

# Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*)

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## Abstract

Monogamy in mammals is characterized by reduced sexual dimorphism in morphology and behaviour. Ten pairs of Eurasian beaver *Castor fiber* were radio-tracked to test how far this concept can be applied to movement behaviour by focusing on sex-related effects on territory sizes and movement patterns. Within monogamous pairs, males and females occupied territories of almost equal size during the whole radio-tracking period and more specifically after parturition. The territories of pair members overlapped on average by  $81.6 \pm 14.0\%$  SD while the territory overlap between residents and their neighbours was small to non-existent (on average between 0.5% and 2.2%). Males had larger 95% utility distributions than did females during the whole tracking period and after parturition. There was no significant difference between the 50% utility distributions for both sexes. Furthermore, males and females spent equal proportions of their time in territory border zones. There was a non-significant trend for males to move greater distances at night than females. Nightly distance moved correlated positively with territory size in females but not in males. Nightly distance moved correlated with neither body weight nor colony size. These results suggest that beavers show reduced sexual dimorphism in space use and movement patterns within adult monogamous pairs.

**Key words:** *Castor fiber*, distance moved, monogamy, radio-tracking, territory

## INTRODUCTION

Monogamy is rare in mammals, occurring in only 3–5% of all species (Kleiman, 1977; Komers & Brotherton, 1997). It is generally referred to as a 'prolonged association and essentially exclusive mating relationship between one male and one female' (Wittenberger & Tilson, 1980). Such a relationship can last over several breeding seasons (Kleiman, 1977; Clutton-Brock, 1989). Facultative monogamy is believed to have evolved as a result of female dispersion and the inability of single males to monopolize more than one female (Kleiman, 1977). Obligate monogamy on the other hand seems to have evolved as a result of the inability of a single female to raise her offspring alone and the need for extensive paternal care (Kleiman, 1977; Clutton-Brock, 1989).

A common feature in monogamous mammals is a reduction of sexual dimorphism both on the morphological and on the behavioural level (Kleiman, 1977). Kleiman (1977) argued that this trend for monomorphism was also applicable to the distribution

of responsibilities regarding the guarding of a joint territory. Although both partners of a pair bond generally contribute to the defence of a territory, especially in obligate monogamous species (Clutton-Brock, 1989), the contribution made by each sex may depend on evolutionary pressures such as parental care and predation pressure (Sommer, 2000). Direct territorial defence, however, is often difficult to quantify. Consequently authors generally focus on space use and movement patterns instead. Even though this has been studied in a variety of mammals (e.g. Blanford's fox *Vulpes cana*: Geffen & Macdonald, 1992; Japanese serow *Capricornis crispus*: Kishimoto & Kawamichi, 1996; Malagasy giant jumping rat *Hypogeomys antimena*: Sommer, 2000; muskrat *Ondatra zibethicus*: Marinelli & Messier, 1993; rock-haunting possum *Petropseudes dahli*: Runcie, 2000), no real consensus has been found on the effects of monogamy on space use.

Both the Eurasian *Castor fiber* and the North American *C. canadensis* beavers are herbivorous, semi-aquatic, mainly nocturnal rodents (Wilsson, 1971; Buech, 1995). They are generally similar, behaviourally and physically (Novak, 1987), but a chromosomal difference of eight chromosomes could potentially affect certain behaviours (Lavrov & Orlov, 1973). Based on typical family

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composition, long-term bonds between male and female adults, similar time budgets of paired adults, and paternal care, beavers are considered to be typical obligate monogamous mammals (Wilsson, 1971; Kleiman, 1977; Svendsen 1989; Sharpe & Rosell, in press). They live in family groups, generally ranging from four to eight individuals (Wilsson, 1971; Müller-Schwarze & Schulte, 1999) and consisting of one adult monogamous breeding pair, kits, yearlings, and possibly one or more sub-adults (Wilsson, 1971; Hodgdon & Lancia, 1983). Beavers are highly territorial (Aleksiuk, 1968; Wilsson, 1971) and family territories are maintained through aggression (Piechocki, 1977) and scent marking (Rosell, 2002) by all members older than 5 months (Wilsson, 1971; Hodgdon & Lancia, 1983). Because the Eurasian beaver has most attributes as discussed by Kleiman (1977), i.e. monogamy, long lasting pair bond and territoriality, it is a suitable model species for investigating the effects of a monogamous mating system on territory size and movement patterns of both members of a mated pair.

From general studies into their behaviour, there is some evidence for sex-related effects on territoriality and space use in beavers (Wilsson, 1971; Hodgdon & Lancia, 1983; Buech, 1995). However, much of the evidence is contradictory and is partly derived from studies on captive animals (Wilsson, 1971). Most of the studies that mention differences in territorial and movement behaviour between the two sexes are based on the adult pair of a single colony (Brady & Svendsen, 1981; Hodgdon & Lancia, 1983; Busher & Jenkins, 1985). Where several males and females have been studied, none of the authors have used paired data for statistical analysis to look at differences within monogamous pairs (Buech, 1995; Wheatley, 1997).

The hypothesis that monogamous mammals exhibit sexual monomorphism in space use and movement behaviour was tested by studying mated Eurasian beavers. It was predicted that mated individuals would show no significant differences in territory size, nightly distance moved, or time spent in territory border zones. Whether nightly distances moved correlated with territory size, body weight and colony size was also investigated.

## METHODS

### Study sites

Data were collected on the rivers Saua and Gvarv in Telemark, south-eastern Norway. Both rivers flow through a semi-agricultural and mixed woodland landscape. Vegetation along the rivers mainly consists of grey alder *Alnus incana* and to a lesser extent of bird cherry *Prunus padus*, common ash *Fraxinus excelsior*, rowan *Sorbus aucuparia*, alpine alder *Sambucus racemosa*, alder-buckthorn *Frangula alnus*, willows *Salix* spp., birch *Betula* spp. and Norway spruce *Picea abies* (O. Boszér & F. Rosell, pers. obs.).

The Saua River forms part of the Telemark Canal, and the study section is delimited at both ends by locks and weirs. The Gvarv River follows a more natural flow pattern

and empties into Lake Nordsjø. The study section on Gvarv included the lower reaches of the river and the upper part of Lake Nordsjø. Both rivers are wide and deep enough to make dam building unnecessary for beavers. Beavers have inhabited the area since the 1920s (Olstad, 1937) and hunting pressure in the study area is low to non-existent.

### Study animals

The study subjects were 20 Eurasian beavers (average  $\pm$  SD weights: males =  $21.6 \pm 1.7$  kg; females =  $22.7 \pm 2.1$  kg), who were the dominant pairs from 10 family group territories. During September (after weaning of kits) 1999 and 2000 and during March–April (before average date of parturition, see below) 2000 and 2001, we live-trapped the animals from a boat using landing nets (Rosell & Hovde, 2001). Permission for capture, handling and surgery was given by the Norwegian Experimental Animal Board and the Norwegian Directorate for Nature Management. To facilitate handling, each beaver was put head-first into a cloth sack. They were then weighed and sexed from the colour of the anal gland secretion (Rosell & Sun, 1999). All beavers were fitted with ear tags by manoeuvring the ear through a small hole in the sack. All individuals were tagged with numbered, coloured plastic ear tags (3.5 cm) (Dalton Continental B.V., The Netherlands) and/or monel metal ear tags (1.5 cm) (National Band and Tag Co., Newport, KY, U.S.A.) and implanted with a subcutaneous microchip (Destron, St. Paul, MN, U.S.A.) in the neck. The beavers did not respond aggressively to the confinement and none was visibly damaged by the procedure. Females were also checked for nipple size. It was assumed that all females gave birth during both years (2000 and 2001). This assumption was based on information from nipple size, presence of kits, sound of kits inside the lodge or bringing of branches into the lodge during July (Wilsson, 1971). Dominance status was determined from previous trapping records of weights, incidence of lactation and behavioural observations (F. Rosell, pers. obs.). Family group size was determined from data collected during an extensive trapping programme that had started in 1998 and was still ongoing at the end of this study. All trapped individuals within a group territory were assigned to age classes based on body weight and size, following Rosell & Pedersen (1999) and Parker *et al.* (2001). Kits (< 1 year old) were not included in group size because they do not take part in active defence of a territory (Wilsson, 1971).

Before the 2000 field season, the beavers from 6 of the 10 pairs were implanted with an Alterra TX30.3A1 intraperitoneal 30 MHz-radio transmitter (63 g) equipped with a temperature and movement sensor (Alterra (IBN/DLO), Wageningen, the Netherlands). The animals were divided into 2 groups, each group receiving a different anaesthetic treatment. Beavers in group 1 were injected with 0.05 mg medetomidine/kg (Domitor 1 mg/ml, Orion Corporation Animal Health, Turku, Finland), 5 mg of ketamine/kg (Narketan 100 mg/ml, Chassot AG, Bern,

Switzerland) and 0.1 mg butorphanol/kg (Torbugesic 10 mg/ml, Fort Dodge Laboratories, IA, U.S.A.). All drugs were injected intramuscularly into the gluteal muscle at the same time with separate syringes. In addition to these drugs, the beavers in group 2 were also injected intramuscularly with 0.25 mg of midazolam/kg (Midazolam 5 mg/ml, Alpharma AS, Oslo, Norway) simultaneously with the other drugs. The addition of midazolam improved the anaesthetic regime. A 6-cm-long ventral midline incision was made to gain access to the peritoneal cavity. The transmitters were soaked in 10 mg/ml benzalkonium chloride, pre-warmed to body temperature and rinsed with sterile saline before being placed to float freely in the peritoneal cavity (Ranheim *et al.*, in press). The incision was closed in 2 layers using a Polydioxanone 1–0 absorbable suture (Ethicon PDS II, Johnson & Johnson International, Sommerville, NJ, U.S.A.) (Ranheim *et al.*, in press).

After surgery the beavers were injected intramuscularly with procaine/benzathine penicillin 100 000 IU/kg (Penikel 15+15, Kela Laboratoria NV, Hoogstraten, Belgium) to minimize the risk of post-operative wound infections. Recovery from anaesthesia was shortened by intramuscularly injecting all animals with 0.25 mg/kg of atipalmezole (Antisedan 5 mg/ml, Orion Corporation Animal Health). All animals were kept in a dark box for 3–5 h before being released and allowed a minimum of 1 week before tracking began to allow them to recover completely. The behaviour and movement of the beavers did not seem to be affected by the implanted transmitters, except for the first 2 days when more time was spent inside the lodges. The transmitter signal was detected using a 1-element loop antenna (Alterra, 6700 AA Wageningen, the Netherlands) and an Icom IC-R10 receiver (Icom Inc., Osaka, Japan). Signal reception range varied between 300 and 600 m from a boat (Nolet & Rosell, 1994).

In 2001, 15 beavers (7 of which had been previously fitted with an intraperitoneal transmitter that had failed and 8 new ones) belonging to 8 of the 10 pairs were fitted with external tail transmitters (Advanced Telemetry Systems Inc., Isanti, MN, U.S.A., Model 16 M ear tag for beaver tail, weight = 38 g) operating at 142 MHz. A belt plier was used to make a hole in 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 screw, washer and nut. A plastic holder was inserted to facilitate the withdrawal of the screw when the transmitter was recovered. No anaesthetics were used for this procedure since beaver tails are mainly composed of adipose tissue and the animals showed no apparent distress. Other researchers have found that the tissue in the tail is too dense for the anaesthetic liquid to penetrate (Rothmeyer, McKinstry & Anderson, 2002). The beavers were released near the capture site < 20 min after capture. Their behaviour did not seem to be affected by the procedure since they were observed showing normal behaviour < 15 min later. The signal was detected using a hand-held RX-98 H tracking receiver with inbuilt foldable antenna (TVP Positioning AB, Lindsberg, Sweden). Mean  $\pm$  SD signal reception range was 353  $\pm$  112 m from a boat.

### Radio-tracking and data collection

Beavers were radio-tracked at night between 15 March and 8 August 2000 and between 8 April and 16 August 2001 resulting in an average of  $6 \pm 3$  tracking nights per animal and  $192.4 \pm 107.8$  fixes per animal. Radio-tracking equipment was used to initially locate the focal animal in its daytime resting-place. When the animal emerged, it was followed until it entered the lodge or burrow in the morning and stayed there for at least 30 min. All radio-tracking was conducted from a boat equipped with an outboard motor, and when dark, the subject was illuminated using spotlights. With due care, disturbance from the spotlights and the noise of the motor was minimal and unlikely to have affected the animals' behaviour (Buech, 1985; Nolet & Rosell, 1994). Both members of a pair were tracked on successive nights. The first member of a pair to be tracked was determined at random. Both members of the pair could not be tracked simultaneously because constant behavioural observations were carried out for 2 separate projects (see Romme Thomsen, 2002; Sharpe & Rosell, in press) on each focal individual throughout the night. Since mated individuals tend to forage independently from each other (J. Herr & F. Rosell, pers. obs.) simultaneous tracking would have interfered with visual observations of behaviour.

Location fixes of the focal animal were taken every 15 min throughout the tracking period and marked on 1:5000 scale field maps to an accuracy of 5 m. If the beaver was on land and out of sight when a location fix was due, its position was determined by taking the crossing of 1 bearing and the riverbank (Nolet & Rosell, 1994). This was appropriate because beavers spend the greatest proportion of their time on land within 1 m of the water's edge (Nolet, Hoekstra & Ottemheim, 1994). All location fixes ( $n = 3847$ ) were later digitized into a geographical information system (GIS) (ArcView 3.2) (Environmental Systems Research Institute, CA, U.S.A.).

### Territory size and overlap

River outlines were digitized onto ArcView GIS from 1:5000 field maps (Gvarv River) or obtained in digitized vector format (Saua River). All digitized location fixes for each beaver were then plotted over the river outlines and minimum convex polygons (MCP) were drawn around each beaver's fixes using the ArcView extension 'animal movement' (Hooge & Eichenlaub, 1997). Male and female territory sizes were expressed as length of riverbank and determined by measuring the total length of both riverbanks delineated by a given MCP. Even though MCPs tend to include stretches of unused habitat, it was felt that they were an accurate representation of the territory. This was based on the idea that territories are essentially linear and hence even unused habitat falling between the territory borders remains essentially unavailable to other beavers. Joint territories were defined as the riverbank included in the MCP based on the fixes from the 2

individuals of mated pairs. Asymptotes for territory size were reached on average after 120 location fixes and autocorrelation of the data was ignored since the MCP method does not require independence of fixes (Harris *et al.*, 1990). Male–female (pair members) territory overlap was defined as the average of the percentage of male riverbank overlapping with female riverbank and the percentage of female riverbank overlapping with male riverbank. Territory overlap between residents and their neighbours was calculated only for animals on the Saua River and expressed as percentage of a resident's (male and female) total riverbank overlapping on average with each known neighbour's (male and female) riverbank. Overlaps were based on MCPs for the whole tracking period only.

### Territory use

The fixed kernel method with an ad hoc smoothing parameter ( $h$ ) (automatically determined by the ArcView extension) was used to compare the utility distributions (UD) of mated beavers within their territories (Worton, 1989). UD maps the intensity of use of riverbank (Powell, 2000) and were expressed as length of riverbank within 95% (used to represent total home range) and 50% (arbitrarily defined as core area) fixed kernel contours (Blundell, Maier & Debeve, 2001). To avoid getting a bias towards stretches of riverbank with lodges or burrows in which the animals spent significant proportions of their time all successive fixes within a lodge or burrow, except the first 1, were discarded from the dataset. Autocorrelation of the data was not taken into account since kernel densities do not require independence of fixes (de Solla, Bonduriansky & Brooks, 1999).

### Time at border

Border zones in territories were arbitrarily defined as the outer parts of the territory containing together 20% of the total length of riverbank within a territory. The number of fixes within these border zones was determined for each territory and the time spent at the border by each animal was expressed as the percentage of the total number of fixes located within such border zones. This analysis was carried out for male, female and joint territories.

### Nightly distance moved

Nightly distance moved was calculated by ArcView and expressed as the sum of all straight-line distances between successive fixes collected during a given radio-tracking night. For each animal the mean nightly distance moved was then calculated.

### Data analysis

All variables described above were analysed by using all data collected on each individual beaver (pairs:  $n = 10$ )

during the whole tracking period. Furthermore, territory size, UD and distance moved were also analysed by only focusing on data collected after parturition (from average date of parturition (1 June) onwards; Wilsson, 1971; F. Rosell, pers. obs.). This analysis was only carried out for pairs ( $n = 7$ ) where each member was tracked for a minimum of 3 nights during the period after parturition to determine whether the presence of kits induced differences in territory size and movement patterns within these pairs. Data collected before parturition could not be analysed separately owing to small sample size of tracking nights per individual.

All statistical analysis was carried out with Minitab version 13 (Minitab Inc., 2000). Data sets were tested for normality and for equal variances using the Anderson–Darling and Levene's test, respectively (Dytham, 1999). Where necessary, square root transformations were used to transform non-normal data sets. All comparisons were based on differences between males and females from mated pairs. Hence paired  $t$ -tests were used on normally distributed data and the Wilcoxon signed-rank test was used on data that deviated from normality. All results are presented as mean  $\pm$  SD. Owing to fundamental flaws with retrospective power analysis, this type of analysis was not used (Hoenig & Heisey, 2001). Since preliminary analysis revealed no interactions between territory size, body weight and colony size, 3 separate Pearson product moment correlations ( $r_p$ ) were used to test whether distance moved correlated with any of these variables (Dytham, 1999). The significance level was set at 0.05, and all tests were 2-tailed.

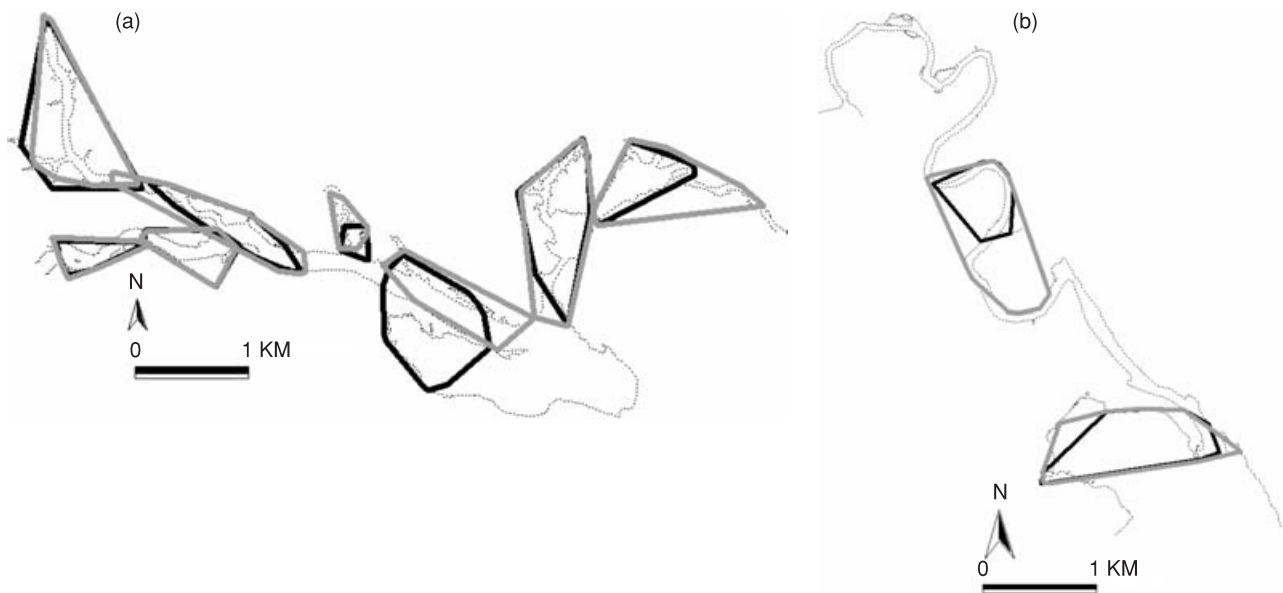
## RESULTS

### Territory size and overlap

No significant difference was found between male and female territory sizes of mated pairs over the whole tracking period (Fig. 1, Table 1). Mean joint territory size over the whole tracking period was  $4429 \pm 1380$  m and the territories of pair members overlapped on average by  $81.6 \pm 14.0\%$ . Territory overlap between neighbours was minimal. Territories of resident males overlapped by only  $2.2 \pm 2.6\%$  and  $1.6 \pm 1.8\%$  with each known male and female neighbour, respectively, while territories of resident females overlapped by only  $0.9 \pm 3.0\%$  and  $0.5 \pm 1.0\%$  with each known male and female neighbour, respectively. During the period after parturition, males and females occupied territories of similar size (Table 2).

### Territory use

The kernel method resulted in the delineation of several disjunct contours per territory. Over the whole tracking period, the length of riverbank delineated by 95% kernel contours was significantly larger in males than in females (Table 1). There was, however, no significant difference between the two sexes during the same period in the length



**Fig. 1.** Male (grey) and female (black) Eurasian beaver *Castor fiber* territories ( $n = 10$ ) delineated by minimum convex polygons based on radio-tracking data from the whole tracking period: (a) Saua River; (b) Gvarv River.

**Table 1.** Means  $\pm$  SD and test statistics for six variables measured on males (M) and females (F) of Eurasian beaver *Castor fiber* pairs ( $n = 10$ ) during the whole tracking period

Variable (units)	Mean $\pm$ SD		Test statistics
	M	F	
Territory size (m of riverbank)	3900 $\pm$ 1514	3483 $\pm$ 1720	$t = 1.07, P = 0.311^d$
95% UD <sup>a</sup> (m of riverbank)	3755 $\pm$ 1707	3098 $\pm$ 1750	$t = 2.33, P = 0.045^d$
50% UD (m of riverbank)	1035 $\pm$ 967	715 $\pm$ 468	$t = 1.37, P = 0.205^d$
Distance moved (m night <sup>-1</sup> )	3756 $\pm$ 2247	2572 $\pm$ 1204	$t = 1.64, P = 0.136^d$
Time at own border <sup>b</sup> (% of total fixes)	28.7 $\pm$ 14.4	27.6 $\pm$ 11.8	$Z = 30.0, P = 0.838^e$
Time at joint border <sup>c</sup> (% of total fixes)	22.8 $\pm$ 11.0	19.6 $\pm$ 11.1	$Z = 39.5, P = 0.241^e$

<sup>a</sup> UD, utility distribution based on kernel contours.

<sup>b</sup> Own border, border within an individual's territory.

<sup>c</sup> Joint border, border within a pair's joint territory.

<sup>d</sup> Paired  $t$ -test.

<sup>e</sup> Wilcoxon signed-rank test.

**Table 2.** Means  $\pm$  SD and test statistics for four variables measured on males (M) and females (F) of Eurasian beaver *Castor fiber* pairs ( $n = 7$ ) after parturition (1 June)

Variable (units)	Mean $\pm$ SD		Test statistics <sup>b</sup>
	M	F	
Territory size (m of riverbank)	4118 $\pm$ 1560	3355 $\pm$ 1709	$t = 2.28, P = 0.063$
95% UD <sup>a</sup> (m of riverbank)	4314 $\pm$ 1809	3329 $\pm$ 1870	$t = 2.52, P = 0.045$
50% UD (m of riverbank)	1273 $\pm$ 1083	757 $\pm$ 403	$t = 1.65, P = 0.149$
Distance moved (m night <sup>-1</sup> )	4664 $\pm$ 2247	3313 $\pm$ 1467	$t = 1.38, P = 0.216$

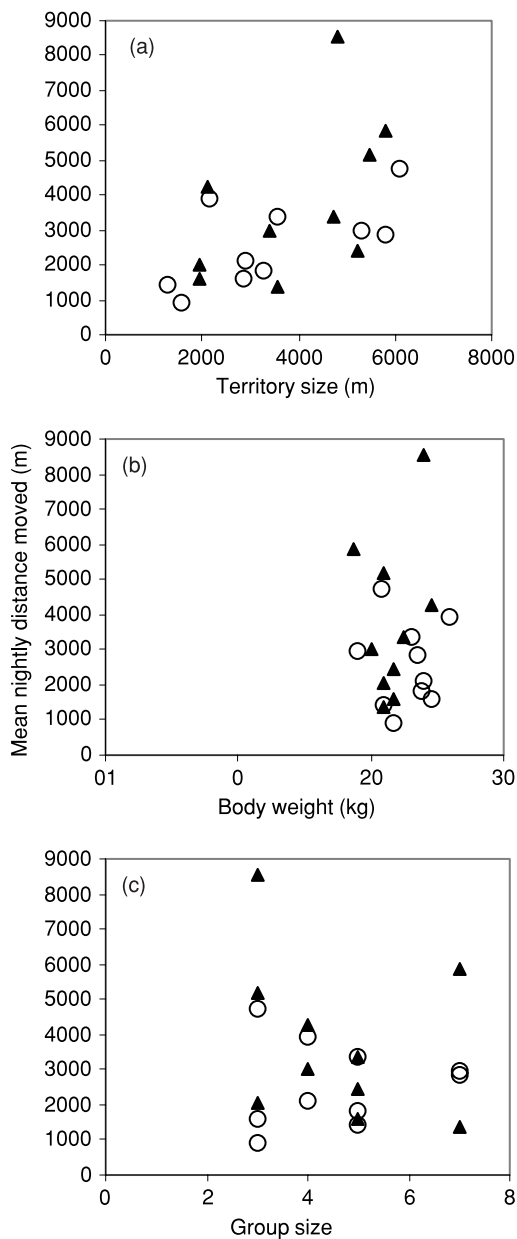
<sup>a</sup> UD, utility distribution based on kernel contours.

<sup>b</sup> Paired  $t$ -test.

of riverbank delineated by 50% kernel contours (Table 1). After parturition, 95% kernel contours delineated significantly longer stretches of riverbank in males than in females (Table 2), but no such difference was found for riverbank delineated by 50% kernel contours (Table 2).

#### Time at border

Over the whole tracking period and within mated pairs, there was no significant difference in the time that each partner spent within border zones of its own individual



**Fig. 2.** Relationship between mean nightly distance moved (m) for male ( $\blacktriangle$ ;  $n = 10$ ) and female ( $\circ$ ;  $n = 10$ ) Eurasian beavers *Castor fiber* during the whole tracking period and: (a) territory size (m); (b) body weight (kg); (c) group size (kits excluded).

territory (Table 1). Similarly, both sexes spent equal proportions of their time within border zones of their joint territories (Table 1).

#### Nightly distance moved

No significant difference was found between nightly distance moved by males and females over the whole tracking period (Table 1). Pearson product moment correlation indicated no significant positive association between nightly distance moved and territory size in males ( $r_p = 0.54$ ,  $n = 10$ ,  $P = 0.108$ ) (Fig. 2a). In females, on

the other hand, a positive significant correlation between nightly distance moved and territory size was found ( $r_p = 0.64$ ,  $n = 10$ ,  $P = 0.045$ ) (Fig. 2a). Nightly distance moved did not correlate with body mass (kg) in males ( $r_p = 0.25$ ,  $n = 10$ ,  $P = 0.478$ ) or females ( $r_p = -0.02$ ,  $n = 10$ ,  $P = 0.961$ ) (Fig. 2b). There was no significant correlation between group size and nightly distance moved by males ( $r_p = -0.30$ ,  $n = 10$ ,  $P = 0.392$ ) or females ( $r_p = 0.08$ ,  $n = 10$ ,  $P = 0.817$ ) (Fig. 2c). After parturition, males and females moved on average equal nightly distances (Table 2).

#### DISCUSSION

Our findings on territory size, territory overlap, nightly distance moved and time spent at borders all suggest little difference in the use of space between adult Eurasian beavers within mated pairs. Even though small sample size probably resulted in low power, no convincing evidence was found to suggest strong sex-related effects on movement behaviour between pair members. Hence the beaver can be regarded as a good model organism for use of space and movement patterns in obligate monogamous mammals because it seems to fit most predictions concerning monomorphism in monogamous mammals (Kleiman, 1977).

#### Territory size, overlap, and use

Territory sizes reported here are in line with territory sizes reported for beavers elsewhere (Davis, 1984; Nolet & Rosell, 1994; Fustec *et al.*, 2001) and lie well within the range of territory sizes (0.5–12.8 km) reviewed by Macdonald *et al.* (1995). However, none of these authors made an attempt to compare male and female territory sizes. Equal home-range sizes have also been described in a range of other monogamous mammals (i.e. Blanford's fox *V. cana*, Geffen & Macdonald, 1992; mahogany glider *Petaurus gracilis*, Jackson, 2000; rock-haunting possum *P. dahli*, Runcie, 2000). The male–female territory overlap of 81% found in this study is in line with territory overlaps among paired adults from other monogamous mammal species (Cape porcupine *Hystrix africaeaustralis*: 75%, Corbet & Van Aarde, 1996; mahogany glider *P. gracilis*: 85.9%, Jackson, 2000; Blanford's fox: 79.9%, Geffen & Macdonald, 1992). Furthermore, minimal intra- and intersex overlaps between residents and neighbours are generally seen as a good indication for strong territorial behaviour of both sexes (Marinelli & Messier, 1993; Powell, 2000). The fact that females had significantly smaller 95% UD's than males indicates that females concentrated their movements on smaller sections of riverbank within their territory. As territory use depends on habitat preferences as well as scent marking activities and because the impact of both types of activities on overall habitat use was not explicitly investigated, it is difficult to determine exactly what caused the trend for larger kernel home ranges in males.

### Time at border

Since beavers rarely move over land for considerable distances, intrusions by neighbours or strangers into a territory will typically occur through the water at the up- and downstream border zones. To prevent such intrusions, patrolling borders should be an important part of the beaver's territorial behaviour. The only two fierce fights observed during the entire study between beavers belonging to different family groups (twice involving at least one dominant female), occurred at territory borders (J. Herr, pers. obs.; L. Romme Thomsen, pers. comm.). Furthermore, an ear-tagged adult, dominant female was found dead at the upstream border of its own territory, showing clear signs of bite wounds. By the time it was found, its position had already been taken over by a new female (F. Rosell & J. Herr, pers. obs.). The fact that both pair members spent equal proportions of their time within these border zones suggests that both sexes are involved in patrolling territory borders.

### Nightly distance moved

Nightly distances moved by our study beavers were comparable to distances reported from *C. fiber* in the Netherlands (Nolet & Rosell, 1994) and *C. canadensis* in North America (Davis, 1984). However, as with territory sizes, these authors did not compare males and females. No evidence was found for significant differences in the nightly distances moved by the two pair members, but there was a trend for males to move longer distances. This could be a consequence of a longer activity period in males (Sharpe & Rosell, in press) or that in two pairs the males moved much longer distances than the females, while distances were similar for all other pairs. Rather than concentrating on distances moved, Brady & Svendsen (1981), Busher & Jenkins (1985) and Buech (1995) looked at the time spent moving by male and female North American beavers. Their results compare with ours in that males spent more time moving than females, from which the authors concluded that patrolling the territory was a typical male-related behaviour. If that were so, we would expect males to move longer distances per night and show a positive correlation between nightly distance moved and territory size. In our study area, both sexes showed a trend for nightly distance moved to increase with territory size. However, this trend was significant only in females, which is another indication that females play a role in the patrol of the territory. However, comparisons between North American studies and ours are limited because the time spent moving cannot be directly equated with distance moved. Furthermore, Brady & Svendsen (1981) and Busher & Jenkins (1985) drew their conclusions from data collected on a single pair and Buech (1995) investigated movement of only three males and four females from three colonies. The stream and lake habitats occupied by these North American beavers are also different from the large rivers occupied by beavers

in our study, which could have impacted on the observed behaviour.

No evidence was found for decreased activity by the females after parturition. Hence, our findings cannot confirm those of Wheatley's (1997) suggesting that females decrease their home-range size and distances moved in the presence of young owing to nursing activities. Equal distances moved by either sex have also been reported in the mahogany glider (Jackson, 2000), Blanford's fox (Geffen & Macdonald, 1992) and muskrats (Marinelli & Messier, 1993), while Sommer (2000) found male Malagasy jumping rats to increase movements when young are present. The fact that distance moved by either sex did not correlate with group size indicates that movements (be they for patrolling or other activities) are not influenced by the total number of individuals in the group. Hence there is no evidence that dominant adults reduce their patrolling activity with an increasing number of subordinate helpers in the colony. Finally, the lack of correlation between nightly distance moved and body weight is probably not surprising considering that differences in body weight between different beavers were fairly small.

Our results suggest that both sexes of adult Eurasian beavers exhibit rather similar use of space and movement behaviour. Unfortunately it is difficult to infer directly equal territoriality from equal use of space in both sexes. In a concurrent study, Romme Thomsen (2002) found similar scent marking patterns in both sexes. However, overall, males deposited more scent marks owing to longer activity periods. Since scent marking is the beaver's main way of defending its territory (Rosell, 2002) these results seem to confirm that Eurasian beavers exhibit little sexual dimorphism, even in a typical territorial behaviour-like scent marking. Romme Thomsen's (2002) results on direct territorial behaviour such as scent marking in conjunction with our results on movement patterns lead us to the conclusion that monomorphism in use of space is probably the result of similar territorial behaviour in both pair members.

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