmots dependent on their status as a neighbour or a stranger. I hypothesise that dominant female yellow-bellied marmots discriminate between the AGS from female neighbors and strangers, and predict that they respond more cautiously (longer sniffing durations) and agonistically (physically) towards AGS from strangers than neighbors, displaying the DEP. I also hypothesize that female yellow-bellied marmots will respond differently to kin and non-kin female neighbors, and predict that



they will respond more aggressively (as seen by enhanced sniffing and physical behavior) to non-kin individuals than to kin.

## **Methods**

### **Study site and population**

The study was conducted between 14 June and 1 August 2009 after the spring breeding season, at the Rocky Mountain Biological Laboratory (RMBL), Gothic, Colorado, USA, a location where yellow-bellied marmots have been studied since 1962 (Blumstein et al. 2006; Armitage 2010). Subjects studied were from 5 different colonies ranging in elevation from 2,867 to 3,008 m, all within 4 km of RMBL: River, Bench, Town, Marmot Meadow and Picnic (Armitage 2003). Within these colonies, marmots were further subdivided into 15 marmot social groups with an average of  $10 \pm 5.2$  SD individuals (Wey & Blumstein 2010) and individuals in these social groups were studied.

### **Scent donors and collection of scent**

Marmots were live-trapped in Tomahawk traps (Tomahawk, WI, USA) baited with Omolene horse feed (Purina<sup>®</sup> Omolene 100, Purina Mills, LLC, St. Louis, MO, USA) between 07:00 to 09:00 h and 16:00 to 18:00 h (Blumstein et al. 2008). Marmots were tagged with metal tags (for permanent identification) and given a fur mark (using Nyanzol fur dye) into their dorsal pelage (Armitage 1982, Blumstein et al. 2008, Olsen & Blumstein 2010). Trapping was carried out every two weeks for individual identification and sampling purposes. Sex was determined by the distance between the anus and the genitals and the reproductive state varied from 3-6 (3: nipples present, 4: nipples prominent; 5/6: lactating). Age was precisely known from longer-term trapping records (2 – 7 years) and hair was collected for relatedness analysis (Olsen & Blumstein 2010; details below).

In the study 30 adult females weighing an average of  $2800 \pm 601$  g were used as scent donors. Prior to collecting the scent samples the area around the papillae was cleaned using an alcohol pad to remove any faeces. Latex gloves were worn when collecting samples to prevent contamination from human odour. The papillae of the anal gland were pressed outward, and the AGS squeezed out and collected with a sterile, wooden-stemmed cotton swab (Express Medical Supply, Inc., Fenton, MO, USA). The cotton swabs with visible secretion were placed directly into 30 mL glass vials with Teflon-lined caps (Lab Safety Supply, Janesville, WI, USA), stored on ice in the field, and frozen at  $-20$  °C within 3 hours. Freezing and thawing is not expected to affect AGS scent (Lassen & Ingdal 2008). Samples were transported on ice to the field for experiments.

Marmots were comparatively docile, showed no signs of obvious distress and were easily restrained when confined in the dark bag. After handling the marmots were released at the point of capture.

For each experiment, stranger and neighbour females of similar characteristics were used, i.e. animals of similar age (< 2 years difference) and similar time of scent collection (< two weeks difference). Neighbours were females whose territory directly abutted the responder's, determined by previous observations. Strangers were selected from territories that were >1 km away from the responder's territory.

### **Kinship**

The relationships between responders and female scent donors were calculated using 12 previously developed microsatellite loci and the relatedness estimator of Queller and Goodnight (1989), using the program KINGROUP 2.0 (Konovalov et al. 2004). Genetic similarity matrices were constructed from pairwise relatedness coefficients (higher  $r$  value = greater kinship) (for details see Olsen & Blumstein 2010).

## **Experimental Design**

All experiments were direct observations undertaken during the morning (between 06:00 and 11:00,  $n = 10$ ) or afternoon (between 14:00 and 18:00,  $n = 5$ ), carried out at a territory's central burrow. Three cotton swabs were used in each experiment; one a plain swab as a control, one with AGS of a neighbour and one with AGS of a stranger. For each observation three tiles measuring 10 cm<sup>2</sup> were placed in a line 2 cm apart to ensure the marmot could differentiate between each scent (Figure 1). The separation of tiles was also to prevent destruction of other cotton swabs within the response to the first. The tiles were placed 1.0 m from the main burrow entrance where marmots would easily smell them (Blumstein & Henderson 1996).

It was unknown whether marmots would respond to an unscented cotton swab therefore a blank was included as a control to assess whether marmots showed interest in a purely novel smell or object within their territory (Rosell et al. 2000). Olfactory stimuli were randomly assigned to each tile to control for order effects. Disposable latex gloves were worn during the placing of the tiles and the addition of the cotton swabs to avoid contamination by human odour. Alcohol pads were used to clean the tiles before the cotton swabs were placed centrally on each tile and attached by a piece of duck tape. All cotton swabs were 5 cm long.

Observers were blind to the treatments during experiments. Given our extensive study of these marmots, we assumed that they were not affected by the human disturbance during experiment installation. Indeed, we observed them retreating into their burrows but they typically re-emerged within minutes. We used 10 x 42 binoculars and/or 15 - 45x spotting scopes to watch the marmot behaviour from a distance of >20 m, so as not to stress animals or influence behaviour (Wey & Blumstein 2010). Each observation was terminated after a response was recorded. If no response was observed within a four-hour period the experiment was repeated at the same site another day, using fresh scents. If a juvenile or male marmot approached the scents, it was scared away by the observer, as were marmots that approached when another was already within 0.5 m of the tiles. After marmots were scared off by the

observer, the experiment was re-set and the observer waited again for a target female to approach the scents. Responses were recorded by using a video camera (Sony® digital video handycam, model no. DCR.SR35E, Komplet.no, Sandefjord, Norway).

For each marmot's response, we recorded 1) the duration of time the marmot spent sniffing each cotton swab (within 5 cm of a swab), 2) duration of time each marmot spent physically responding to the swabs (pawing, and/or biting) and 3) frequency of scent marking the swabs (bite or rub). Interpreting time at stimulus as an indication of an agonistic response by yellow-bellied marmots can be justified based on previous experimental and observational evidence (Johns & Armitage 1979, Brady & Armitage 1999).

### **Statistical analysis**

The data did not fit assumptions of distribution and homogeneity of variance for parametric analysis (Sokal & Rohlf 1995), and therefore nonparametric statistics were used (Siegel & Castellan 1988). I used a Friedman's test for three related samples to identify differences in duration of responses by resident marmots to the neighbour, stranger and control. To further investigate the differences in duration between the cotton swabs I used a Wilcoxon's matched pairs test (two-tailed, Siegel & Castellan 1988). A Spearman's Rank correlation was used to investigate the influence of kinship on the duration of time sniffing the cotton swabs. All data analyses were performed using the statistical package SPSS software version 19 (IBM, Chicago, IL, USA).

### **Results**

Female sniffed different amounts of time in response to neighbours, strangers and control stimuli (Friedman's test:  $F = 0.003$ ,  $P < 0.01$ ). Females spent more time sniffing neighbours' AGS than a control ( $Z = -2.922$ ,  $P = 0.001$ ), and more time sniffing strangers' AGS than a control ( $Z = -3.052$ ,  $P = 0.001$ ). However, no difference in sniffing time was detected between

the neighbour and the stranger AGS ( $Z = -0.599$ ,  $P = 0.857$ ). Only one female was observed to display any physical response to the AGS. The individual responded to both the neighbour (41 s) and stranger (16 s) AGS by scent marking on rocks around her burrow.

The coefficient of relationship between strangers and responders was 0 to 0.12, while it ranged from 0 to 0.55 for neighbors and responders. We found that the duration of time a female spent sniffing the AGS did not increase with relatedness to a neighbour ( $r_s = 0.997$ ,  $p = 1.000$ ) (Figure 1).

## **Discussion**

This study examined the relationships between territorial neighbours by investigating whether female yellow-bellied marmots possess a dear enemy response to anogenital scent marks. My prediction that yellow-bellied marmot females would respond more cautiously (via sniffing) and agonistically (physical behaviour) towards AGS from female strangers than neighbours was not upheld. Therefore, my findings do not support the DEP of increased agonistic behaviour towards strangers as has been reported in many other species (Ferkin 1988, Harris & Murie 1982, Murdock & Randall 2001, Palphramand & White 2007, Rosell et al. 2008). However, I did find a significant difference between the response of female marmots to the neighbour and stranger scents compared to the control, showing that their behaviour was a direct response to the AGS and not purely a response to the presence of novel objects within their territory (Rosell et al. 2000).

As demonstrated in my study, DEP is not always displayed by female rodents that are polygamous, form matrilineal groups and have home range overlap without strict territory borders (Andreassen et al. 1998, Rosell et al. 2008). For example, Rosell et al. (2008) found that female root voles did not display DEP when field dyadic arena trials were conducted between strangers and neighbours of the same sex. However, these behavioral experiments did provide

evidence for DEP in male root voles, which suggests that female root voles are less territorial than males (see Andreassen et al. 1998). This could also explain the lack of DEP in marmots.

Raynaud and Dobson (2011) carried out a study using olfactory secretions with the philopatric female Columbian ground squirrel. They found support for DEP because squirrels sniffed stranger's perioral secretions longer than neighbor's secretions. However, in their investigation they also found that the physical behaviour of the female ground squirrels did not differ significantly between the neighbour and stranger perioral scent. In my study all females sniffed the AGS but all were passive to the presented scents and none displayed any immediate territorial behaviour in response to them. Interestingly the one female that did show agonistic behaviour vigorously over marked around her burrow entrances and surrounding rocks after responding. Observations of marmot scent marking behaviours show that marmots choose rocks as their favoured scent marking object (Armitage 1976, Brady & Armitage 1999).

In his review Temeles (1994) concluded that the DEP is not a permanent feature but may vary throughout the year according to the adaptive value of neighbour-stranger discrimination (see also: Briefer et al. 2008). Many, but not all, of my experiments were conducted after pups were weaned and had emerged from their natal burrows (personal observation). However, adult females exhibited a seasonal peak in scent-marking during the gestation and lactation periods (May – June) and rates of scent marking decline over time (Armitage 1999, Armitage 2003, Cross 2012). It is possible that had I looked for DEP earlier in the year, specifically during the period of peak marking, we would have detected it. Thus, there is room for future study into DEP in marmots.

In addition, Ostfeld (1985) suggests that because grass (in meadows) tends to be evenly distributed, abundant, and is highly renewable females of species that rely largely on grasses should be non territorial. As marmots forage on grass as well as forbs (Armitage 1979), it is possible that during the summer when resources are abundant neither neighbours nor strangers

are perceived as sufficiently threatening to warrant agnostic behaviour in response to scent marks.

In conclusion, I found that female yellow-bellied marmots did not appear to display traits of the DEP in response to scent marks of AGS although their lack of response to the control demonstrates that they do respond to AGS as a scent mark. The absence of agonistic response to the scents could reveal a lack of territorial behaviour in female yellow-bellied marmots but this needs further study.

## **Acknowledgements**

I would like to thank The Rocky Mountain Biological Laboratory marmot field crew of 2009 and my supervisors Frank Rosell, Daniel Blumstein and Susan Jojola for the help I received both out in the field and in the processing of the data, through time, knowledge and patience. The funding and resources made available to me by Telemark University College, Norway, were invaluable in enabling my research. Animals were trapped under permits issued annually by the Colorado Division of Wildlife.



## References

- Andreassen, H. P., Hertzberg, K., & Ims, R. A. 1998: Space-use response to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. *Ecology* **79**, 1223-1235.
- Armitage, K. B. 1975: Social behaviour and population dynamics of marmots. *Oikos* **26**, 341-354.
- Armitage, K. B. 1976: Scent marking by yellow-bellied marmots. *J. Mammal.* **57**, 583-584.
- Armitage, K. B. 1979: Food Selectivity by Yellow-Bellied Marmots. *J. Mammal.* **60**, 628-629.
- Armitage, K. B. 1981: Sociality as a life-history tactic of ground squirrels. *Oecologia* **48**, 36-49.
- Armitage, K. B. 1991: Social and population-dynamics of yellow-bellied marmots - results from long-term research. *Annual Review Ecology and Systematics* **22**, 379-407.
- Armitage, K. B. 1999: Evolution of Sociality in marmots. *J. Mammalogy* **80**, 1-10.
- Armitage, K. B. 2003: Marmots (*Marmota monax*) and allies. In: *Wild mammals of North America: biology, management, and conservation*. 2<sup>nd</sup> ed. (Feldhamer, G. A., Thomsen B. C., Chapman, J. A., eds). Johns Hopkins University Press. Baltimore, pp. 188-210.
- Armitage, K. B. 2010: Individual fitness, social behaviour and population dynamics of yellow-bellied marmots. In: *The Ecology of Place: Contributions of Place-Based Research to Ecological Understanding*. (Billick, I., Price, M. V., eds.) University of Chicago Press, Chicago, pp 209-247.
- Armitage, K. B. & Downhower, J. F. 1974: Demography of Yellow-bellied marmot populations. *Ecology* **55**, 1233-1245.
- Armitage, K. B., Van Vuren, D. H., Ozgul, A. & Oli, M. K. 2011: Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. *Ecology* **92**, 218-227.
- Bee, M. A. 2003: A test of the “dear enemy effect” in the strawberry dart-poison frog (*Dendrobates pumilio*). *Behavioural Ecology and Sociobiology* **54**, 601-610.

- Blumstein, D. T. & Armitage, K. B. 1999: Cooperative breeding in marmots. *Oikos* **84**, 369-382.
- Blumstein, D.T. & Henderson, S. J. 1996: Cheek-rubbing in golden marmots (*Marmota caudata aurea*). *J. Zool. Lond.* **238**, 113-123.
- Blumstein, D. T., Ozgul, A., Yovovich, V., Van Vuren, D. H. & Armitage, K. B. 2006: Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. *J. Zool. Lond.* **270**, 132-138.
- Blumstein, D. T. 2007: The evolution, function, and meaning of marmot alarm communication. *Advances in the study of behaviour* **37**: 371-400..
- Blumstein, D. T., Richardson, D. T., Cooley, L., Winternitz, J. & Daniel, J. C. 2008: The structure, meaning and function of yellow-bellied marmot pup screams. *Anim Behav* **76**, 1055-1064.
- Booksmythe, I., Jennions, M. D. & Backwell, P. R. Y. 2010: Investigating the ‘dear enemy’ phenomenon in the territory defence of the fiddler crab, *Uca mjoebergi*. *Anim. Behav.* **79**, 419-423.
- Bradbury, J. W. & Vehrencamp, S. L. 1998: Principles of animal communication. Sunderland, Massachusetts: Sinauer.
- Brady, K. M. & Armitage, K. B. 1999: Scent-marking in the yellow-bellied marmot (*Marmota flaviventris*). *Ethol. Ecol. and Evol.* **11**, 35-47.
- Briefer, E., Rybak, F. & Aubin, T. 2008: When to be a dear enemy: flexible acoustic relationships of neighbouring skylarks, *Alauda arvensis*. *Anim. Behav.* **76**, 1319-1325.
- Brown, J. L. 1964: The evolution of diversity in avian territorial systems. *Wilson Bulletins* **76**, 160-168.
- Cross, H. 2011: Kinship affects scent marking rates in female yellow-bellied marmots. Unpublished MSc. Supervised Study. Norway: Telemark University College.

- Davies, N. B. & Houston, A. I. 1984: Territory economics, behavioural ecology: an evolutionary approach, 2<sup>nd</sup> ed. Sunderland, Massachusetts: Sinauer. pp. 148-169
- Ferkin, M. H. 1988: The effect of familiarity on social interactions in meadow voles, *Microtus pennsylvanicus*: a laboratory and field study. *Anim. Behav.* **36**, 1816-1822.
- Frase, B. A. & Armitage, K. B. 1984: Foraging patterns of yellow-bellied marmots: role of kinship and individual variability. *Behav. Ecol. Socio.* **16**, 1-10.
- Frase, E. A. & Hoffman, R. S. 1980: *Marmota flaviventris*. *Mamm sp.* **135**, 1-8.
- Harris, M. A. & Murie, J. O. 1982: Responses to oral glands scents from different males in Columbian ground squirrels. *Anim. Behav.* **30**, 140-148.
- Hurst, J.L. & Benyon, R. J. 2010: Making progress in genetic kin recognition among vertebrates. *J. Bio.* **13**.
- Johns, D. W. & Armitage, K. B. 1979: Behavioral ecology of alpine yellow-bellied marmots. *Behav. Ecol. Socio.* **5**, 133-157.
- Jojola, S. M. 2011: Yellow-bellied marmots do not display neighbor-stranger discrimination of oral and cheek gland secretions. Unpublished PhD chapter. Norway: Telemark University College.
- Konovalov, D. A., Manning, C. & Henshaw, M. T. 2004: KINGROUP: a program for pedigree relationship reconstruction and kin group assignments using genetic markers. *Mol Ecol Notes* **4**, 779-782.
- Lachish, S. & Goldizen, A. W. 2004: Responses to neighbours and non-neighbours in the buff-banded rail (*Gallirallus philippensis*): no dear-enemy relationships. *Australian J. Zool.* **52**, 369-378.
- Lassen, B. A. & Ingdal, K. 2008: Chemical composition of perioral, orbital and anal gland secretion of yellow-bellied marmot (*Marmota flaviventris*): glandular differences and coding for sex. Unpublished Masters Thesis. Norway: Telemark University.

- Le Roux, A., Cherry, M. I. & Manser, M. B. 2008: The effects of population density and sociality on scent marking in the yellow mongoose. *J. Zool. Lond.* **275**, 33-40.
- Maher, C. R. & Lott, D. F. 1995: Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Anim. Behav.* **49**, 1581-1597.
- Murdock, H. G. & Randall, J. A. 2001: Olfactory communication and neighbor recognition in giant kangaroo rats. *Ethology* **107**, 149-160.
- Nee, J. A. 1969: Reproduction in a population of yellow-bellied marmots (*Marmota flaviventris*). *J. Mammal.* **50**, 756-765.
- Olsen, L.E. & Blumstein, D. T. 2010: Applying the coalitionary-traits metric: sociality without cooperation in male yellow-bellied marmots. *Behav. Ecol.* **21**, 957- 965.
- Ostfeld, R. S. 1985: Limiting resources and territoriality in microtine rodents. *The American Naturalist* **126**, 1-15.
- Palphramand, K. L. & White, P. C. L. 2007; Badgers, *Meles meles*, discriminate between neighbour, alien and self scent. *Anim. Behav.* **74**, 429-436.
- Queller, D. C. & Goodnight, K. F. 1989: Estimating relatedness using genetic markers. *Evolution* **43**, 258-275.
- Randall, J. A., Hekkala, E. R., Cooper, L. D. & Barfield, J. 2002: Familiarity and flexible mating strategies of a solitary rodent, *Dipodomys ingens*. *Anim Behav.* **64**, 11-21.
- Rausch, R. L. & Bridgens, J. G. 1989: Structure and function of sudoriferous facial glands in nearctic marmots, *Marmota spp.* (Rodentia: sciuridae). *Zool. Anz.* **223**, 265-282.
- Raynaud, J. & Dobson, S. F. 2011: Scent communication by female Columbian ground squirrels, *Urocitellus columbianus*. *Behav. Ecol. Socio.* **65**, 351-358.
- Rosell, F., G. Johansen & Parker, H. 2000: Eurasian beavers (*Castor fiber*) behavioural response to simulated territorial intruders. *Canadian J. Zool.* **78**, 931-935.
- Rosell, F. & Bjørkøyli, T. 2002: A test of the dear enemy phenomenon in the Eurasian beaver. *Anim. Behav.* **63**, 1073-078.

- Rosell, F., Gundersen, G. & Galliard, J. F. 2008: Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defence. *Behav. Ecol. Socio.* **62**, 1559-1568.
- Rosell, F., Jojola, S. M., Ingdal, K., Lassen, B. A., Swenson, J. E., Arnemo, J. M. & Zedrosser, A. 2011: Brown bears possess anal sacs and secretions may code for sex. *J. Zool. Lond.* **283**, 143-152.
- Siegel, S. & Castellan, N. J. Jr. 1988: Nonparametric statistics for the behavioural sciences. 2nd ed. New York, USA: McGraw-Hill.
- Sokal, R. R. & Rohlf, F. J. 1995: Biometry. The principles and practice of statistics in biological research. 3rd ed. New York, USA: W.H. Freeman and Co.
- Sun, L. & Müller-Schwarze, D. 1999: Chemical signals in beaver – one species, two secretions, many functions? In: Advances in chemical signals in vertebrates VIII (Johnston, R. E., Muller-Schwarze, D. & Sorenson, P.W. eds). Kluwer Academic/Plenum Publishers. New York, USA, pp. 281-288.
- Tegt, J. L. 2004: Coyote (*Canis latrans*) recognition of relatedness using odor cues in faeces, urine, serum, and anal sac secretions. Thesis. Utah, USA: Utah State University, Dept. of Forest, Range and Wildlife Sciences.
- Temeles, E.J. 1994. The role of neighbours in territorial systems: when are they “dear enemies”? *Anim. Behav.* **47**, 339-350.
- Wey, T. W. & Blumstein, D. T. 2010: Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Anim. Behav.* **79**, 1343-1352.
- Yuan, H., Liu, D., Sun, L., Wei, R., Zhang, G. & Sun, R. 2004: Anogenital gland secretions code for sex and age in the giant panda, *Ailuropoda melanoleuca*. *Canadian J. Zool.* **82**, 1596-1604.
- Zenuto, R. R. 2010: Dear enemy relationships in the subterranean rodent *Ctenomys talarum*: the role of memory of familiar odours. *Anim. Behav.* **79**, 1247-1255.

Zhang, J-X., Ni, J., Ren, X-J., Sun, L., Zhang, Z-B., Wang ,Z-W. 2003: Possible coding for recognition of sexes, individuals and species in anal gland volatiles of *Mustela evermanni* and *M. sibirica*. *Chemical Senses* **28**, 381-388.

## **Figure Legend**

Figure 1. Typical presentation of scents and control on the tiles

Figure 2. Total time responders spent sniffing the neighbour scent and relatedness between responders and neighbours.

Figure 1





**Figure 2**

