ethology international journal of behavioural biology

Ethology

Sex Discrimination via Anal Gland Secretion in a Territorial Monogamous Mammal

Hannah B. Cross*, Andreas Zedrosser*†, Owen Nevin‡ & Frank Rosell*

* Department of Environmental and Health Studies, Faculty of Arts and Sciences, Telemark University College, Bø i Telemark, Norway
† Department of Integrative Biology, Institute of Wildlife Biology and Game Management, University of Natural Resources and Applied Life Sciences, Vienna, Vienna, Austria
‡ CQ University Australia, Bryan Jordan Drive, Gladstone, Qld, Australia

Correspondence
Frank Rosell, Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark University College, 3800 Bø i Telemark, Norway.
E-mail: frank.rosell@hit.no

Received: December 2, 2013
Initial acceptance: March 1, 2014
Final acceptance: June 11, 2014
(M. Manser)

doi: 10.1111/eth.12277

Keywords: anal gland secretion, beavers, *Castor fiber*, mammals, mated pairs, monogamy, scent marking, territoriality

The copyright line for this article was changed on 6 October 2014 after original online publication

Abstract

Monogamy in mammals is relatively unusual, only occurring in 3–5% and to an even lesser degree in rodents. Monogamy exists in two forms, facultative which evolved due to female dispersion and obligate when male care is needed for offspring survival. Most monogamous rodents use scent marking as a form of territorial defence to obtain exclusive access to vital resources. Intrasexual competition occurs in many species to maintain pair bonds and also to signal presence within a territory. In this study, we tested the hypothesis that resident obligate monogamous Eurasian beaver (*Castor fiber*) can discriminate between the sexes when investigating anal gland secretions (AGS) from unknown (stranger) mated pairs. We predicted that, due to intrasexual competition, dominant territorial male and female beavers will display a stronger response to AGS of same-sex conspecifics. Territorial intrusion by mated pair strangers was simulated by the formation of experimental scent mounds (ESM) with AGS. Our results showed that both sexes (1) displayed a stronger response to the male AGS in sniffing duration, (2) physically responded for longer durations towards male AGS and (3) overmarked male AGS more frequently. We infer that obligate monogamous mammals can determine the sexual identity of intruding conspecifics of a mated pair via AGS and that intruding males may pose more of a threat to resident males via intrasexual competition and resident females due to the long-term costs, such as infanticide and abortion, of a new dominant male.

Introduction

Monogamy generally implies that a mated pair remains together throughout several breeding seasons (Lack 1968; Kleiman 1977). Monogamy only occurs in 3–5% of all mammals and to an even lesser degree in rodents (Kleiman 1977; Dunbar 1984). Monogamy exists in two forms, facultative which evolved due to female dispersion (Komers & Brotherton 1997) and obligate when male care is needed for offspring survival (Brotherton & Manser 1997). Pair bonds are established to enable sufficient resources to be acquired for breeding and survival (Wickler & Seibt 1983; Gubernick & Teferi 2000), and in most monogamous pairings, at least one, if not both sexes, defend a territory. Territorial codefence is exercised by monogamous mammals such as Kirk's dik–dik (*Madoqua kirkii*) (Brotherton et al. 1997), Malagasy giant jumping rat *(Hypogeomys antimena)* (Sommer 2005) and California mouse (*Peromyscus californicus)* (Gubernick & Teferi 2000). Many species maintain and defend territories to obtain exclusive access to vital resources such as mates, food and nest sites, which are not always mutually exclusive and can often be multipurpose breeding territories (Temeles 1994; Wyatt 2014).

Glandular secretions are often employed as olfactory signals, that is, scent marks, to define territories and their ownership (Gosling 1982; Sillero-Zubiri & Macdonald 1998; Roberts 2007). Mammalian scent marking is usually carried out by both sexes (Gosling & Roberts 2001; Roberts 2007), for example spotted hyena (*Crocuta crocuta*) (Burgener et al. 2009), and several types of glands are used for these purposes. Anal gland secretion (AGS) in the yellow mongoose (*Cynictis penicillata*) and other herpestids function as long lasting marks (Le Roux et al. 2008).

Sexual dimorphism in monogamous mammals with territorial codefence exists due to sex-specific roles (Jannett 1986) and has been identified in the compounds of some mammalian olfactory secretions including AGS (Jordan et al. 2011). In some species, for example the monogamous aardwolf (*Proteles cristatus*), both sexes deposit AGS as a form of territorial defence; however, males often scent mark more frequently than females (Thiessen & Rice 1976; Wyatt 2003; Skinner & Chimimba 2005; Müller-Schwarze 2006). In monogamous codefending mammals, individuals are expected to display more agonistic responses to same-sex conspecifics due to strong intrasexual competition over resources such as food, shelter and mates (Boydston et al. 2001; Gosling & Roberts 2001; Cant et al. 2002).

Little information has been gained about the duration of sniffing and/or physical destruction of scent marks with regard to intrusions of same-sex conspecifics, and therefore, the response of individuals to intruders in this manner is unknown. However, a common response to encountered scent marks of same-sex conspecifics is ‘overmarking’: when an individual places its scent mark directly on top of a previous scent mark deposited by a different individual (Johnston 2008; Jordan et al. 2011; Wyatt 2014), which is often considered a form of intrasexual competition (Rich & Hurst 1999; Müller & Manser 2008; Jordan et al. 2011; Clapham et al. 2012). Ferkin et al. (2004) and Woodward et al. (2000) suggest that in monogamous species, individuals should overmark same-sex intruders more often than opposite-sex intruders to maintain pair bonds and also to signal their presence within the territory. This is supported by Ferkin and Pierce (2007) who suggest that although scent marking is a costly activity, individuals should overmark same-sex conspecifics to avoid competition and eavesdropping. Little is known about the response of individuals of monogamous mated pairs after encounters with scent marks from same-sex conspecifics especially in wild populations (but see Woodward et al. 2000).

The obligate monogamous Eurasian beaver (*Castor fiber*) lives in family units consisting of a dominant adult pair with current year kits, yearlings and sometimes subadults (Wilsson 1971; Campbell et al. 2005). Copulations occur around late January to early February, at a time when environmental constraints such as, cold temperatures, snow and ice often reduce mobility (Wilsson 1971). Kits are born mid-May (Parker & Rosell 2001), weaned at approx. 1–2 mo and emerge from the lodge during July (Wilsson 1971). Beavers usually disperse as 2-yr-olds to the nearest available site, although delayed dispersal is common in high-density populations (Hartman 1997). Beavers are not sexually size-dimorphic (Osborn 1955; Muller-Schwarze 2011) but do display sexual dimorphism in their parental care. Males primarily invest their time through indirect care via construction behaviours and territorial defence, whilst the females provide the direct care such as providing food and huddling with the young (Nolet & Rosell 1994; Woodard 1994; Sharpe & Rosell 2003). Beavers are highly territorial, and both sexes and all age classes (>5 mo) participate in territory defence, with the dominant pair being the main contributors (Wilsson 1971; Rosell & Thomsen 2006). Aggressive encounters are common, bite wounds from conspecifics are a common cause of death and often occur in May when the subadults are dispersing and new territories are likely to be established (Nolet & Rosell 1994). Beavers settle in a new territory or take over a territory both as a pair and individually, when an individual holds a territory it is likely to be shortly joined by a new mate to form a pair. Intruding beavers usually establish themselves in previously occupied territories when one or both residents have died, although mated pairs have been observed to evict territory owners (Nolet & Rosell 1994; F. Rosell, unpubl. data).

Scent marking peaks in spring (Apr. and May) (Rosell & Nolet 1997; Rosell et al. 1998), and males scent mark more frequently than females, particularly in summer (Jun.and Jul.) when females are lactating (Rosell & Thomsen 2006). Adults of both sexes remove scent mounds and overmark where conspecifics, other than the family group, have marked, but it is unknown whether individuals remove scent mounds and/or overmark same sex and/or opposite sex (Rosell et al. 2000; Rosell & Bjørkøyli 2002; Tinnesand et al. 2013).

Both Eurasian and North American (*Castor canadensis*) beavers deposit scent in the form of castoreum or AGS. Castoreum is produced in the castor sacs; urine is mixed with the contents of the castor sac resulting in a castor fluid, and AGS has sebaceous, wax esters and fatty acids that form the major constituents (Grønneberg 1979; Grønneberg & Lie 1984; Sun 1996). These secretions have been shown to provide information regarding species (Rosell 2002) and subspecies identification (Rosell & Steifetten 2004), but only AGS enables beavers to discriminate between sex, individuals and kin (Grønneberg 1979; Sun 1996; Sun & Müller-Schwarze 1997, 1998a; Rosell & Sundsdal 2001; Rosell 2003).

This study investigates the potential for sex discrimination in anal gland secretion in the Eurasian beaver. By presenting scent marks, we simulated simultaneous territorial intrusions by an established mated pair in a free living population of Eurasian beavers. We hypothesised that dominant monogamous territorial males and females can discriminate between the sexes via the odorant signal of AGS. We predicted that, due to intrasexual competition, dominant monogamous territorial males and females will exhibit stronger responses to the scent of same-sex conspecifics via response durations (sniffing and physical i.e. pawing behaviour with front and/or back feet) and over-marking frequencies.

Materials and Methods

Study Area and Study Animals

The study was conducted between 30th May–26th Jul. 2008 and 19th Apr.–19th Jun. 2010 on the Straumen, Saua and Gvarv rivers in Telemark County, south-eastern Norway (59°23 , 09°09E). The mean monthly temperature is below 0°C between Nov. and Mar. All rivers contain lakes along part of their length, resulting in only limited fluctuations in water temperature along the main river channels and thus reduced ice cover in winter. All three rivers form part of the catchment of Lake Nordsjø (Campbell et al. 2012). The beaver population in the study area is near carrying capacity (Parker & Rosell 2001; Campbell et al. 2005, 2012), all territories are adjacent to each other with no unoccupied stretches of river (Herr & Rosell 2004) and hunting pressure is low. Beavers in the study area are part of a long-term study that began in 1998, and we were thus able to use trapping records to determine the dominant adults of each sex (Sharpe & Rosell 2003; Campbell et al. 2012, 2013).

Scent Donors and Collection of Scent Samples

Beavers were trapped at night using landing nets from a boat (Rosell & Hovde 2001). All live trapping was under licence from the Norwegian Experimental Animal Board and the Norwegian Directorate for Nature Management and met the guidelines approved by the American Society of Mammologists (Gannon & Sikes 2007). AGS samples were collected from 44 live-trapped beavers (22 mated pairs, *X*weight ± SD = 20.3 ± 1.97 kg, range 18.0–25.5 kg, age 3–12 yr). Before collecting AGS samples, the tail was lifted and the rectum emptied. The cloaca area was then rinsed with distilled water. The papillae of the anal gland were pushed out separately and the AGS squeezed out. Live-trapped beavers were sex-determined by the colour and viscosity of their AGS (Rosell & Sun 1999). Pregnant/lactating females were determined by the size of the nipples >0.5 cm and kits seen/trapped in the territory that year (Campbell et al. 2012, 2013). No beaver was handled for more than 20 min. AGS samples were stored in glass vials with Teflon lids (La-Pha-Pack®) and placed in cool bags surrounded by ice blocks to maintain them at a low temperature during transportation to or from the laboratory. AGS samples were stored in a freezer at −20°C until used in an experiment. Freezing and thawing does not affect the composition or smell of the AGS (Sun 1996).

Experimental Design

Samples collected from mated pairs from other watersheds located >15 km away from the experimental sites were designated as 'strangers' (Sun et al. 2000; Rosell & Bjørkøyli 2002). Mated pairs were used as donors in this study to ensure an environmental similarity of the two scents. For all 22 experiments, stranger mated pairs with similar characteristics to the territory holders were selected, that is, animals of similar age (<2 yr), weight (<3 kg difference) and similar season of scent collection (<2 mo difference). AGS samples of 0.25 g were used for the experiments (Rosell & Bjørkøyli 2002). The selected AGS was placed in a plastic cap (2.5 cm diameter and 1.5 cm high) placed on an experimental scent mound (ESM), as this was deemed to be a suitable receptacle for use in the field, and the small circumference of the cap reduces the evaporation surface area (Schulte 1998; Rosell & Bjørkøyli 2002). Beavers do not respond to untreated ESM; therefore, none were included as a control (Schulte et al. 1995; Rosell et al. 2000).

The ESM were established 30–60 min (17:00–18:00 h) before the anticipated emergence of any beaver family member from the lodge (Rosell & Bjørkøyli 2002). All experiments were carried out within 50 m of the lodge of a territory, and ESM were located where beavers could smell and readily access them from the water (Rosell & Bjørkøyli 2002). For each experiment, two ESM were constructed 30 cm apart and within 50 cm of the water's edge (Fig. 1).

Fig. 1: Experimental setup with ESM containing male and female AGS and a responding dominant resident.

The 30-cm separation distance between ESM enabled beavers to differentiate between the scents and provided the opportunity of responding initially to one ESM then separately to the other. It also prevented the destruction of the second ESM during response to the first (Sun & Müller-Schwarze 1997; Rosell & Bjørkøyli 2002). Simultaneous presentation controls for temporal variation in motivation of the resident and thus provides a more sensitive test of discriminatory abilities (Sun & Müller-Schwarze 1997; Rosell & Bjørkøyli 2002; White et al. 2003).

Disposable gloves were worn during construction of ESM to avoid contamination with human odour. ESM were formed by scraping mud from the bottom of the river or the riverbank to create a low dome shape. Each ESM was approx. 15 cm wide and 10 cm high (Rosell & Bjørkøyli 2002). Both scent mounds within a pair were approximately equal in size and shape and constructed from the same material. Any other scent mounds found in the locality were destroyed prior to construction of the ESM. The bottle cap containing either male or female AGS from the stranger mated pair was placed in the centre of the ESM, the top of the cap even with the surface of the mound. During scent preparation, a coin toss was used to randomly determine the position of the male/female scent at each ESM site, but observers were blind to the scents to avoid bias during experiments and analysis. Each observation was terminated after a response was recorded or when fading daylight prevented further observations. At termination, the caps and scents were removed, and the mounds were destroyed. If no response was observed, the experiment was repeated on another night, using fresh scents from the same donor beaver.

Response Measures

Responses were recorded using a tripod mounted video camera (Sony DCR-SR35E) set to record continuously. The camera was placed approx. 10 m directly behind the experimental site and was always handled with latex gloves to avoid human odour. Video recordings were analysed manually using Microsoft Windows Media Player (Microsoft®). Three response patterns were classified: (1) sniffing, defined as when a beaver was within 5 cm of the mound, facing the mound with its nose; (2) physical, defined as when a beaver used its front and back feet to change the shape of the mound; and (3) overmarking, defined as when a beaver was standing on a mound in an overmarking position with the papillae visible (Rosell & Bjørkøyli 2002; Rosell & Sanda 2006).

Sniffing duration was recorded in seconds as a measure of time required to identify scents, as well as a sign of level of interest. Physical response duration was measured in seconds to indicate strength of any triggered agonistic behavioural response, that is, the longer the response, the more agonistic it was considered to be (Sun & Müller-Schwarze 1997; Rosell & Bjørkøyli 2002). Interpreting physical behaviour at a stimulus as an indication of an agonistic response in Eurasian beaver can be justified based on previous experimental and observational evidence (Rosell et al. 2000; Rosell & Bjørkøyli 2002). Overmarking duration was not recorded as overmarking lasts less than a second. Therefore, only the presence or absence of overmarking was recorded. Only the response of the first beaver and only responses from the dominant male or female of the territory were included in the analysis (Sun & Müller-Schwarze 1997). An experiment was terminated when the beaver re-entered the water or was >5 m from the ESM.

Statistical Analysis

We evaluated the duration of the sniffing response and the physical response of dominant territorial beavers towards AGS from intruding beavers with generalised linear mixed effects models (GLMM) with a Poisson error structure (Zuur et al. 2009), which are commonly used to analyse such experiments (Palphramand & White 2007; Tinnesand et al. 2013). The model evaluating the sniffing duration (in seconds) of the dominant territorial beaver included the sex of both the donor beaver and responding dominant beaver (as a factor with the levels male or female). Age and body mass were not included in the analysis as they had been controlled for in the experimental design.

A physical reaction seemed to be dependent upon the presence of a preceding sniffing reaction; no physical responses were observed without a prior sniffing response. The model evaluating the duration (in seconds) of a physical response of a resident dominant beaver therefore included the sex of the donor and responder as well as the duration (in seconds) of a sniffing response preceding a physical response.

We used a GLMM with a binomial error structure to evaluate the probability for overmarking. As a response variable, we used the occurrence of an intruding beaver overmarking an AGS sample or not (0 = no overmarking, 1 = overmarking), and as explanatory variables, we included the sex of both the donor beaver and responding dominant beaver (as a factor with the levels male or female). In addition, we controlled for the absence or presence of a physical reaction prior to overmarking.

Due to the pairwise presentation of the AGS samples to dominant territorials, we nested the random effects of the dominant territorial's identity within the random effects of the experimental identity in all explanatory models (Bates 2010). We used a backward procedure to select the best models, based on p-values with a significance level of $\alpha = 0.05$, starting with a full model of all covariates and relevant second-order interactions (Crawley 2007). The function lmer in the 'lme4' package in R 2.14.20 (www.R-project.org) was used to fit GLMM with Poisson distribution, and the 'nlme' package with the function glmmPQL was used to fit GLMM with Poisson distribution corrected for overdispersion (Zuur et al. 2009).

We used chi-square tests to analyse whether dominant resident beavers reacted first to AGS of male or female intruders. The statistical software R 2.14.20 (www.R-project.org) was used in all analyses.

Results

We recorded responses of 22 dominant territorial beavers (13 males, nine females). Dominant resident beavers of both sexes responded significantly more often first to the AGS of a male intruding beaver than to the AGS of a female intruding beaver (chi-square test, $N_{\text{1st response to male}} = 19$, $N_{\text{1st response to female}} = 3$, $\chi^2 = 5.133$, df = 1, p = 0.024).

The results of a GLMM analysing the sniffing response showed that resident dominant beavers spent significantly more time sniffing AGS from males than females of an intruding mated pair (Table 1; Fig. 2). The sex of the responding dominant beaver was not significant ($\beta = -0.157$, p = 0.578) and therefore removed from the analysis.

Table 1: Generalised linear mixed models explaining A) the time of the sniffing response (in seconds) of resident dominant beavers of both sexes to an intruding mated pair of beavers.; B) the time of the physical response (in seconds) of resident dominant beavers of both sexes to an intruding mated pair of beavers.; C) the probability of overmarking of resident dominant beavers of both sexes to an intruding mated pair of beavers. Number of observations = 44 and number of trials = 22. β = estimated coefficient, SE = standard error, *z*/*t* = *z*-value for models A and C and *t*-value for model B

Variables	β	SE	*z*/*t*	p-Value
A) Duration of sniffing response				
Intercept	2.593	0.145	17.821	<0.001
Intruding mated pair			4.648	<0.001
Female	0	0		
Male	0.324	0.070		
B) Duration of physical response				
Intercept	0.573	0.478	1.173	0.254
Intruding mated pair			12.415	<0.001
Female	0	0		
Male	2.111	0.517		
C) Probability of overmarking				
Intercept	−4.579	1.613	−2.839	0.005
Physical duration	0.256	0.098	2.616	0.009
Intruding mated pair			2.226	0.026
Female	0	0		
Male	3.101	1.393		

The results of a GLMM analysing the physical response showed that resident dominant beavers spent significantly more time physically responding to the AGS from males than females of an intruding mated pair (Table 1; Fig. 2). The sex of the resident dominant beaver ($\beta = 0.355$, p = 0.317) and the length of the preceding sniffing response ($\beta = 0.003$, p = 0.774) were not significant and therefore removed from the analysis.

The probability of overmarking significantly increased with the duration of the preceding physical reaction towards the AGS of an intruding mated pair, and the AGS of the intruding male was overmarked significantly more often than the AGS of the intruding female (Table 1). Of the 22 donor females, 10 were pregnant/lactating, and seven of the nine responding females were pregnant/lactating. A *post-hoc* test with a chi-Square analysis indicated that it was marginally significant for pregnant dominant females to overmark AGS of an intruding male more often than non-pregnant dominant females (chi-square test, $\chi^2 = 2.933$, df = 1, p = 0.087). Due to a small sample size, no tests were carried out on the durations of sniffing and physical responses.

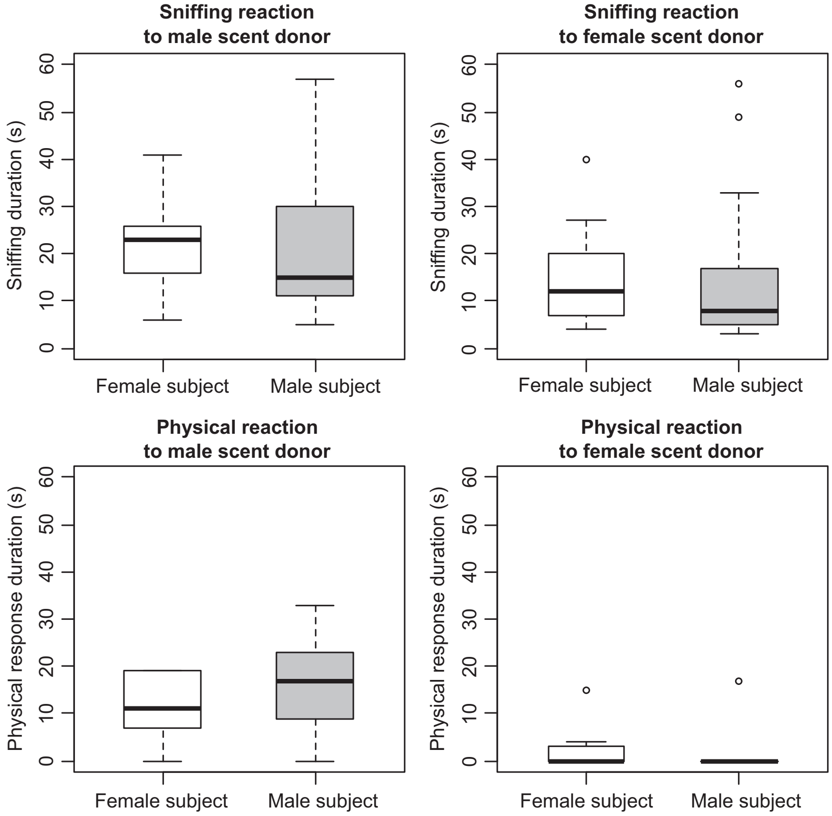

Fig. 2: Duration (in seconds) of the sniffing and physical responses of dominant territorial female (female subject, white box) and male (male subject, grey box) beavers to experimental scent mounds with anal gland secretion of a male and female scent donor from a mated pair. The bars indicate the maximum and minimum durations, the circles indicate outliers.

Discussion

Our findings that both sexes of territory holding monogamous beavers respond towards the AGS of the stranger pair male for longer durations indicate that paired territory holders can distinguish between male and female AGS. This supports the hypothesis that dominant territorial monogamous beavers can discriminate between stranger adults of a mated pair via the odorant signal of AGS. This is consistent with other mammalian species where AGS is known to code for sex and considered to be important for social communication (Jordan et al. 2010). Our results only support our prediction that dominant monogamous territorial males and females will exhibit stronger responses to the scent of same-sex conspecifics, with regard to the males and not the females which, opposite to our prediction, responded for longer durations and overmarked more frequently, the AGS of male intruders. Our results also suggest that both sexes of a pair of dominant resident beavers consider stranger mated-pair males to pose a greater threat than stranger mated-pair females.

Our study does not support Sun and Müller-Schwarze (1999) who found no evidence that the North American beaver (*C. canadensis*), which is behaviourally similar to the Eurasian beaver, respond more agonistically to AGS of either sex. However, in their study, ESMs were constructed in the evening, left unobserved and returned to the next day with no continuous knowledge (e.g. continual observation direct or film) of the ESM during the intervening hours. It is possible that more than one beaver from the same colony visited the ESMs, resulting in differential responses being masked by collective responses of several individuals.

We predicted a more agonistic response to same-sex conspecifics by a territorial monogamous mammal due to strong intrasexual competition over resources such as food, shelter and mates (Boydston et al. 2001; Gosling & Roberts 2001; Cant et al. 2002). A laboratory study on the monogamous prairie vole (*Microtus ochrogaster*) found individuals overmarked same-sex conspecifics more frequently than opposite-sex conspecifics when placed in neutral arenas (Ferkin 1999; Woodward et al. 2000). Our study agreed with these findings with regard to males, but not regarding females; however, none of the female voles were pregnant or lactating at the time of their experiment, whereas in our study, many of the females were, which may affect marking behaviour.

Monogamous males increase their reproductive success by defending a territory to secure a breeding space with adequate food resources to support a pregnant female and later offspring (Busher & Jenkins 1985; Clutton-Brock 1989). Male intruders to a territory pose more of a threat to a male territory holder due to intrasexual competition. Although intrasexual competition is often stronger in polygamous species, monogamous populations with high densities, such as our study population, have strong competition for mates and territories. In the monogamous Alpine marmot (*Marmota marmota*) intruding individuals, both males and females can 'force' a divorce of a pairing (Lardy et al. 2011). This is also occasionally observed in our study population, though mainly due to intruding males (F. Rosell, unpubl. data).

Ferkin et al. (2004) and Ferkin and Pierce (2007) suggested that overmarking of opposite-sex conspecifics could be to advertise sexual receptiveness or interest; however, most of the females that responded in our experiment were pregnant or lactating, as beavers mate in late January and early February, and also, the individuals used in the experiments were all long-term mated pairs. Female residents may infer that male intruders pose more of a threat than females as in some species males can determine their relatedness to young (Blumstein 1997; Sun & Müller-Schwarze 1997, 1998b; Hackländer & Arnold 1999), and therefore, a mate change during the breeding season would expose the young to the risk of infanticide, although definite evidence of infanticide in beavers is lacking (But see Haines 1955; Sun 2003).

In monogamous species, the male biological parent of the young is essential for parental care and offspring survival and therefore could reduce the likelihood of extra-pair copulations (EPCs). EPCs are also low in species in which mobility is difficult during the mating season due to environmental constraints, such as ice and snow, (Nolet & Rosell 1994) and have not been found in our study population (H.V. Tinnesand, M. Sæbo and F. Rosell, unpubl. data). Additionally, in some species, for example Alpine marmots, females can abort their unborn offspring (i.e. the Bruce effect) when there is a new dominant male in a territory, which reduces time and energy costs (Agrell et al. 1998; Hackländer & Arnold 1999). Aborting or losing young due to infanticide is very costly to females especially in obligate monogamous mammals that only mate once a year and therefore reduce their fitness (Agrell et al. 1998; Hackländer & Arnold 1999).

Our study suggests that in accordance with similar studies, and our prediction, territorial obligate monogamous mammals can determine the sexual identity of intruding conspecifics of a mated pair via AGS and that they regard the male of an intruding mated pair as posing a greater threat than the female. Intruding males may pose more of a threat to resident males via intrasexual competition and to resident females due to the long-term costs, such as infanticide and abortion, of a new dominant male.

Acknowledgements

We would like to thank Christian A. Robstad, Manuel Esteban Echeverria, Patricia M. Graf, Róisin Campbell-Palmer and Helga Veronica Tinnesand for help in the field, and Telemark University College for funding to enable this work.

Literature Cited

Agrell, J., Wolff, J. & Ylönen, H. 1998: Counter-strategies to infanticide in mammals: costs and consequences. Okios **83**, 507—517.

Bates, DM. 2010. lme4: Mixed-Effects Modeling with R. Springer, New York.

Blumstein, D. 1997: Infanticide among golden marmots (*Marmota caudate aurea*). Ethol. Ecol. Evol. **9**, 169—173.

Boydston, E., Morelli, T. & Holekamp, K. 2001: Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, *Crocuta crocuta*). Ethology **107**, 369—385.

Brotherton, P. & Manser, M. 1997: Female dispersion and the evolution of monogamy in the dik-dik. Anim. Behav. **54**, 1413—1424.

Brotherton, P., Pemberton, J., Komers, P. & Malarky, G. 1997: Genetic and behavioral evidence of monogamy in a mammal, Kirk's dik–dik (*Madoqua kirkii*). Proc. R. Soc. Lond. B **1382**, 675—681.

Burgener, N., Dehnhard, M., Hofer, H. & East, M. L. 2009: Does anal gland scent signal identity in the spotted hyaena? Anim. Behav. **77**, 707—715.

Busher, P. & Jenkins, S. 1985: Behavioral patterns of a beaver family in California. Biol. Behav. **10**, 41—54.

Campbell, R. D., Rosell, F., Nolet, B. A. & Dijkstra, V. A. A. 2005: Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? Behav. Ecol. Sociobiol. **58**, 597—607.

Campbell, R., Nouvellet, P., Newman, C., Macdonald, D. & Rosell, F. 2012: The influence of mean climate trends and climate variance on beaver survival and recruitment dynamics. Glob. Chang. Biol. **18**, 2730—2742.

Campbell, R. D., Newman, C., Macdonald, D. W. & Rosell, F. 2013: Proximate weather patterns and spring green-up phenology effect Eurasian beaver (*Castor fiber*) body mass and reproductive success: the implications of climate change and topography. Glob. Chang. Biol. **19**, 1311—1324.

Cant, M., Otali, E. & Mwanguhya, F. 2002: Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. Ethology **108**, 541—555.

Clapham, M., Nevin, O., Ramsey, A. & Rosell, F. 2012: A hypothetico-deductive approach to assessing the social function of chemical signalling in a non-territorial solitary carnivore. PLoS ONE **7**, e35404.

Clutton-Brock, T. 1989: Mammalian mating systems. Proc. R. Soc. Lond. B **236**, 339—372.

Crawley, M. J. 2007: The R Book. John Wiley, Chichester.

Dunbar, R. 1984: The ecology of monogamy. New Sci. **103**, 12—15.

Ferkin, M. 1999: Meadow voles (*Microtus pennsylvanicus, Arvicolidae*) over-mark and adjecent-mark the scent marks of same-sex conspecifics. Ethology **105**, 825—837.

Ferkin, M. & Pierce, A. 2007: Perspectives on over-marking: is it good to be on top?. J. Ethol. **25**, 107—116.

Ferkin, M., Li, H. & Leonard, S. 2004: Meadow voles and prairie voles differ in the percentage of conspecific marks they over-mark. Acta Ethol. **7**, 1—7.

Gannon, W. & Sikes, R. 2007: Guidelines of the American Society of Mammalogists for the use of wild animals in research. J. Mammal. **88**, 809—823.

Gosling, L. 1982: A reassessment of the function of scent marking in territories. J. Comp. Ethol. **60**, 89—118.

Gosling, L. & Roberts, S. 2001: Scent marking by male mammals: cheat-proof signals to competitors and mates. Adv. Study Behav. **30**, 169—217.

Grønneberg, T. 1979: Analysis of a wax ester fraction from anal gland secretion of beaver (*Castor fiber*) by chemical ionization mass spectrometry. Chem. Scr. **13**, 56—58.

Grønneberg, T. & Lie, T. 1984: Lipids of the anal gland secretion of beaver (*Castor fiber*). Chem. Scr. **24**, 200—203.

Gubernick, D. & Teferi, T. 2000: Adaptive significance of male parental care in a monogamous mammal. Proc. R. Soc. Lond. B **1439**, 147—150.

Hackländer, K. & Arnold, W. 1999: Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). Behav. Ecol. Sociobiol. **10**, 592—597.

Haines, A. 1955: Osborne Russell's Journal of a Trapper. Univ. of Nebraska Press, Lincoln, Nebraska.

Hartman, G. 1997: Notes on age at dispersal of beaver (*Castor fiber*) in an expanding population. Can. J. Zool. **75**, 959—962.

Herr, J. & Rosell, F. 2004: Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*). J. Zool. **262**, 257—264.

Jannett, F. 1986: Morphometric patterns among microtine rodents. I. Sexual selection suggested by relative scent gland development in representative voles (*Microtus*). In: Chemical Signals in Vertebrates. (Duvall, D., Müller-Schwarze, D. & Silverstein, eds). Plenum Press, New York. pp. 541—550.

Johnston, R. E. 2008: Individual odors and social communication: individual recognition, kin recognition, and scent over-marking. Adv. Study Behav. **38**, 439—505.

Jordan, N. R., Mwanguhya, F., Kyabulima, S., Rüedi, P. & Cant, M. A. 2010: Scent marking within and between groups of wild banded mongooses. J. Zool. **280**, 72—83.

Jordan, N. R., Manser, M. B., Mwanguhya, F., Kyabulima, S., Rüedi, P. & Cant, M. A. 2011: Scent marking in wild banded mongooses: 1. Sex-specific scents and over-marking. Anim. Behav. **81**, 31—42.

Kleiman, D. 1977: Monogamy in mammals. Q. Rev. Biol. **52**, 39—69.

Komers, P. & Brotherton, P. 1997: Female space use is the best predictor of monogamy in mammals. Proc. R. Soc. Lond. B **264**, 1261—1270.

Lack, D. 1968: Ecological Adaptations for Breeding in Birds. Methuen, London.

Lardy, S., Cohas, A., Figueroa, I. & Allainé, D. 2011: Mate change in a socially monogamous mammal: evidences support the "forced divorce" hypothesis. Behav. Ecol. **22**, 120—125.

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. **275**, 33—40.

Müller, C. A. & Manser, M. B. 2008: Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew. Ethology **114**, 174—185.

Muller-Schwarze, D. 2011: The Beaver: Its Life and Impact. Cornell Univ. Press, Ithaca, USA.

Müller-Schwarze, D. 2006: Chemical Ecology of Vertebrates. Cambridge Univ. Press, Cambridge, UK.

Nolet, B. & Rosell, F. 1994: Territoriality and time budgets in beavers during sequential settlement. Can. J. Zool. **72**, 1227—1237.

Osborn, D. J. 1955: Techniques of sexing beaver, *Castor canadensis*. J. Mammal. **36**, 141—143.

Palphramand, K. L. & White, P. C. L. 2007: Badgers, *Meles meles*, discriminate between neighbour, alien and self scent. Anim. Behav. **74**, 429—436.

Parker, H. & Rosell, F. 2001: Parturition dates for Eurasian beaver *Castor fiber*: when should spring hunting cease? Wildl. Biol. **7**, 237—241.

Rich, T. & Hurst, J. 1999: The competing countermarks hypothesis: reliable assessment of competitive ability by potential mates. Anim. Behav. **58**, 1027—1037.

Roberts, S. C. 2007: Scent Marking. The Univ. of Chicago Press, Chicago.

Rosell, F. 2002: The function of scent marking in beaver (*Castor fiber*) territorial defense. PhD, Norwegian University of Science and Technology.

Rosell, F. 2003: Territorial scent marking behaviour in the Eurasian beaver (*Castor fiber L.*). Biologiezentrum Linz/Austria **2**, 147—161.

Rosell, F. & Bjørkøyli, T. 2002: A test of the dear enemy phenomenon in the Eurasian beaver. Anim. Behav. **63**, 1073—1078.

Rosell, F. & Hovde, B. 2001: Methods of aquatic and terrestrial netting to capture Eurasian beavers. Wildl. Soc. Bull. **29**, 269—274.

Rosell, F. & Nolet, B. 1997: Factors affecting scent-marking behavior in Eurasian beaver (*Castor fiber*). J. Chem. Ecol. **23**, 673—689.

Rosell, F. & Sanda, J. 2006: Potential risks of olfactory signalling: the effect of predators on scent marking by beavers. Behav. Ecol. Sociobiol. **17**, 897—904.

Rosell, F. & Steifetten, Ø. 2004: Subspecies discrimination in the Scandinavian beaver (*Castor fiber*): combining behavioral and chemical evidence. Can. J. Zool. **82**, 902—909.

Rosell, F. & Sun, L. 1999: Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *Castor fiber*. Wildl. Biol. **5**, 119—123.

Rosell, F. & Sundsdal, L. 2001: Odorant source used in Eurasian beaver territory marking. J. Chem. Ecol. **27**, 2471—2491.

Rosell, F. & Thomsen, L. 2006: Sexual dimorphism in territorial scent marking by adult Eurasian beavers (*Castor fiber*). J. Chem. Ecol. **32**, 1301—1315.

Rosell, F., Bergan, F. & Parker, H. 1998: Scent-Marking in the Eurasian Beaver (*Castor fiber*) as a Means of Territory Defense. J. Chem. Ecol. **24**, 207—219.

Rosell, F., Johansen, G. & Parker, H. 2000: Eurasian beaver (*Castor fiber*) behavioral response to simulated territorial intruders. Can. J. Zool. **78**, 931—935.

Schulte, B. 1998: Scent marking and responses to male castor fluid by beavers. J. Mammal. **79**, 191—203.

Schulte, B., Müller-Schwarze, D., Tang, R. & Webster, F. 1995: Bioactivity of beaver castoreum constituents using principle component analysis. J. Chem. Ecol. **21**, 941—957.

Sharpe, F. & Rosell, F. 2003: Time budgets and sex differences in the Eurasian beaver. Anim. Behav. **66**, 1059—1067.

Sillero-Zubiri, C. & Macdonald, D. 1998: Scent marking and territorial behaviour of Ethiopian wolves (*Canis simensis*). J. Zool. **245**, 351—361.

Skinner, J. & Chimimba, C. 2005: The Mammals of the Southern African Sub-Region, 3rd edn. Cambridge Univ. Press, Cambridge, UK.

Sommer, S. 2005: Major histocompatibility complex and mate choice in a monogamous rodent. Behav. Ecol. Sociobiol. **58**, 181—189.

Sun, L. 1996: Chemical kin recognition in the beaver (*Castor canadensis*): Behavior, relatedness and information coding. PhD, State University of New York, Syracuse.

Sun, L. 2003: Monogamy correlates, socioecological factors, and mating systems in beavers. In: Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals. (Reichard, U. & Boesch, C., eds). Cambridge Univ. Press, Cambridge, UK. pp. 138—146.

Sun, L. & Müller-Schwarze, D. 1997: Sibling recognition in the beaver: a field test for phenotype matching. Anim. Behav. **54**, 493—502.

Sun, L. & Müller-Schwarze, D. 1998a: Anal gland secretion codes for relatedness in the beaver, *castor canadensis*. Ethology **104**, 917—927.

Sun, L. & Müller-Schwarze, D. 1998b: Beaver response to recurrent alien scent: scent fence or scent match? Anim. Behav. **55**, 1529—1536.

Sun, L. & Müller-Schwarze, D. 1999. Chemical signls in the beaver: One species, two secretions, many functions?. Plenum, New York.

Sun, L., Müller -Schwarze, D. & Schulte, B. 2000: Dispersal pattern and effective population size of the beaver. Can. J. Zool. **78**, 393—398.

Temeles, E. 1994: The role of neighbours in territorial systems: when are they "dear enemies"? Anim. Behav. **47**, 339—350.

Thiessen, D. & Rice, M. 1976: Mammalian scent gland marking and social behavior. Psychol Bull. **83**, 505—539.

Tinnesand, H. V., Jojola, S., Zedrosser, A. & Rosell, F. 2013: The smell of desperadoes? Beavers distinguish between dominant and subordinate intruders Behav. Ecol. Sociobiol. **67**, 1—10.

White, M., Swaisgood, R. & Zhang, H. 2003: Chemical communication in the giant panda (*Ailuropoda melanoleuca*): the role of age in the signaller and assessor. J. Zool. **259**, 171—178.

Wickler, W. & Seibt, U. 1983: Monogamy: An ambiguous concept. In: Mate Choice (Ed. by Bateson, P.). Cambridge Univ. Press, Cambridge, UK, pp. 33—50.

Wilsson, L. 1971: Observations and experiments on the ethology of the European beaver (*Castor fiber*). Viltrevy **8**, 115—266.

Woodard, E. L. 1994: Behavior, Activity Patterns and Foraging Strategies of Beaver (*Castor Canadensis*) on Sagehen Creek. Univ. of California, Berkeley, CA.

Woodward, R. L., Bartos, K. & Ferkin, M. H. 2000: Meadow Voles (*Microtus pennsylvanicus*) and Prairie Voles (*M. ochrogaster*) Differ in Their Responses to Over-Marks from Opposite- and Same-Sex Conspecifics. Ethology **106**, 979—992.

Wyatt, T. 2003: Pheromones and Animal Behavior: Communication by Smell and Taste. Cambridge Univ. Press, Cambridge, UK.

Wyatt, T. D. 2014: Pheromones and Animal Behavior: Chemical Signals and Signatures, 2nd edn. Cambridge Univ. Press, Cambridge, UK.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. 2009: Mixed Effects Models and Extensions in Ecology with R. Springer, New York.