

SEXUAL DIMORPHISM IN TERRITORIAL SCENT MARKING BY ADULT EURASIAN  
BEAVERS (*Castor fiber*)

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**Abstract**—Mammalian scent marking is often associated with territorial defense. However, males and females may demonstrate different activity pattern and play different roles. Female mammals nurture the young during lactation, while males purportedly perform other tasks more frequently, such as territorial maintenance and defense. This paper investigates the contribution made by mated pairs of adult males and females to territorial scent-marking in the obligate monogamous Eurasian beavers (*Castor fiber*). We hypothesized that both sexes should show territorial behavior and predicted that they deposit a higher proportion of scent marks at borders. We also hypothesized that a sexual dimorphism exists due to reproductive constraints on the females and predicted that males should invest significantly more in scent-marking behavior than females during summer. We obtained behavioral data by radio-tracking six mated pairs of Eurasian beavers during spring and summer 2000-2001 on two rivers in south-eastern Norway. Our results showed that both males and females clustered their scent marks near territorial borders, but males deposited a significantly larger number of scent marks than females and spent significantly more time at borders. Males were also found to have a significantly higher scent marking rate and scent marks per night than females during summer, but not during spring. Overall, scent marks per night were significantly higher in males than females. We conclude that both males and females Eurasian beavers carry out territorial behavior by scent marking, but males carry a larger part of the territorial defense during summer when females lactate. Our results are discussed in the light of the co-defense hypothesis.

**Key Words**—*Castor fiber*, monogamy, parental care, co-defense, territoriality.

## INTRODUCTION

Several nonexclusive hypotheses have been proposed to explain why animals scent-mark (see Back et al., 2002; Begg et al., 2003; Miller et al., 2003). Scent marks might serve several functions, which may change or vary with time of year or location of the mark. However, it is widely accepted that mammals scent mark their territories to advertise their occupancy and ownership of the territory (e.g. Gosling, 1982; Sillero-Zubiri and Macdonald, 1998), but it is still under debate how scent marks actually function in terms of territory maintenance (Gorman, 1990; Gosling, 1990; Richardson, 1991, 1993).

The "scent-matching" hypothesis posits that scent marks provide an olfactory link between a resident owner and his territory, and that this enables intruding animals to recognize the chance of escalated conflicts (Gosling, 1982; Gosling and Roberts, 2001). By matching the scent of a territory owner with those of nearby scent marks, an intruder employs the unique property of olfactory signaling that includes the provision of both a historical and a spatial record of a territorial individual's behavior. Territory owners can thus signal their status to intruders in a way that cannot be mimicked and that is to their advantage in subsequent encounters (Gosling, 1982). Intruding animals (independent of gender), upon entering a foreign territory, quickly discover that the area is already occupied as scent marks are placed at the border (Gorman and Mills, 1984; Richardson, 1993). The threat of being detected and possibly becoming involved in a fight should keep intruders to the border region, when it does not completely deter them from intruding (Sliwa and Richardson, 1998). According to the hypothesis, territory owners should also remove or replace marks of others (Gosling, 1986). It is thus crucial that both sexes maintain their scent marks in such a way that maximizes the success of matching (see Gosling, 1986; Gosling and Roberts, 2001; Roberts and Lowen, 1997). This is achieved both by replenishing their own scent marks on a regular basis and by removing or replacing marks of competitors within their territory (Rich and Hurst, 1999; Roberts, 1998).

Both sexes usually scent mark in mammals (e.g. Kleiman, 1981; Heymann, 1998; Gosling and Roberts, 2001). However, males and females may demonstrate different activity patterns and play different roles. Female mammals nurture the young during lactation, while males purportedly perform other tasks more frequently, such as territorial maintenance and defense. If one sex ranged further than the other did, the former may encounter more intruders or unmarked regions and respond by marking at higher rates. Selection could then favor individuals of this sex with relatively larger or more active scent structures (Rosell and Schulte, 2004). Also, a seasonal difference in scent marking activity may have been developed due to energy constraints on females during summer.

The Eurasian beaver (*Castor fiber*) is a typical obligate monogamous species (Wilsson, 1971; Kleiman, 1977). They defend territories, invest in their territories by the construction of dams and lodges, have young with an extended period of maturation, and the adult male exhibits a relatively high degree of both direct and indirect parental care (Wilsson, 1971; Rosell, 2002). They live in family units consisting of an adult pair and their offspring (Wilsson, 1971; Nolet and Rosell, 1994). Breeding pairs maintain long-term pair-bonds and copulate during January-March (Wilsson, 1971). Kits which are born on average June 1<sup>st</sup> and the adult male as well as subadults of both sexes help rearing them (Wilsson, 1971). Some behavioral differences in adult males and females have been observed, especially during spring and summer when young are reared (Wilsson, 1971). Two recent studies on mated male and female Eurasian beavers suggest that males have significantly larger kernel home ranges during the whole tracking period (March-August) and after parturition (Herr and Rosell, 2004), and that males allocate significantly more time to travel (Sharpe and Rosell, 2003).

In beavers there are no external differences between the sexes except for visible nipples in lactating females (Wilsson, 1971). Both sexes possess two anal glands and two castor sacs where retention of urine creates the fluid castoreum (Rosell, 2002). During scent marking their territories, castoreum is deposited on scent mounds or on the ground (Rosell and Sundsdal, 2001). The number of scent marks is significantly higher in spring when subadults disperse (Rosell et al., 1998). The

anal gland secretion is occasionally deposited; however its role in territorial scent marking is not yet fully understood (Rosell and Bergan, 1998; Rosell and Sundsdal, 2001). Both sexes and all age classes (> 5 months) participate in scent marking (Wilsson, 1971).

A variety of hypotheses have been assumed for scent marking in the two beaver species, i.e. the Eurasian beaver and the North American beaver (*C. canadensis*) (see review in Rosell, 2002). However, by testing alternative hypotheses, Houlihan (1989) confirmed the territorial function of North American beaver scent marks and rejected other interpretations (see also Schulte, 1998). Scent marking in the Eurasian beavers likewise serves a territorial function (Rosell, 2002). Scent marks are concentrated near territorial borders, apparently to maximize the signal effect to potential trespassers on or before entering the territory (Rosell and Nolet, 1997; Rosell et al., 1998).

More information is needed about frequency of marking by different group members (age, social status, and sex) and behavioral context in which the signal is deposited. In this scenario and given the obligate monogamous nature of the Eurasian beaver it is interesting to investigate whether scent marking behavior is similar between the sexes and if a seasonal difference exists. Previous studies of sex differences in scent marking in North American beavers have either focused on the reaction to experimentally constructed scent marks (Butler and Butler, 1979; Svendsen and Huntsman, 1988; Müller-Schwarze and Houlihan, 1991), or when based on direct observation of scent marking, included unequal numbers of males and females (Buech, 1995). From Eurasian beavers only anecdotal information exists, based on animals in captivity (Wilsson, 1971). None of the studies above used observations of mated pairs.

This paper investigates the contribution made by mated pairs of adult males and females to scent-marking in Eurasian beavers. We hypothesized that both sexes should show territorial behavior and predicted that they deposit a higher proportion of scent marks at borders. We also hypothesized that a sexual dimorphism exists due to reproductive constraints on the females and predicted that males should invest significantly more in scent-marking behavior than females during summer. We examined the sexual dimorphism issue by presenting the rate of marking, activity

patterns, and the marking context.

## METHODS AND MATERIALS

*Study Area and Study Animals.* We collected data in Eurasian beaver territories along the Gvarv and Saua Rivers in Telemark, southeastern Norway, during spring and summer 2000 and 2001. Both rivers meander through a semi-agricultural and mixed forest landscape. The Saua River forms part of the Telemark Canal, and at either end of the area studied are canal locks and weirs. The Gvarv River follows a more natural flow regime and discharges into Lake Nordsjø, part of which forms a section of one of the territories. Both rivers are either too wide for beavers to build dams or too deep to make it necessary. Beavers have inhabited the area since the 1920s (Olstad, 1937). Hunting pressure within the study area is either very low or non-existent, and the beavers are used to human presence.

Subjects were 12 Eurasian beavers ( $\bar{X} \pm \text{SD}$  weights: males:  $21.3 \pm 1.4$  kg; females:  $22.8 \pm 2.6$  kg), which were the reproducing pairs in six territories. Assessment of pairs was based on previous trapping records of weights, incidence of lactation and behavioral observations (F. Rosell, unpublished data). We caught animals from a boat, using landing nets, during September, March and April 1999–2001 (Rosell and Hovde, 2001). Permission for capture, handling, and surgical procedures was provided by the Norwegian Experimental Animal Board and the Norwegian Directorate for Nature Management. Licensed veterinarians carried out all surgical procedures. To facilitate handling and tagging, each beaver was placed head first into a cloth sack and restrained while another researcher applied eartags by maneuvering the beaver's ear out through a small hole cut in the sack. No beavers responded aggressively while confined in the sack; they tended to remain comparatively docile, and none was visibly injured by the procedure. Individuals were tagged with numbered plastic eartags (3.5 cm, Dalton Continental B.V., Lichtenvoorde, The Netherlands) or monel metal eartags (1.5 cm, National Band and Tag Co., Newport, Kentucky,

U.S.A.) or both. Each beaver was weighed, implanted with a microchip measuring 1 cm (Destron 490, Villaume Ave, St Paul, Minnesota, U.S.A.) in the neck, and sexed by the color of the anal gland secretion (Rosell and Sun, 1999; Rosell and Bjørkøyli, 2002). We assumed that all females gave birth during both 2000 and 2001 based on observations of nipple size, presence of kits, sound of kits inside the lodge and transport of branches into the lodge during July (Wilsson, 1971).

During September, March, and April, prior to the 2000 field season, the beavers from five of the six pairs studied were implanted with an Alterra TX30.3A1 intraperitoneal 30 MHz-radio transmitter (63g) equipped with temperature and movement sensor (Alterra (IBN/DLO), 6700 AA Wageningen, the Netherlands) (Ranheim et al., 2004). To recover completely all animals were allowed a minimum of one week before tracking began. However, the behavior and movement of the beavers did not appear to be affected by the implanted transmitters, except for the first two days when more time was spent inside the lodges. The transmitter signal was detected using a one-element loop antenna (Alterra, 6700 AA Wageningen, the Netherlands) and an Icom IC-R10 receiver (Icom Inc., 6-9-16 Kamigashi, Osaka 547, Japan). Signal reception range varied between 300-600 m from a boat (Nolet & Rosell 1994). In April 2001, the last two beavers (plus one with an failed intraperitoneal transmitter) were fitted with external tail transmitters (Advanced Telemetry Systems Inc., Isanti, MN, USA, Model 16 M ear tag for beaver tail, weight=38g) operating at 142 MHz (F. Rosell, unpublished data). Belt pliers were used to perforate the tail approximately 10 cm from the base of the tail and 3.1-2.4 cm from the lateral edge. The transmitter was secured with a bolt, washer, and nut. A plastic holder was inserted to facilitate the withdrawal of the bolt when the transmitter was recovered. The beavers were released near the capture site less than 10 minutes after capture. Animals showed normal behavior less than 15 min after their release. Signals were detected using a hand-held RX-98 H tracking receiver with built-in foldable antenna (TVP Positioning AB, Box 53, SE-71132 Lindsberg, Sweden). Mean ( $\pm$ SD) signal reception range from a boat ranged from  $353\pm 112$  m (F. Rosell, unpublished data).

*Ethical Considerations.* Please refer to Sharpe and Rosell (2003) and Herr and Rosell (2004) for detailed information on animal welfare issues and Ranheim et al. (2004) for descriptions of surgical procedures.

*Data Collection.* The study was conducted between March 7<sup>th</sup> and August 8<sup>th</sup> 2000, and between April 8<sup>th</sup> and July 31<sup>st</sup> 2001. Three beaver pairs were followed both years, two additional pairs only in 2000, and one extra pair only in 2001. On average each beaver was followed 6.8 nights (range 4-10), adding to a total of 82 nights, equally divided between males and females. Data were collected by a two-person team (one observer and one recorder). A boat with outboard motor was used to follow the beavers. During dark periods a spotlight was used to illuminate the animals. Noise from the engine and the light did not seem to affect normal behavior in the beavers as long as they were approached with care (Nolet and Rosell, 1994; Rosell and Hovde, 2001, personal observation). Binoculars were used when needed. Focal animal sampling (Altmann, 1974; Martin and Bateson, 1999) was used and a single beaver was followed throughout each observation night. The predetermined focal animal was initially located in its daily resting place by the signal from its radio transmitter. After the animal emerged, the observation team attempted to stay in visual contact with it throughout the night. Whenever an animal disappeared from view, the radio signal was used to locate it again. Both members of a pair were followed on consecutive nights in order to obtain "paired observations" and to reduce the effects of seasonal changes in weather conditions and behavior. Which member of a pair was to be followed first was determined at random by tossing a coin.

Beavers are nocturnal and usually have one activity period during each night (Wilsson, 1971; Nolet and Rosell, 1994). Thus, an observation session began when the focal animal emerged from its daily resting-place in the evening and was terminated after the break of dawn when the animal had spent  $\geq 30$  minutes inside a lodge or burrow. This period of activity was defined as the "principal activity period" (Corp et al., 1997). If a beaver left its daily resting-place undetected, the activity period was set to begin midway between the last time the animal was known to be in the



resting-place and the time it was discovered to have left. The same procedure was used to determine the end of the period. Behavior was recorded continuously throughout observation sessions and classified into eight categories (Altman, 1974; Martin and Bateson, 1999) along with time and position (Table 1). We assigned the last behavioral pattern prior to scent marking and the first after scent marking as the “context prior” and “context after”, respectively. Positions were recorded on a 1:5000 scale map of the study area. During each observation night, seven environmental variables were recorded every two hour: Air temperature (°C), water temperature (°C), precipitation (presence/absence), moon (presence/absence), mist (presence/absence), cloud cover (pct.), and wind (5 categories).

**[Table 1 near here]**

*Scent Marking Rate and Scent Marks per Night.* We used scent marking rate (SMR) and scent marks per night (SM/night) to compare scent marking activity between male and female beavers. To obtain standardized scent marking rates, we divided the number of scent marks by the length (in hours) of the principal activity of the respective beaver, subtracted by the time the animal was either out of sight or its behavior could not be deduced. Nightly visits to lodges or burrows were included, as scent marking has not been reported to occur here. Males had longer activity periods than females ( $\bar{X} \pm SD$  minutes per night: Males=570.0±97.5; Females=493.0±144.7; Wilcoxon-Signed ranks test:  $W=725.5$ ,  $P=0.0001$ ). Therefore, a rate like SMR will not reflect the actual contribution of a beaver to the total number of scent marks deposited each night. Thus, we also compared scent marks per night (SM/night). Before doing so we checked whether we had managed to keep track of males and females equally well, i.e. whether the percentage of time we had the beaver “in sight” (see above) during the principal activity period was the same for both sexes. Not surprisingly we had more minutes of “in sight” data on males due to the longer principal activity periods ( $\bar{X} \pm SD$

minutes per night: Males= 495.0±112.1; Females=442.0±131.3; W=683.5, P=0.001). However, the percentage of time we had the beaver in sight was equal between the sexes albeit marginal ( $\bar{X} \pm SD$  percent: Males= 86.2±0.083; Females=89.8±0.068; W=280.0, P=0.0511). Thus, we chose to use the visible counts of scent marking instead of adjusting them for time not in sight.

We divided our data into two periods: (1) spring (before parturition) and (2) summer (from parturition onwards). Parturition usually takes place around June 1<sup>st</sup>, and was therefore chosen as the division date (Wilsson, 1971; F. Rosell, unpublished data).

*Spatial Distribution.* Beaver territories can be considered as one-dimensional as only a narrow strip of land is used along riversides (Nolet et al., 1994). Locations of territory borders used in this study were obtained from Campbell (2000) and Herr and Rosell (2004) who established borders based on minimum convex polygons (MCP) by fixes found during radio-tracking performed concurrently with this study. We divided each beaver territory into two zones: 1) “border”: 100 m bank length on both riversides at shared borders and 2) “core”: the central part of the territory. A territory with two neighboring territories would thus have 400 m of border length. Border length did not vary considerably with territory size and thus a fixed length of 100 m bank length was used in all cases. Overlap between territories is minimal (Herr and Rosell, 2004) and 100m bank length would therefore be sufficient to encompass overlapping sections. Furthermore the territories of pair members overlapped on average by 81.6±14.0% SD (Herr and Rosell, 2004).

*Data Analysis.* Normality was tested using Shapiro-Wilk test (SPSS inc., 1999) and homogeneity of variance using Levene’s test (Dytham, 1999). If assumptions about continuity, normality, and homogeneity were met, parametric tests were used. When assumptions of normality could not be met even after transformation of data, the equivalent non-parametric tests were used for statistical testing. SMR and SM/night were normally distributed for overall year data and thus One-way ANOVA could be used to compare scent marking between pairs and Pearson Correlation to investigate correlations within pairs (Sokal and Rohlf, 1995). We choose to use the non-parametric Wilcoxon signed-ranks tests to compare SMR and SM/night between males and females

due to the low sample size and problems of obtaining normality during seasons (Sokal and Rohlf, 1995). The sampling unit for paired statistics was the individual beaver in order to avoid the "pooling fallacy" (Machlis et al., 1985; Martin and Bateson, 1999) which implies not to treat repeated measures of the same subject as independent samples. Chi-square tests were used to analyze spatial distribution of scent marks (Sokal and Rohlf, 1995). Before statistical testing, expected frequencies of scent marks in each zone were adjusted for bank length, as core bank lengths were much larger than border bank lengths. The Spearman rank correlation was used to compare context of male and female scent marking (Sokal and Rohlf, 1995). Data from males and females were pooled in order to obtain enough data in each behavioral category. Spearman Rank correlation was used to control for environmental influences. The Bonferroni adjustment for multiple comparisons was applied due to the high number of correlations (Sokal and Rohlf, 1995). Two-tailed tests were used in all analyses and  $P = 0.05$  was used as the level of significance. Statistical tests were run in SPSS version 10.0 (SPSS inc., 1999) and Analyze-it (version 1.71).

## RESULTS

*Territorial Function.* A total of 806 scent marks (SM) were registered (males = 480 and females = 326; Table 2). Three animals (two males and one female) were the main contributors to the total number of scent marks deposited, with 20.5 %, 26.8 %, and 28.7 %, respectively (Table 2). Those three animals came from two pairs (L2a and L2b) which accounted for 55.5 % and 29.4 % of all scent marks deposited by the six pairs (Table 2). The remaining four pairs each contributed 6.1 % or less. Both SMR and SM/night varied significantly between pairs (One-way ANOVA; SMR:  $F_{5,6} = 11.17$ ,  $P = 0.005$ ; SM/night:  $F_{5,6} = 12.81$ ,  $P = 0.004$ ). Within pairs, male and female SMR and SM/night were significantly correlated (Pearson correlation; Spring:  $R^2 = 0.88$ ,  $N = 6$ ,  $P = 0.019$ ; Summer:  $R^2 = 0.92$ ,  $N = 6$ ,  $P = 0.010$ ).

**[Table 2 near here]**

All but four scents marks (three made by two females, one by a male), were deposited within the marker's own territory (border zone included). Males and females scent marked significantly more in the border zones than expected when compared to the time spent in border and core zones (Table 3, males:  $\chi^2=1101.429$ ,  $df=1$ ,  $P<0.001$ ; females:  $\chi^2=1142.36$ ,  $df=1$ ,  $P<0.001$ ). Both sexes also scent marked significantly more in the border zones than would be expected if the deposition had been according to bank length (Table 3, males:  $\chi^2=935.348$ ,  $df=1$ ,  $P<0.001$ ; females:  $\chi^2=696.193$ ,  $df=1$ ,  $P<0.001$ ).

**[Table 3 near here]**

*Sexual Dimorphism.* Within each pair most scent markings observed were made by males, the percentage ranging from about 52-75 %, except for pair L1 where the male made more than 90 % of all scent marks (Table 2). There was no difference in SMR between the sexes when looking at the overall study period (Fig. 1-a.I). However this was due to only one female having a higher rate of marking than her mate. SM/night was significantly higher in males than females (Fig. 1-b.I). From spring to summer five males increased their marking rates and of these, four males had a higher SM/night during summer. Amongst the females an equal pattern was seen with four females having a higher SMR and five a higher SM/night in summer than in spring. In the couple from territory L2a both SMR and SM/night dropped considerably between seasons (Fig. 1-aI-II; b.I-II). During summer both SMR and SM/night was significantly higher in males than females. During spring there was no difference in SMR with two females having a higher rate than their mates. The same was true for SM/night, however only one female caused the difference (Fig. 1-aI-II; b.I-II).

**[Figure 1 near here]**

Males and females deposited the same proportion of their scent marks in border and core zones (Table 3,  $\chi^2=0.818$ ,  $df=1$ ,  $P=0.366$ ). However, males spent significantly more time in the border zones than females and spent a significantly higher proportion of their total activity time there (Table 4). This was also true when looking at the spring season. In the summer season only absolute time was significantly different between the sexes, whereas proportion of time spent at borders was marginally non-significant (Table 4). Males would deposit significantly more scent marks and females significantly less scent marks than would be expected if the sexes had contributed equally to scent marking in each zone (Table 3, border:  $\chi^2=9.993$ ,  $df=1$ ,  $P=0.00167$ ; core:  $\chi^2=19.167$ ,  $df=1$ ,  $P<0.001$ ).

[Table 4 near here]

All eight behavioral contexts of scent marking (Table 5), both prior and after, were significantly correlated between males and females (prior:  $r_s = 0.82$ ,  $N = 8$ ,  $P = 0.012$ ; after:  $r_s = 0.86$ ,  $N = 8$ ,  $P = 0.006$ ). There was a significant correlation between behavior prior to and after scent marking in both sexes (males:  $r_s = 0.72$ ,  $N = 8$ ,  $P = 0.045$ ; females:  $r_s = 0.90$ ,  $N = 8$ ,  $P = 0.002$ ). The most common context of scent marking in both sexes, prior to as well as after scent marking, was swimming (32.8-37.9 %). The second most common context was scent marking (30.0-34.3 %), i.e. about one third of scent markings would be succeeded by renewed scent marking (multiple marking). All but 1 of 122 (0.82 %) and 1 of 91 (1.01 %) multiple markings made by males and females respectively occurred at borders. Foraging came third (14.8-21.2 %). All other events contributed with less than 6 %.

[Table 5 near here]

SMR was not correlated with any of the weather variables nor with date in either sex (Spearman correlation with Bonferroni method for multiple comparisons:  $r_s$ , all  $P > 0.05$ ). This was also true for each season separately.

## DISCUSSION

*Territorial Function.* The “scent-matching” hypothesis has received support by studies of scent marking in both the North American beaver (Sun and Müller-Schwarze, 1998) and then Eurasian beaver (Rosell, 2002; Rosell and Bjørkøyli, 2002; Rosell and Steifetten, 2004). By scent-matching, competitors or mates match the odor from scent marks with the odor of conspecifics they encounter (Gosling, 1982; Gosling and McKay, 1990). It is thus crucial that both sexes of beavers maintain their scent marks in such a way that maximizes the success of matching (see Gosling, 1986; Gosling and Roberts, 2001; Roberts and Lowen, 1997). The high proportion of scent marks deposited at borders by both sexes confirms that scent marking serves a major function in territorial defense in Eurasian beavers (e.g. Nolet and Rosell, 1994; Rosell, 2002). Also, all (except one) multiple makings occurred at borders. This is in accordance with our first hypothesis and prediction and in agreement with earlier studies of the Eurasian beaver (Rosell and Nolet, 1997; Rosell et al., 1998). However, in these studies no information about sex was provided. Both sexes of beavers frequently replenishing their own scent marks on a regular basis (this study) and remove or replace marks of competitors within their territory (e.g. Rosell, 2002), further supporting the hypothesis.

A high degree of individual variation in scent marking was found in this study, varying more between pairs than within. Moreover scent marking behavior was correlated between mated pairs. Thus, apparently the sex of the beaver has less influence on scent marking than scent marking by their mate. This suggests that marking rates in beavers are regulated by the individual beaver in response to outside stimuli and that both members of a pair respond in a similar way to these stimuli. Number of scent marks varies spatially and temporally in populations of most species of

mammals and can be correlated with food availability, breeding activity, levels of dominance, and individual density (Ralls, 1971; Johnson, 1973; Gosling, 1990). It is possible that differences in these factors between the territories in the present study may explain the differences in scent marking. Furthermore the two territories with the highest degrees of scent marking (L2a and L2b) were assumed to have an ongoing dispute over position of territory borders possibly due to a split into two separate territories.

*Sexual Dimorphism.* Our second hypothesis that a sexual dimorphism exists due to reproductive constraints on the females was only partly supported. The low sample size may have resulted in low statistical power and an inability to detect any further differences. Also, a wide application of our findings to other habitats should be done with some caution. Nevertheless, the data provide no convincing evidence of any biological effects that were undetected by statistical analysis (i.e. means, median and percentages for males and females were similar).

Overall (spring and summer), SM/night was significantly higher in males than females. Males were also found to have a significantly higher SMR and SM/nights than females during summer, but not during spring. This is in accordance with our prediction. Scent marking involves investment both in terms of time and energy (Gosling, 1986). For instance scent marking at higher intensity has been shown to reduce growth rate and body size in mice (Gosling et al., 2000). Patrolling the territory in connection with scent marking is time-consuming and could be energetically costly for beavers. It thus seems likely that males invest more time in territorial defense than females during the breeding period, because males do not need extra energy to develop a fetus and cannot initially provide direct care to newly born offspring. During summer kits have been born and are reliant on milk from the female (all females were assumed to give birth in our study). Thus, females are more constrained by parental care than males and have less time and energy to spend on territorial activities. Lactation and infant care impose heavy burdens and constrains on female mammals (e.g. Campbell and Reece, 2002).

This coincides with the fact that we found that males deposited a significantly larger number of scent marks and spent significantly more time at borders. This finding is also in accordance with Sharpe and Rosell (2003) who in a study concordant with this showed that males spend more time traveling, and with Rosell and Schulte (2004) who suggested that a difference in territorial behavior between male and female has led to differential investment in scent structures. They suggested that female have larger castor sacs (low flushing rates) and smaller anal glands (infrequent use) because of reduced employment of both glands for territorial purposes, whereas males have just the opposite configuration because of enhanced use of both glands in territorial demarcation. Hence, behavioral dimorphism might select for morphological dimorphism in signal producing structures, even in an obligate monogamous species.

*Co-defense.* Our results coincide with the general picture of obligate monogamous mammals where both sexes participate in the defense of a joint territory (Clutton-Brock, 1989). However, most mammals are intra-sexually territorial, but several findings suggest that beavers are intra- and inter sexually territorial. Adult beavers of both sexes countermark where other conspecifics (of both sexes) have marked (Rosell et al., 2000; Rosell, 2002; Rosell and Steifetten, 2004). A display ("stick display") used in territorial context is used both intra- and inter-sexually (Thomsen et al., submitted). Beavers are able to recognize relatedness by a pheromone in the anal gland secretion. This would deter extra-pair copulations (EPCs) by females, since their mate would be able to detect young unrelated to him and could treat them unfavorably or potentially kill them, and consequently favor monogamy (Sun, 2003). Furthermore it would make mate change during the breeding season unlikely because the kits would be exposed to risk of infanticide if a stranger of either sex enters the territory, although definite proof of infanticide in beavers is lacking (see however Haines, 1955). Since beavers evolved in northern latitudes and mating occur in late winter when mobility is restricted by environmental conditions, male roving costs would also be high (Nolet and Rosell, 1994) and therefore the potential for EPCs low.



For a territorial species like the beaver, there are benefits to co-defending the territory (e.g. Mathews, 2002). No other socially monogamous rodent shows the same degree of construction activities or foraging and food storage behavior as the beaver (Baker and Hill, 2003). The benefits of defending a large territory rather than only the immediate vicinity of the lodge is likely to lie in the long-term payoff of reducing the rate of resource depletion within the site and thus increasing the long-term viability of the territory (Campbell et al., in press). Campbell et al. (in press) argue that the settlement pattern and reproductive history have a lasting impact on the territorial system of beavers due to a combination of the low adult mortality, high dispersal costs, and avoidance of resource depletion. All these factors lower the individual energetic investment in defense and thus reduce the risk of being evicted from the territory. Male beavers exhibit a relatively high degree of both direct and indirect parental care (Wilsson, 1971; Novak, 1987; Rosell, 2002), for instance males will bring food to offspring. Hence, defending a territory could be seen as an effort to secure a breeding space with adequate food resources to support a pregnant female and later offspring, ultimately increasing the males' reproductive success (Busher and Jenkins, 1985; Clutton-Brock, 1989). Likewise territory defense by females is likely to be resource defense (Clutton-Brock, 1989).

Thus, co-operation between male and female should raise the odds of maintaining control over a large resource-rich territory in which young can be raised successfully. Male parental care, combined with the benefits of defending a larger territory, could have lead to the evolution of co-defense and consequently a high degree of monomorphism in scent marking. Further studies comparing allocation by either sex to territorial behavior (e.g. scent marking) outside the breeding season could confirm the hypothesis that females contribute less to the defense during certain times of the year due to reproductive constraints.

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TABLE 1. CATEGORIES OF EURASIAN BEAVER BEHAVIOR AND DESCRIPTION OF EACH CATEGORY

Behavior category	Description of behavior
Swimming	Swimming for more than 2 minutes in one direction or more than 25m
Scent marking	Depositing castoreum, including behavior initiating scent marking
Foraging	On land foraging, eating food, or diving for aquatics
Grooming	Grooming own fur
Amicable interaction	Nosing, social grooming, ‘play wrestling’ <sup>a</sup> , and other social interactions between family members
Agonistic interaction	Chasing, biting, ‘stick display’ <sup>b</sup> , or other agonistic behavior towards non-family or family members
On bank	Entering bank for a shorter or longer period, sitting, walking, or sniffing the ground, but without performing any other characteristic behavior
Other	Any behavior not mentioned above

<sup>a</sup>Moving of the head in a circle in an exaggerated manner, signaling to a group member (Wilsson 1971).

<sup>b</sup>A display behavior involving the use of tools where the beaver holds an object, usually a stick, in its mouth while moving its upper body rapidly up and down (Thomsen LR, Campbell RD, Rosell F unpublished data).

TABLE 2. NUMBER OF OBSERVATION NIGHTS IN SIX EURASIAN BEAVER TERRITORIES, NUMBER OF SCENT MARKS OBSERVED, AND RELATIVE CONTRIBUTION (IN PERCENT) TO TOTAL NUMBER OF SCENT MARKS WITHIN PAIRS, BETWEEN PAIRS AND BETWEEN PAIRS WITH THE SEXES COMBINED

Territory	Nights	No. scent marks		Contribution within pairs (%)		Contribution between pairs (%)		Contribution between pairs -
		male	female	male	female	male	female	sexes
								combined (%)
L1	14	27	2	93.1	6.9	3.3	0.2	3.6
L2a	20	231	216	51.7	48.3	28.7	26.8	55.5
L2b	18	166	72	69.6	30.4	20.5	8.9	29.4
L5	8	27	21	57.1	42.9	3.5	2.6	6.1
L6	14	18	11	62.1	37.9	2.2	1.4	3.6
N2	8	11	4	73.3	26.7	1.4	0.5	1.9
SUM	82	480	326					

TABLE 3. SCENT MARKING BY MALE AND FEMALE EURASIAN BEAVERS IN THE BORDER AND CORE ZONES OF THEIR TERRITORIES. NUMBER OF SCENT MARKS OBSERVED AND NUMBER OF SCENT MARKS EXPECTED ACCORDING TO TIME SPENT IN EACH ZONE AND EXPECTED ACCORDING TO BANK LENGTH OF THE BORDER AND CORE ZONES RESPECTIVELY

		<b>Border</b>	<b>Core</b>
Males	Obs <sup>*</sup>	311	168
	Exp <sup>†</sup>	64 / 72	415 / 407
	% <sup>‡</sup>	64.9	35.1
Female s	Obs	231	92
	Exp	39 / 53	294 / 270
	%	70.9	29.1

<sup>\*</sup>Observed number of scent marks.

<sup>†</sup>Expected number if scent marks had been randomly distributed according to time in zone/length of bank in zone.

<sup>‡</sup>Observed number of scent marks in percent.

TABLE 4. MEAN ( $\pm$ SD) RESULTS OF MINUTES PER NIGHT SPENT AT BORDERS AND TIME SPENT AT BORDERS IN PERCENTAGE OF TOTAL ACTIVITY TIME (*ITALICS*) BY MALE (M) AND FEMALE (F) EURASIAN BEAVER DURING SPRING, SUMMER AND OVERALL. SIGNIFICANT RESULTS ( $P < 0.05$ ) ARE MARKED WITH AN ASTERISK

Season	Sex	Mean ( $\pm$ SD)	T	d.f.	P
			paired t-test		
Spring <sup>a</sup>	M	45.86 (51.27)	5.11	4	0.007*
		<i>7.82 (7.66)</i>	<i>-5.08</i>		<i>0.007*</i>
	F	24.14 (36.44)			
		<i>5.34 (6.46)</i>			
Summer <sup>b</sup>	M	36.06 (45.88)	3.05	5	0.028*
		<i>5.96 (7.30)</i>	<i>-2.13</i>		<i>0.086</i>
	F	19.58 (22.68)			
		<i>3.43 (3.91)</i>			
Overall	M	38.74 (46.98)	6.70	5	0.001*
		<i>6.53 (7.24)</i>	<i>-4.11</i>		<i>0.009*</i>
	F	23.04 (30.34)			
		<i>4.18 (5.21)</i>			

<sup>a</sup>March 7<sup>th</sup> – June 1<sup>st</sup> (before parturition).

<sup>b</sup>June 1<sup>st</sup> – August 8<sup>th</sup> (after parturition).

TABLE 5. BEHAVIORAL CONTEXT OF SCENT MARKING BY EURASIAN BEAVERS.  
 PERCENTAGE DISTRIBUTION OF BEHAVIORS PRIOR TO AND AFTER SCENT  
 MARKING EVENTS AND NUMBER OF EVENTS RECORDED IN EACH CATEGORY.  
 DATA FROM EACH SEX POOLED

Behavior <sup>a</sup>	Males	Males	Females	Females
	prior	after	prior	after
Swim	33.0	37.9	32.8	37.2
SM <sup>b</sup>	30.0	30.0	34.3	32.9
Forage	21.2	15.3	18.9	14.8
Agonistic	4.7	3.9	1.9	1.8
Amicable	3.0	3.0	3.4	2.2
On bank	3.0	3.0	4.9	5.8
Groom	2.7	2.5	1.9	1.1
Other	2.5	4.4	1.9	4.3
Number of events	406	406	265	277

<sup>a</sup>See Table 1 for description of behaviors.

<sup>b</sup>SM=scent marking.

## Figure Legend

Fig. 1a-b. Mean (SD) scent marking rates (SMR) (a) and scent marks per night (SM/night) (b) by the dominant male (*black bars*) and female (*grey bars*) Eurasian beaver. Results of Wilcoxon-Signed Ranks test shown. I: overall (March 7<sup>th</sup> – August 8<sup>th</sup>), II: spring (March 7<sup>th</sup> – June 1<sup>st</sup>), and III: summer (June 1<sup>st</sup> – August 8<sup>th</sup>). Significant results ( $P < 0.05$ ) are marked with an asterisk.

[Figure 1a,b]

