

# **SCENT MARKING IN THE EURASIAN BEAVER (*Castor fiber*) AS A MEANS OF TERRITORY DEFENSE**

**FRANK ROSELL\*, FRODE BERGAN AND HOWARD PARKER**

Telemark College, Department of Environmental Sciences, N-3800 Bø, Norway.

\* To whom correspondence should be addressed

**Abstract-** Beaver (*Castor* spp.) normally scent mark by depositing castoreum and/or anal gland secretion on scent mounds close to the water's edge. The aim of this study was to investigate the hypothesis that the Eurasian beaver (*C. fiber*) scent marks as a means of territory defense. Scent marking behavior was studied during an entire year (1 April 1995 - 31 March 1996) in 7 adjacent territories along 9.2 km of the Bø River in Telemark County, Norway. The number and location of fresh scent marks were recorded biweekly. The main results showed that: 1) the number of scent marks in territories was significantly higher in spring, when dispersal of subadults normally occurs, than during the rest of the year; 2) the number of scent marks was clumped near territorial borders; and 3) the number of scent marks were significantly greater upstream than downstream of the lodge.

**Key words-** Beaver, *Castor fiber*, *Castor canadensis*, castoreum, anal gland secretion, scent mound, scent marking, territorial behavior, Norway.

## **INTRODUCTION**

Communication and social recognition in many mammals are based on olfactory signals (Wynne-Edwards, 1962; Ralls, 1971; Schulte, et al., 1994). Scent marking has high persistence and is effective even in the absence of the sender (Wynne-Edwards, 1962; Bollinger, 1980). Olfactory communication can be defined as the process whereby a chemical signal is generated by a presumptive sender and transmitted (generally through the air) to a presumptive receiver, who by means of adequate receptors, can identify, integrate and respond (either behaviorally or physiologically) to the signal (Eisenberg and Kleimann, 1972).

Mammalian scent marking is often associated with territorial defense (Gosling, 1990). It is widely accepted that mammals scent mark their territories to advertise their occupancy and ownership of the territory (Peters and Mech, 1975; Macdonald, 1980; Erlinge et al., 1982; Gosling, 1982; Gorman and Mills, 1984; Smith et al., 1989), but it is still under debate how scent marks actually function in terms of territory maintenance (Gorman, 1990; Gosling, 1990; Richardson, 1991). For many years it was believed that scent marks help deter intruders from entering a territory, or at least to intimidate them (Hediger, 1949; Geist, 1964; Johnson, 1973). Although scent marks are unlikely to totally exclude all intruders from exploiting resources within a territory, they may limit the degree (in time and space) to which the territory is intruded, and hence indirectly protect its resources. The fact that not all territorial intruders are obviously intimidated has stimulated the search for new explanations as to how scent marks function in territory maintenance (Gosling, 1982; Gosling, 1990; Richardson, 1993).

The beaver (*Castor* spp.) defends a territory and usually lives in colonies consisting of an adult pair, kits, yearlings, and sometimes subadults (Bradt, 1938; Aleksiuk, 1968; Bergerud and Miller, 1977; Novak, 1977; Svendsen, 1980a; Svendsen, 1989; Nolet and Rosell 1994). In a review of 13 earlier studies of the Eurasian beaver (*C. fiber*), Rosell and

Parker (1995) found an average colony size of 3.8 (SD = 1.0, range = 2.4-5.5). The beaver is monogamous, which is rare amongst the Rodentia, and can occupy the same lodge for many years (Wilsson, 1971; Svendsen, 1980a; Hodgdon and Lancia, 1983; Svendsen, 1989).

Olfactory communication is likely to be important to beaver as they have poorly developed long-distance acoustic communication (with the exception of tail-slapping), are primarily nocturnal, and therefore are less reliant upon visual communication (e.g. Wilsson, 1971; Schulte, 1993). The beaver possesses two pairs of organs used in scent marking (Hodgdon, 1978; Walro and Svendsen, 1982; Valeur, 1988). These are located in two cavities between the pelvis and the base of the tail, and consist of two castor sacs and two anal glands. Both castoreum from the castor sacs and/or oil from the anal glands are secreted onto small piles of mud and debris close to the water's edge (Wilsson, 1971; Svendsen, 1980b; Rosell and Nolet, 1997), though castoreum is probably used the most (Bollinger, 1980; Tang et al., 1993; Schulte et al., 1994). All age classes and both adults mark within the territory (Aleksiuk, 1968; Wilsson, 1971; Butler and Butler, 1979; Svendsen, 1980b; Buech, 1995).

One of the main functions of scent marking appears to be the maintenance of territorial rights in both North American (*C. canadensis*) (Houlihan, 1989; Welsh and Müller-Schwarze, 1989), and Eurasian beaver (Rosell and Nolet, 1997). If the primary function of scent marking is territorial defense, then marking is predicted to be most frequent when transient animals from other families are most likely to enter occupied areas, i.e. in spring or early summer when dispersal of subadult beaver normally occurs (Beer, 1955; Bergerud and Miller, 1977; Molini et al., 1980; Svendsen, 1980a).

The central problem facing all animals that scent mark their territories is where to place their marks. Given the constraints of time and energy, scent marks should not be deployed at random, but instead in an organized pattern that maximizes their chance of being

discovered by the individuals to whom they are directed, to give the earliest possible warning to a potential trespasser. Such a place might be territorial borders (Gosling, 1982; Gorman, 1990), and the upstream edge of the territory should be most frequently marked if the movement of dispersing individuals is predominantly downstream. The pay-off to the owner is the reduced costs of competition (Gosling, 1986; Gosling and Mckay, 1990).

In this paper we focus on the temporal and spatial distribution of scent marking in the Eurasian beaver during an entire year to illustrate seasonal differences in the pattern of marking. We investigated the hypothesis that Eurasian beaver scent mark as a means of territory defense. The following two predictions were tested: 1) the number of scent marks in territories is highest during spring when dispersion of subadults normally occurs; and 2) scent marks are not randomly placed inside the territory.

## METHODS AND MATERIALS

*Study Area.* The study was conducted on a 9.2 km section of the Bø River in the municipality of Bø ( $59^{\circ} 25' N$ ,  $09^{\circ} 03' E$ ), Telemark County, Norway. The part of the river studied averages 35 m in width and meanders through mixed woodland and agricultural countryside dominated by marine and fluvial deposits (Bergan, 1996). Vegetation along the river consists mainly of alder (*Alnus incana*) with lesser amounts of willow (*Salix* spp.), birch (*Betula pubescens*), aspen (*Populus tremula*), rowan (*Sorbus aucuparia*), Norwegian spruce (*Picea abies*), and Scots pine (*Pinus sylvestris*). During winter, a hydroelectric power station further upstream regulates flow, keeping the river ice-free. This provided us with the opportunity to study scent marking behavior uninhibited by the usual constraints of winter ice. The river has been occupied by beaver since the 1930s (Olstad, 1937).

*Study Animals and Colonies.* The study was conducted between 1 April 1995 and 31 March 1996. The number of animals in each colony was determined by direct counts using

light sensitive binoculars. Counts were made from the river bank or from a canoe around dawn and dusk, at approximately 14-days intervals, both in August and September of 1995. The animals were classified as kits, yearlings, and adults  $\geq$  2-years-old based on body size, tail size (length x width) and weight (Townsend, 1953; Patric and Webb, 1960; Jackson, 1991; Van Deelen, 1994). The sound of the tail-slap also gave a good indication of the age-class of the animal, as smaller animals make lighter "slap-sounds".

*Delineation of Territories.* Territorial borders for each colony were determined from regular sight observations of animals moving up and downstream of the lodge throughout the year. Individual movements were plotted on maps. Particular notice was made of the extreme distances moved away from the lodge in both directions. The borderline between territories was drawn at a point midway between the extremes of neighboring territory holders. The two colonies at the outskirts of the study area (colony 1 and 7) were naturally delineated from colonies outside the study area by waterfalls or riffles, which also constituted territorial boundaries. The closest neighbor was found by measuring the midstream distance between the two occupied lodges. The territory size was defined as the total length of river bank (sum of both sides) between upper and lower territorial borders of a colony.

*Scent Marking.* Each side of the river within the study area was searched once every 14 days (biweekly) for newly used scent mounds from 1 April 1995 to 31 March 1996 using a canoe. Scent mounds are small piles, usually of mud and debris, scraped together by beaver upon which secretion from the castor sacs and/or anal glands are deposited (Aleksiuk, 1968; Wilsson, 1971). A freshly marked scent mound, i.e. with a scent detectable by the human nose at 2 cm or more, was termed a "scent mark". This definition also included marks directly on the ground or on tussocks. Minimum distance between two different scent mounds was 10 cm. If a scent mound did not have a smell detectable by the human nose, it was thought to be old and excluded from analysis (see however Bollinger, 1980; Schulte, 1993). Each scent

mark was labelled for recognition, either with a small wooden stake placed 0.5 - 1 m behind the mark, or by writing the number on natural objects such as trees. All scent marks found during each biweekly trip were registered on a 1:5000 map. After each land visit, boots were cleaned in water to minimize transport of scent from one area to another. Whenever possible, marks were smelled from the canoe, i.e. without actually stepping out.

The year was divided into 4 periods which roughly coincided with 4 different behavioral events for the beaver: breeding (January-March) (Wilsson, 1971), dispersal of subadults (April-June) (e.g. Molini et al., 1980; Svendsen, 1980a), kits emerging from the lodge (July-September) (Wilsson, 1971) and winter preparations (October-December) (e.g. Wilsson, 1971).

*Statistical Methods.* Mean values are presented with standard errors. We used nonparametric statistics in accordance with Siegel and Castellan (1988). Nonparametric tests were corrected for ties. Probability values are two-tailed and 5 % was used as the level of significance. Mean values  $\pm$  2 standard error gives approximately 95 % confidence intervals.

## RESULTS

Seven colonies were located within the study area. A total of 2628 scent marks ( $\bar{X} = 375 \pm 85$  colony $^{-1}$  year $^{-1}$ , range 197-431) were found within the 7 territories during the study. From 30 November 1995 to 9 March 1996 all scent marks were located on snow (N=380). Twenty-eight beaver were recorded by sight observations during the intensive sight observation periods in August and September 1995. Colony size varied from 3 to 7 ( $\bar{X} = 4 \pm 0.6$ , N=7). Seventy-one percent were adults, 22 % were 1-year-olds and 7 % were kits. Only colony 7 produced young in 1995 (two kits were born). All colonies, except colony 4, had one yearling. The study area had a density of 0.76 colonies and 3.0 animals per kilometre stream length. Average territory size was  $2.6 \pm 0.3$  km (length of both banks, range 1.5-3.4). No

seasonal difference in territory size was observed, and the borders were stable throughout the year.

*Number of Scent marks.* No significant correlation was found between total number of scent marks of a colony and distance from its main lodge to the main lodge of the nearest neighboring colony (Spearman rank-correlation coefficient  $r_s=0.095$ ,  $N=7$ ,  $P=0.840$ ), nor between the number of scent marks and territory size ( $r_s=0.564$ ,  $N=7$ ,  $P=0.187$ ). Beaver in colonies with two neighboring territories ( $N=5$ ) scent marked on the average  $373 \pm 44$  times, not significantly different from colonies ( $N=2$ ) with only one neighboring territory ( $\bar{X}=382 \pm 49$ , Mann-Whitney U-test,  $U=4.0$ ,  $P=0.699$ ).

*Seasonal variation.* There was a significant difference in the mean number of scent marks per colony between each of the four seasons (Kruskal-Wallis one-way ANOVA,  $X^2=21.04$ ,  $df=3$ ,  $P=0.001$ ) (Figure 1). The mean number of scent marks per colony ( $N=7$ ) was higher during the dispersal of subadults ( $\bar{X}=199 \pm 11$ ), than during the other three periods (kits emerging from the lodge =  $87 \pm 15$ ; winter preparations =  $26 \pm 5$ ; breeding =  $63 \pm 10$ ). Scent marking was most frequent in May (weeks 18-21). A peak in the number of scent marks occurred in all colonies between the beginning of April (week 14/15) and the end of May (week 20/21). On 21 June 1995 at 14:15 we observed a beaver (probably a subadult) on land inside the territory of colony 5. It entered the water, and we followed the animal at a distance by canoe as it moved downstream in a head wind. It swam rapidly past the lodge and through the territory of colony 6. When entering the border area between colony 6 and 7 it slowed down, and approached a site at the shoreline with a high density of scent marks, while simultaneously making up-and-down sniffing movements with the head. It then swam close to shore at a lower speed until reaching the lodge of colony 7, into which it dove. We assume that this was a dispersing subadult from colony 7.

Scent marking almost ceased during weeks 22/23 when a flood raised water levels by 90 cm. Scent marking increased briefly thereafter, then gradually declined when kits emerged from the lodge and during winter preparations. The number of scent marks increased again in January-February (weeks 2-9) during breeding, and then decreased briefly, before increasing again during the dispersal of subadults.

*Location of Scent Marks.* The majority of scent marks were clumped near territorial borders within a zone of about 150 m throughout the year (Figure 2). During the winter preparation period, beaver scent marked almost exclusively at territorial borders. Beaver in the two colonies at the peripheries of the study area (colonies 1 and 7) concentrated scent marks only along the territorial border adjacent to their single neighbor colony.

Significantly more scent marks were located between the lodge and the upstream territorial border ( $\bar{X} = 267 \pm 46$ , N=7) than between the lodge and the downstream border ( $\bar{X} = 107 \pm 35$ , N=7) (Mann-Whitney U-test, U=6.0, P=0.018) (Figure 2). Beaver in all colonies, except 1 and 2, scent marked significantly more upstream of the lodge than downstream. This was true, even when the nearest neighbor's lodge was located downstream (Figure 2).

## DISCUSSION

*Temporal distribution.* The number of scent marks was highest in spring (April - May). This is in accordance with our first prediction and in agreement with earlier studies for both species of beaver (e.g. Butler and Butler, 1979; Müller-Schwarze and Heckman, 1980; Rosell and Nolet, 1997; Svendsen, 1980b). The random observation of the apparently dispersing beaver from colony 7 was analogous to that described by Hodgdon (1978) for a beaver dispersing through an occupied territory. Fresh scent marks were indeed found in the

immediate vicinity of the on-land observation of this beaver, and may be the explanation for why colony 5 scent marked more frequently during the spring than the other colonies.

The considerable and rapid increase in water level at the end of May 1995 probably led to a constant washing out of scent marks, and hence to a low number of recordings in that particular period. A similar phenomenon was observed in the Netherlands (Rosell and Nolet, unpublished).

Hodgdon (1978) suggested that the intense marking activity following ice-out might have been a delay of marking activity caused by the physical barrier of winter ice, and thus not a true reflection of actual marking cycles. He suggested that an analysis of resident family scent marking cycles at more southerly latitudes, where the ice barrier was absent, should provide an assessment of any relationship between gonadal activity and marking. Indeed, despite its northerly location, the Bø River remains ice-free throughout the year due to hydroelectric regulation. Results from our study therefore suggest that the high frequency of scent marking in spring probably is primarily associated with a peak in dispersal of subadults at this time, and is not a delay in the scent marking peak due to winter ice. However, prolonged low temperatures and ice can limit beaver activity (Wilsson, 1971; Lancia et al., 1982; Hodgdon and Lancia, 1983). Though initial natal dispersal appears to occur most commonly in spring (e.g. Molini et al., 1980; Svendsen, 1980a), it may occur at other times of the year. Van Deelen and Pletscher (1996) found that the dispersal date was highly variable ranging from 7 April to 20 August (mean 17 May), as was settlement date (mean: 24 July; range: 9 April-12 November). Hodgdon (1978) found that dispersal took place from March to September. Hartman (1994) found that three of nine beaver in his study dispersed as yearlings in early fall, and one in early winter. If waters are icebound, dispersal will be impossible until ice break-up. However, if freeze-up does not occur, beaver may be highly mobile throughout the year (Payne, 1984). Exploratory movements outside the natal

territory have been observed in several studies (Wilsson, 1971; Payne, 1982; Van Deelen, 1991; Hartman, 1997), and presumably can develop into true dispersal. A substantial drop in temperature and an eventual freeze-up might, on the other hand, drive some explorers back to the natal colony. The continually ice-free state of the Bø River allows dispersion throughout the entire year. However low water temperatures make prolonged swimming a very costly activity (e.g. Nolet and Rosell, 1994).

*Spatial distribution.* If the primary function of beaver scent marking was territory defense, then markings might be expected to cluster near territorial boundaries. Hediger (1949) commented that many species deposit scent where they meet or expect rivals; e.g. near territory borders. Peters and Mech (1975) reported that wolves (*Canis lupus*) concentrated scent marks at the periphery of the territory. The same pattern was also found in the Chinese water deer (*Hydropotes inermis*) (Sun et al., 1994), in the aardwolves (*Proteles cristatus*) (Richardson, 1991), in Tigers (*Panthera tigris*) (Smith et al., 1989), and in the badger (*Meles meles*) (Kruuk, 1978; Kruuk et al., 1984). Aleksiuk (1968) found most marking points for the North American beaver at the edge of territories, but some also were located near the lodge. Richard (1967) suggested that the Eurasian beaver marked most frequently near territorial boundaries. Rosell and Nolet (1997) also found a higher number of scent marks near the borders. Nitsche (1985a,b), in contrast, found that the central part of a territory was more intensively marked than the peripheries (Eurasian beaver).

In this study, scent marks were clumped near territorial borders, which is in accordance with our second prediction. In this manner, intruding beaver, upon entering a foreign territory, quickly discover that the area is already occupied. This general pattern was maintained throughout the year. From October to December, when marking activity was minimal, almost all marking occurred at territorial borders. In this manner, beaver presumably

maximize the effect of the scent marking process at a time of the year when time and energy are mainly allocated to preparation for winter.

More scent marks were located upstream than downstream of the lodge, which is also in accordance with our second prediction. This was the case regardless of the location (up- or downstream) of the nearest neighbor. Colonies 1 and 2 were exceptions. Colony 1 had no close neighbors upstream, and therefore presumably had less reason to scent mark intensively here. As for colony 2, we have no explanation for why it deviated in this respect. In contrast, Müller-Schwarze (1992) found no difference in the frequency of upstream and downstream marking, and concluded that if scent marking provides information by water-borne chemicals, it is not reflected in the number of scent mounds built by downstream beaver.

Whether marking activity is concentrated up or downstream of the lodge may be dependent upon the predominating direction of dispersal in a particular watershed. Downstream dispersal would presumably be the most energy efficient, in which case concentrating most scent marks at the upstream border would be the most effective means of informing potential intruders. We do not know the main direction of dispersal in our study area, though beaver have been shown to disperse both upstream and downstream (Leege, 1968; Van Deelen and Pletscher, 1996). Another explanation for a predominance of upstream marking would be that intruders entering from a downstream direction automatically receive an almost continual flow of chemical scent information in the surface film from all upstream territories. Thus the water segment of a beaver's territory presumably is readily covered in this manner. Indeed, swimming beaver keep their nostrils at the water level, thus enabling them to sense chemical messages from neighboring beaver concentrated within the surface film (Grønneberg and Lie, 1984).

*Acknowledgments*-We thank Dr. Per Christian Hagen for statistical advice, Frøydis Nævdal Bergan, Dr. Göran Hartman, Prof. D. Müller-Schwarze, Dr. Bart A. Nolet, Dr. Bruce Schulte, Dr. Lixing Sun and Dr. Fran Tattersall for valuable comments on an earlier draft, and Bjørnar Hovde, Øyvind Steifetten and Gisle Uren for help in the field. The study was supported financially by the Telemark County Conservation Department.

## REFERENCES

- ALEKSIUK, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). *J. Mammal.* 49:759-762.
- BEER, J. R. 1955. Movements of tagged beaver. *J. Wildl. Manage.* 19:492-493.
- BERGAN, F. 1996. Duftmarkering hos europeisk bever (*Castor fiber* Linnaeus, 1758) i Bøelva, Telemark. Fordeling i tid og rom gjennom et år. Hovedoppgave Høgskolen i Telemark, institutt for natur- og miljøforvaltning. Bø i Telemark, 45 pp.
- BERGERUD, A. T., and MILLER, D. R. 1977. Population dynamics of Newfoundland beaver. *Can. J. Zool.* 55:1480-1492.
- BOLLINGER, K. S. 1980. Scent marking behavior of beaver (*Castor canadensis*). MS thesis. University of Massachusetts, Amherst, 186 pp.
- BRADT, G. W. 1938. A study of beaver colonies in Michigan. *J. Mammal.* 19:139-162.
- BUECH, R. R. 1995. Sex differences in behavior of beavers living in near-boreal lake habitat. *Can. J. Zool.* 73:2133-2143.
- BUTLER, R. G., and BUTLER, L. A. 1979. Toward a functional interpretation of scent marking in the beaver (*Castor canadensis*). *Behav. Neural Biol.* 26:442-454.
- EISENBERG, J. F., and KLEIMANN, D. G., 1972. Olfactory communication in mammals. National Zoological Park. Smithsonian Institution. Washington, DC.

- ERLINGE, S., SANDELL, M., and BRINCK, C. 1982. Scent-marking and its territorial significance in stoats, *Mustela erminea*. *Anim. Behav.* 30:811-818.
- GEIST, V. 1964. On the rutting behavior of the mountain goat. *J. Mammal.* 45:551-568.
- GORMAN, M. L. 1990. Scent marking strategies in mammals. *Rev. Suisse Zool.* 97:3-29.
- GORMAN, M. L., and MILLS, M. G. L. 1984. Scent marking strategies in hyaenas (Mammalia). *J. Zool. Lond.* 202:535-547.
- GOSLING, L. M. 1982. A reassessment of the function of scent marking in territories. *Z. Tierpsychol.* 60:89-118.
- GOSLING, L. M. 1986. Economic consequences in mammalian territoriality, pp 385-395 in D. Duval, D. Müller-Schwarze, and R. M. Silverstein (eds.). *Chemical signals in vertebrates 4*. Plenum Press, New York.
- GOSLING, L. M. 1990. Scent marking by resource holders: Alternative mechanisms for advertising the costs of competition, pp 315-328 in D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk (eds.). *Chemical signals in vertebrates*. V. Oxford, Oxford University Press.
- GOSLING, L. M., and MCKAY, H. V. 1990. Competitor assessment by scent matching: an experimental test. *Behav. Ecol. Sociobiol.* 26:415-420.
- GRØNNEBERG, T. Ø., and LIE, T. 1984. Lipids of the anal gland secretion of beaver (*Castor fiber*). *Chemica Scripta* 24:100-103.
- HARTMAN, G. 1994. Ecological studies of a reintroduced beaver (*Castor fiber*) population. PhD dissertation. The Swedish University of Agricultural Sciences, Uppsala.
- HARTMAN, G. 1997. Notes on age at dispersal of beaver (*Castor fiber*) in an expanding population. *Can. J. Zool.* 75:959-962.
- HEDIGER, H. 1949. Säugetier-Territorien und ihre Markierung. *Bijdr. Dierkd.* 28:172-184.

HODGDON, H. E. 1978. Social dynamics and behavior within an unexploited beaver (*Castor canadensis*) population. PhD dissertation. University of Massachusetts, Amherst, 292 pp.

HODGDON, H. E., and LANCIA, R. A. 1983. Behaviour of the North American beaver (*Castor canadensis*). *Acta Zool. Fennica* 174:99-103.

HOULIHAN, P.W. 1989. Scent mounding by beaver (*Castor canadensis*): Functional and semiochemical aspects. MS thesis. State University of New York College of Environmental Science and Forestry, Syracuse, New York.

JACKSON, M. D. 1991. Beaver dispersal in western Montana. MS thesis. University of Montana, Missoula, 77 pp.

JOHNSON, R. P. 1973. Scent marking in mammals. *Anim. Behav.* 21:521-535.

KRUUK, H. 1978. Spatial organisation and territorial behaviour of the European badger *Meles meles*. *J. Zool.* 184:1-19.

KRUUK, H., GORMAN, M., and LEITCH, A. 1984. Scent-marking with the subcaudal gland by the European badger, *Meles meles* L. *Anim. Behav.* 32:899-907.

LANCIA, R. A., DODGE, W. E., and LARSON, J. S. 1982. Winter activity patterns of two radio-marked beaver colonies. *J. Mamm.* 63:598-606.

LEEGE, T. A. 1968. Natural movements of Beaver in southeastern Idaho. *J. Wildl. Manage.* 32:973-976.

MACDONALD, D. W. 1980. Patterns of scent marking with urine and feces amongst carnivore communities. *Symp. Zool. Soc. Lond.* 45:106-121.

MOLINI, J. J., LANCIA, R. A., BISHIR, J., and HODGDON, H. E. 1980. A stochastic model of beaver population growth, pp. 1215-1245, in J. A. Chapman and D. Pursey (eds.). Proceedings, Worldwide furbearer Conference. Frostburg, Maryland.

- MÜLLER-SCHWARZE, D. 1992. Castoreum of beaver (*Castor canadensis*): function, chemistry and biological activity of its components, pp 457-464, in R. L. Doty and D. Müller-Schwarze (eds.). Chemical signals in vertebrates 6. Plenum Press, New York.
- MÜLLER-SCHWARZE, D., and HECKMAN, S. 1980. The social role of scent marking in beaver (*Castor canadensis*). *J. Chem. Ecol.* 6:81-95.
- NITSCHE, K. A. 1985a. Reviermarkierung beim Elbebiber (*Castor fiber albicus*). *Mitt. Zool. Ges. Braunau* 4:259-273.
- NITSCHE, K. A. 1985b. Zum Markierungsverhalten des Elbebibers (*Castor fiber albicus* MATSCHIE, 1907). *Säugetierkd. Inf.* 2:245-253.
- NOLET, B. A., and ROSELL, F. 1994. Territoriality and time budgets in beavers during sequential settlement. *Can. J. Zool.* 72:1227-1237.
- NOVAK, M. 1977. Determining the average size and composition of beaver families. *J. Wildl. Manage.* 41:751-754.
- OLSTAD, O. 1937. Beverens (*Castor fiber*) utbredelse i Norge. Statens viltundersøkelser. Særtrykk av Nytt magasin for naturvidenskapene 77:217-273.
- PATRIC, E. F. and WEBB, W. L. 1960. An evaluation of three age determination criteria in live beavers. *J. Wildl. Manage.* 24:37-44.
- PAYNE, N. F. 1982. Colony size, age, and sex structure of Newfoundland beaver. *J. Wildl. Manage.* 46:655-661
- PAYNE, N. F. 1984. Population dynamics of beaver in North America. *Acta Zool. Fennica.* 172:263-266.
- PETERS, R. P., and MECH, L. D. 1975. Scent-marking in wolves. *Am Sci.* 63:628-637.
- RALLS, K. 1971. Mammalian Scent marking. *Science* 171: 443-449.
- RICHARD, P. B. 1967. Le determinisme de la construction des barrages chez le castor du Rhone. *La terre et la vie* 4:21-470.

- RICHARDSON, P. R. K. 1991. Territorial significance of scent marking during the non-mating season in the aardwolf *Proteles cristatus* (Carnivora: Proteidae). *Ethology* 87:9-27.
- RICHARDSON, P. R. K. 1993. The function of scent marking in territories: a resurrection of the intimidation hypothesis. *Trans. Roy. Soc. S. Afr.* 48:195-206.
- ROSELL, F., and NOLET, B. A. 1997. Factors affecting scent-marking behavior in Eurasian beaver (*Castor fiber*). *J. Chem. Ecol.* 23:673-689.
- ROSELL, F., and PARKER, H. 1995. Forvaltning av bever: dagens tilstand og fremtidige behov. (Beaver management: present practice and Norway's future needs). Høgskolen i Telemark, avdeling for økonomi-, miljø- og idrettsfag. Bø, Norway, 137 pp.
- SCHULTE, B. A. 1993. Chemical communication and ecology of the North American beaver (*Castor canadensis*). PhD dissertation. State University New York, Syracuse, 194 pp.
- SCHULTE, B. A., MÜLLER-SCHWARZE, D., TANG, R., and WEBSTER, F. X. 1994. Beaver (*Castor canadensis*) responses to major phenolic and neutral compounds in castoreum. *J. Chem. Ecol.* 20:3063-3081.
- SIEGEL, S., and CASTELLAN, N. J. 1988. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.
- SMITH, J. L. D., MCDOUGAL, C., and MIQUELE, D. 1989. Scent marking in free-ranging tigers. *Panthera tigris. Anim. Behav.* 37:1-10.
- SUN, L., BING, X., and DAI, N. 1994. Scent marking behaviour in the male Chinese water deer. *Acta Theriol.* 39:177-184.
- SVENDSEN, G. E. 1980a. Population parameters and colony composition of beaver (*Castor canadensis*) in Southeast Ohio. *Am. Midl. Nat.* 104:47-56.
- SVENDSEN, G. E. 1980b. Patterns of scent-mounding in a population of beaver (*Castor canadensis*). *J. Chem. Ecol.* 6:133-148.

- SVENDSEN, G. E. 1989. Pair formation, duration of pair-bonds, and mate replacement in a population of beavers (*Castor canadensis*). *Can. J. Zool.* 67:336-340.
- TANG, R., WEBSTER, F. X., and MÜLLER-SCHWARZE, D. 1993. Phenolic compounds from male castoreum of the North American beaver, *Castor canadensis*. *J. Chem. Ecol.* 19:1491-1500.
- TOWNSEND, J. E. 1953. Beaver ecology in western Montana with special reference to movements. *J. Mammal.* 34:459-479.
- VALEUR, P. 1988. Beverens territorial-atferd som populasjonsregulerende faktor. (Territorial behavior as factor in regulation of populations in beaver.) *Fauna* 41:20-34.
- VAN DEELEN, T. R. 1991. Dispersal pattern of juvenile beavers in western Montana. MS thesis. University of Montana, 91 pp.
- VAN DEELEN, T. R. 1994. A Field Technique for Aging Live Beavers, *Castor canadensis*. *Can. Field. Nat.* 108:361-363.
- VAN DEELEN, T. R., and PLETSCHER, D. H. 1996. Dispersal characteristics of two-year-old Beavers, *Castor canadensis*, in western Montana. *Can. Field-Naturalist* 110:318-321.
- WALRO, J. M., and SVENDSEN, G. E., 1982. Castor sacs and anal glands of the North American beaver (*Castor canadensis*): their histology, development, and relationship to scent communication. *J. Chem. Ecol.* 5:809-819.
- WELSH, R. G., and MÜLLER-SCHWARZE, D. 1989. Experimental habitat scenting inhibits colonization by beaver, *Castor canadensis*. *J. Chem. Ecol.* 3:887-893.
- WILSSON, L. 1971. Observations and experiments on the ethology of the European Beaver (*Castor fiber L.*). *Viltrevy* 8:115-266.
- WYNNE-EDWARDS, V. C. 1962. Animal dispersal in relation to social behaviour. Oliver and Boyd, Edinburgh, Scotland.

## **FIGURE LEGENDS**

**Fig. 1.** Mean number of scent marks in 7 adjacent territories along the Bø River observed at 14-day intervals throughout one year (1 April 1995 - 31 March 1996). Vertical bars show the 95 % confidence intervals. N is the total number of scent marks for each 14-day period in all 7 territories combined. A flood during weeks 22/23 hampered scent marking activity.

**Fig. 2.** Total number of scent marks in each 100 m zone during each of the four 3-month periods, and for all periods pooled, for 7 adjacent territories along the Bø River during one year (1 April 1995 - 31 March 1996). "B" indicates the location of borders between territories based on the movement patterns of colony members. Numbers indicate the approximate position of the lodge in territories 1-7. Zone 1 is positioned furthest upstream.

Fig. 1, Rosell et al.

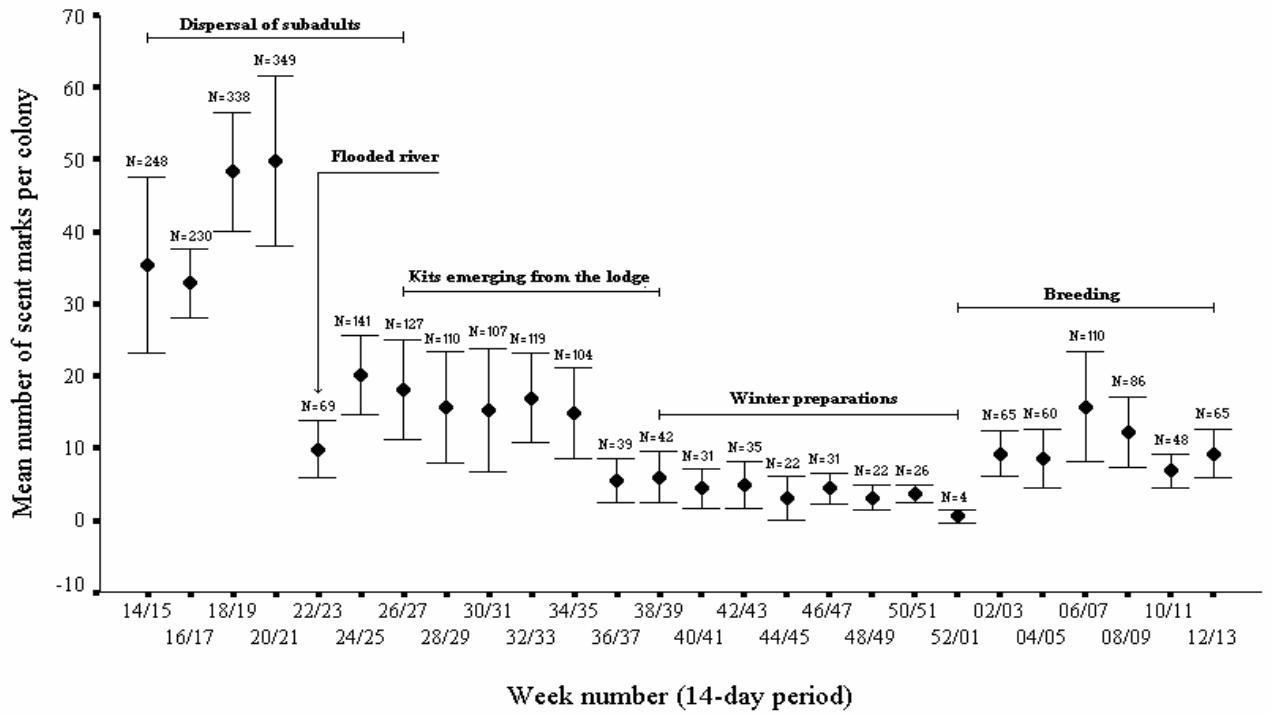


Fig. 2, Rosell et al.

