# Do marmots display a 'dear enemy phenomenon' in response to anal gland secretions?

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## 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 strangers. We tested philopatric female yellow-bellied marmots (*Marmota flaviventris*) for the presence of DEP. We hypothesized that dominant females discriminated between the anal gland secretion (AGS) from female neighbours and strangers, and predicted that they would respond more agonistically (as reflected by the duration of both sniffing and physical behaviour) towards AGS from strangers than neighbours. We also hypothesized that female marmots would respond differently to kin and non-kin female neighbours, and predicted a reduced agonistic response to related individuals. Direct observations of resident marmot's 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. We conclude that, although female yellow-bellied marmots detect AGS, they do not seem to discriminate between neighbours and strangers via AGS scent marks. Other secretions may be used in territorial identification.

## Introduction

A territory is an area or part of a home range defended by an individual or a group (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 may include the time spent defending an area, an increased risk of predation associated with territorial advertisements (acoustic, olfactory or visual signalling), and increased risks of injury from physical encounters (Bradbury & Vehrencamp, 1998). Once territorial boundaries have been established, residents may possess information regarding neighbours and therefore treat them as less of a threat, resulting in reduced defence costs. However, interactions with strangers (non-territorial floaters) are unpredictable as they may be seeking a territory and therefore an aggressive response might be worth the cost of time and energy (Fisher, 1954; Temeles, 1994). This difference of response intensity towards neighbours and strangers has been termed the 'dear enemy phenomenon' (DEP) as well as the familiarity hypothesis (Fisher, 1954; Randall et al., 2002; Briefer, Rybak & Aubin, 2008; Booksmythe, Jennions &

Backwell, 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, Gundersen & Galliard, 2008).

The presence of DEP tends to depend on the type of territory being defended; it has been frequently found to occur in multi-purpose foraging territories, but rarely in feeding territories (Temeles, 1994). The stability of both the group and the territory may be a key driver for the presence of DEP because 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 and strangers (Bee, 2003; Lachish & Goldizen, 2004; Jordan et al., 2011).

Mammals have a variety of scent-producing glands, and the glandular secretions potentially involved in DEP have been studied in Columbian ground squirrels (*Urocitellus columbianus*) (Harris & Murie, 1982; Raynaud & Dobson, 2011), woodchucks (*Marmota monax*; Meier, 1991) and Eurasian beavers (*Castor fiber*; Rosell & Bjørkøyli, 2002). In many species, the anal/anogenital gland secretion (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 yellow mongoose (*Cynictis penicillata*) and other herpestids are used to produce long-lasting marks (Le Roux, Cherry & Manser, 2008). Rosell & Bjørkøyli (2002) found that Eurasian beavers displayed the DEP when presented with AGS from a neighbour and a stranger; however, to our knowledge, no other studies have focused specifically on AGS in relation to DEP in free-ranging rodents.

In addition to neighbour familiarity, kinship may also influence the response to an olfactory signal (Hurst & Benyon, 2010). 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 (Maeto, 2002; Hurst & Benyon, 2010). This has been demonstrated in coyotes (*Canis latrans*; Tegt, 2004), Belding's ground squirrels (Maeto, 2002), Columbian ground squirrels (Raynaud & Dobson, 2011), root voles (Rosell *et al.*, 2008), North American beaver (*C. canadenesis*; Sun & Müller-Schwarze, 1999) and ring-tailed lemurs (*Lemur catta*; Hurst & Benyon, 2010). However, only Raynaud & Dobson (2011) have considered kinship between females when investigating DEP, although in philopatric societies, neighbours may often be close kin and therefore may pose less of a threat than truly unrelated strangers (Ferkin, 1988). Genetic relatedness therefore must 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 (*M. flaviventris*) are diurnal, semi-fossorial sciurid rodents (Frase & Hoffman, 1980; Blumstein, 2007) that are active for 4 to 5 months annually (Armitage, 2003). Marmots dig numerous burrows that serve as refuges within their 0.015 $km^2$ home ranges (Armitage, 1975) and typically occupy 'multipurpose/breeding' home ranges. Marmots mate just before or just after emerging from their hibernation burrows. Pups are born a month after emergence (Armitage & Downhower, 1974), and pups are weaned at 25–35 days (Nee, 1969; Armitage, 1982). Marmots are a harem-polygamous social species and form matrilines, 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 as 2-year-olds (Blumstein & Armitage, 1999). Males occasionally control more than one matriline (Armitage *et al.*, 2011; Olson *et al.*, 2012), and therefore, it is expected that some neighbours are related by sharing a father. Resident adult females should respond aggressively towards intrusions by strange females because their reproductive success is increased by ensuring that 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).

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 (Rosell *et al.* unpubl. data). To date, most scent related behavioural studies in marmots have focused on facial rubbing behaviour (Armitage, 1976; Brady & Armitage, 1999; Olsen & Blumstein, 2010) and no behavioural studies have focused on AGS. Therefore, the function of AGS in marmots is still unknown (Armitage, 1975; Rausch & Bridgens, 1989).

In this study we investigated the use of AGS as an olfactory cue to aid in the assessment of the threat imposed by intruding female yellow-bellied marmots based on their status as a neighbour or a stranger. We hypothesised that dominant female yellow-bellied marmots would discriminate between the AGS from female neighbours and strangers, and predicted that they would respond more cautiously (longer sniffing durations) and agonistically (physically) towards AGS from strangers than neighbours. If so, marmots would be inferred to display DEP. We also hypothesised that female yellow-bellied marmots would respond differently to kin and non-kin female neighbours, and predicted that they would respond more agonistically to non-kin individuals than to kin.

## Methods and materials

### 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). The subjects studied were from five different colonies ranging in elevation from 2867 to 3008 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 ± 5.2 (SD) individuals (Wey & Blumstein, 2010).

### Scent donors and collection of scent

Marmots were live-trapped in Tomahawk traps (Tomahawk, WI, USA) baited with Omolene horse feed (Purina® 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.*, 2008a). 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.*, 2008a; Olsen & Blumstein, 2010). Trapping was carried out every 2 weeks for individual identification and sampling purposes. Sex was determined by measuring the distance between the anus and the genital pore, and the reproductive state varied from 3 to 6 (3, nipples present; 4, nipples prominent; and 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).

We used 30 dominant adult females, weighing an average (SD) of 2800 ± 601 g as scent donors. We wore latex gloves when collecting samples to prevent contamination from human odour. Prior to collecting the scent samples, we cleaned the area around the papillae using an alcohol pad to remove any faeces. The papillae of the anal gland were then pressed outward, and the AGS squeezed out and collected with a sterile, wooden-stemmed cotton swab (Express Medical Supply, Inc., Fenton, MO, USA). We placed the cotton swabs with visible secretion directly into 30 mL glass vials with Teflon-lined caps (Lab Safety Supply, Janesville, WI, USA), which we stored on ice in the field, and placed in a freezer at –20°C within 3 h. We transported the samples on ice to the field for experiments.

The vast majority of marmots were 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, we used stranger and neighbour females with similar age (< 2 years difference) and time of scent collection (< 2 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 and with whom focal subjects would have had no prior exposure.

## Kinship

The relationships between responders and female scent donors were calculated using 12 previously developed microsatellite loci and the relatedness estimator of Queller & Goodnight (1989), using the program KINGROUP 2.0 (Konovalov, Manning & Henshaw, 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 h, $n = 10$) or afternoon (between 14:00 and 18:00 h, $n = 5$), 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 neighbour's AGS, and one with stranger's AGS. For each observation, a swab was placed on one of three sealed and impermeable tiles measuring 10 cm$^2$ placed 2 cm apart to ensure the marmot could differentiate between each scent. The tiles were separated to prevent a subject interacting with one title from stepping on or otherwise inadvertently manipulating another swab. The tiles were placed 1.0 m from the main burrow entrance where marmots could easily smell them (Blumstein & Henderson, 1996).

We did not know whether marmots would respond to an unscented cotton swab, so we included a blank, as a control to assess whether marmots showed interest in a purely novel smell (the cotton swab) or object within their territory (Blum-

stein, Barrow & Luterra, 2008b). Olfactory stimuli were randomly assigned to each tile to control for order effects. We wore disposable latex gloves while manipulating both the tiles and swabs to avoid contamination by human odour. We used alcohol pads 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. Simultaneous choice tests are powerful ways to test discrimination and our experimental design was based on previous studies by Brady & Armitage (1999) and Blumstein & Henderson (1996) that successfully elicited different olfactory responses between treatments in yellow-bellied marmots.

Observers were blind to the treatments during experiments. Given our extensive study of these marmots, we assumed that they were not affected by human disturbance during experiment installation. Indeed, we observed them retreating into their burrows, but they typically re-emerged within minutes. We used 10 × 42 binoculars and/or 15-45× spotting scopes to watch the marmot's 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 4-h period, the experiment was repeated, using fresh scents, at the same site another day. We scared away juvenile or male marmots that approached the scents, and marmots that approached when another was already within 0.5 m of the tiles. After the marmots were scared off, we reset the experiment and waited for a target female to again approach the scents. Responses were recorded by using a video camera (Sony® digital video handycam, model no. DCR.SR35E, Komplett.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) the duration of time each marmot spent physically responding to the swabs (pawing, and/or biting); and (3) the frequency of scent marking the swabs (bite or rub). Interpreting physical behaviour at a stimulus as an indication of an agonistic response in 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 meet assumptions of distribution or homogeneity of variance for parametric analysis (Sokal & Rohlf, 1995). Because we could not transform them to meet distributional assumptions, we used non-parametric statistics (Siegel & Castellan, 1988). We used a Freidman's test for three related samples to identify differences in response duration by resident marmots to the odours of the neighbour, stranger and control. To further investigate the differences in duration between the cotton swabs, we 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). Finally, we calculated Cohen's *d*-scores as a measure of the effect size of the main comparison.

## Results

Females sniffed for different amounts of time in response to the odours of neighbours, strangers and control stimuli (Friedman's test: $F = 0.003$, $P < 0.001$, Fig. 1). 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 other 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, and ranged from 0 to 0.55 for neighbours and responders. We found that the duration of time a female spent sniffing the AGS did not increase with relatedness to a neighbour ($r_s = 0.001$, $P = 1.000$; Fig. 2).

The effects sizes of the dataset show that the effect of the treatment is large (compared to the control) (neighbour–control = Cohen's *d*: 0.956, stranger–control = Cohen's *d*: 1.544) and we had sufficient sample sizes to detect these large effects. The effect of the neighbour stranger comparison is very small (Cohen's *d*: 0.127) and we would need a much larger sample size to detect this difference. Regardless, the effect of being exposed to a neighbour or a stranger is
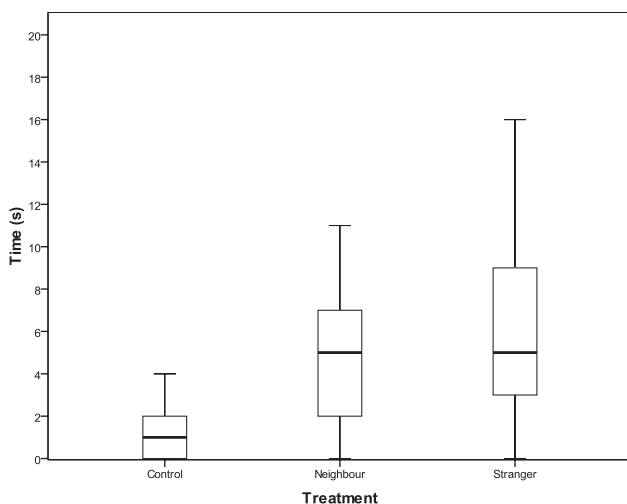
relatively small and likely to be minimally important to the marmots.

## Discussion

This study examined the relationships between territorial neighbours by investigating whether female yellow-bellied marmots exhibit a dear enemy response to anogenital scent marks. Our 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 supported. Therefore, our findings do not support the DEP of increased agonistic behaviour towards strangers, as has been reported in many other species (Harris & Murie, 1982; Ferkin, 1988; Murdock & Randall, 2001; Palphramand & White, 2007; Rosell *et al.*, 2008). However, we 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 potentially novel objects within their territory (Blumstein *et al.*, 2008b).

Our results suggest that DEP is not always displayed by female rodents that are polygamous, form matrilines and have home range overlap without strict territory borders (Andreassen, Hertzberg & Ims, 1998; Rosell *et al.*, 2008). For example, Rosell *et al.* (2008) found that female root voles did not display DEP when dyadic arena trials were conducted between strangers and neighbours of the same sex. However, these behavioural 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 female marmots.
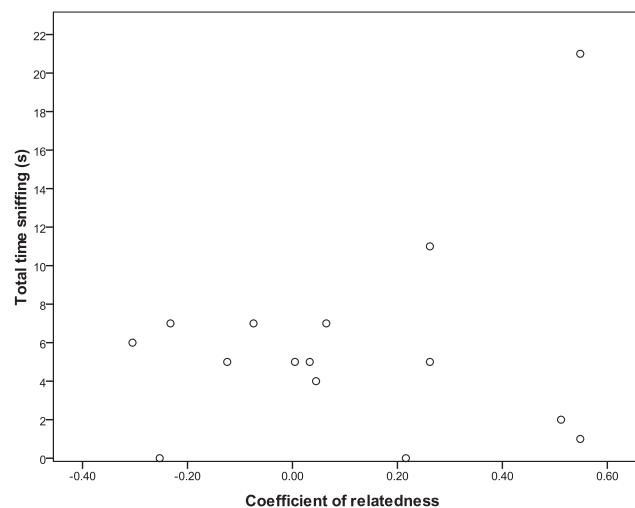


**Figure 1** Response length (s), of female yellow-bellied marmots to AGS from the neighbour, stranger and control. The line in the boxplot indicates the median; the lower and upper ends indicates the 25% and 75% values, respectively; and the two whiskers indicate the distance from the end of the boxplot to the largest and smallest observed values.



**Figure 2** Total time yellow-bellied marmots spent sniffing the AGS of the neighbour and the relatedness between responders and neighbours. KINGROUP 2.0 produces relatedness estimators, and therefore, some marmots have a relatedness estimated to be less than 0.

Raynaud & Dobson (2011) carried out a study using olfactory secretions with the philopatric female Columbian ground squirrels. They found support for DEP because squirrels sniffed stranger's perioral secretions longer than neighbour'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 our study, all females sniffed the AGS but only one displayed any immediate territorial marking behaviour in response to them. Interestingly, the one female that did show agonistic behaviour, vigorously overmarked 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 objects (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 our experiments were conducted after pups were weaned and had emerged from their natal burrows. 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). It is possible that had we looked for DEP earlier in the year, specifically during the period of peak marking, we might have detected it. However, females are defensive following pup emergence and it is also likely that territorial behaviour would be maintained to reduce the risk of infanticide by neighbouring females.

In addition, Ostfeld (1985) suggested that because herbaceous vegetation (in meadows) tends to be evenly distributed, abundant and is highly renewable, females of species that rely largely on herbaceous vegetation should be non-territorial. Marmots are generalist herbivores (Frase & Armitage, 1984), and it is possible that during the summer, when resources are abundant, neither neighbours nor strangers are perceived as sufficiently threatening to warrant agonistic behaviour in response to scent marks.

In conclusion, we found that female yellow-bellied marmots did not appear to have a 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 potentially biologically important scent mark. The absence of agonistic responses to the scents could reveal a lack of territorial behaviour in female yellow-bellied marmots but this needs further study.

## Acknowledgements

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