

**The function of scent marking in beaver
(*Castor fiber*) territorial defence**

Frank Rosell

Dr. scient. thesis

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The author's address:

Faculty of Arts and Sciences
Department of Environmental and Health Studies
Telemark University College
N-3800 Bø i Telemark
Norway

E-mail: Frank.Rosell@hit.no

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Preface

I saw my first beaver on 19 July, 1990, at 5:14 PM. Little did I know then that this sight would change my life. I was studying chemistry at the time, but felt an increasing desire to pursue follow-up studies in zoology, and shortly thereafter began a Master of Science thesis in ethology. The study animal of my choice was destined to be the beaver, and the topic of my thesis a combination of chemistry and ethology. I'm therefore greatly indebted to my Master of Science supervisors, professor Yngve Espmark, Dr. Göran Hartman and Dr. Bart A. Nolet. I thank Bart for kindly allowing me to work on his reintroduction project in the Biesbosch region of the Netherlands, and Bart and Göran for their friendship, and for sharing their extensive knowledge of beavers with me. I also thank Göran for always replying to my endless stream of e-mails! Yngve was also one of my PhD supervisors. I thank him for his support and help.

The person I'm in greatest debt to is my other PhD supervisor and beaver colleague since October 1994, Dr. Howard Parker. Without his generous, enthusiastic and cooperative attitude and help this thesis would never have been realized. His critical and constructive comments, both written and oral, have always been helpful, and I have really appreciated all our lunch discussions. Thanks, Howard, for all your help, support and friendship. After all these years, I have never seen him in bad mood! He has always opened his door, both home and office for me, and I will always remember that. Thanks also for "taking care" of me during various meetings in Spain, Russia, Scotland and Norway. I really have enjoyed your company!

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I also want to thank my parents, Roy and Thoril Rosell, for their support. My father started my interest in animals when he first taught me about birds. Thanks to both of them for the many nice hikes over the years, for always “pointing” me in the right direction when the way forward was confusing, and for reminding me occasionally of what’s best to do.

And last, but not least, I sincerely thank my live-in companion, Randi Pettersen, for her undying patience during my many evenings/nights of fieldwork during our past 6 years together. She has always listened to all of my new ideas and current new findings, endured the writing of my beaver book a few years back, and has been supportive in every way! Thanks for your incredible understanding, and for joining me at meetings in Spain and Poland and during our stay in Syracuse. I love you!

I further thank professors Yngve Espmark, Michael H. Ferkin, Martyn L. Gorman, Hans Kruuk, Dietland Müller-Schwarze, Bruce Schulte and Lixing Sun, and Drs. Howard Parker and Craig Roberts for valuable discussions and comments on earlier drafts of the introductory chapter. To avoid forgetting anyone, additional assistance is given credit under “acknowledgements” in the respective papers of this thesis.

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Frank Rosell
Telemark University College
Bø i Telemark
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List of individual papers

This dr. scient. thesis is based on the six papers listed below (referred to below and later by their Roman numerals **I-VI**).

- I** Rosell, F. & Nolet, B.A. 1997. Factors affecting scent-marking behavior in Eurasian beaver (*Castor fiber*). *Journal of Chemical Ecology* 23:673-689.
- II** Rosell, F., Bergan, F. & Parker, H. 1998. Scent-marking in the Eurasian beaver (*Castor fiber*) as a means of territory defense. *Journal of Chemical Ecology* 24:207-219.
- III** Rosell, F. & Sundsdal, L.J. 2001. Odorant source used in Eurasian beaver territory marking. *Journal of Chemical Ecology* 27:2471-2491.
- IV** Rosell, F., Johansen, G. & Parker, H. 2000. Eurasian beavers (*Castor fiber*) behavioral response to simulated territorial intruders. *Canadian Journal of Zoology* 78:931-935.
- V** Rosell, F. & Bjørkøyli, T. In press. A test of the dear enemy phenomenon in the Eurasian beaver. *Animal Behaviour* xx:xx-xx.
- VI** Steifetten, Ø. & Rosell, F. Submitted. Differential territorial response toward conspecific and heterospecific scent marks by the Eurasian beaver (*Castor fiber*). *Behavioral Ecology*.

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Sammendrag (Summary in Norwegian)

Denne avhandlingen eksaminerer hvordan duftmarkeringer fungerer i territorieforsvaret hos eurasiatisk bever (*Castor fiber*). Beveren avsetter vanligvis duft (castoreum fra bevergjelpungene og/eller sekret fra analkjertlene (AKS)) på små hauger av leire og planterester, og alle aldersgrupper og begge kjønn deltar i markeringen. Jeg satte fram hypotesen at duftmarkeringer spiller en viktig rolle i territorieforsvaret til fritt levende eurasiatisk bever, og undersøkte følgende spørsmål. (1) Hvilke faktorer virker inn på duftmarkeringsatferden? (2) Hvordan er duftmarkeringer fordelt i tid og rom i løpet av et helt år? (3) Er castoreum og/eller AKS brukt i forsvaret av territoriet? (4) Hvordan reagerer denne arten på simulerte inntrengere i territoriet? (5) Kan den eurasiatiske beveren diskriminere mellom duft fra naboer og fremmede, og mellom duft fra sin egen art og den nordamerikanske beveren (*C. canadensis*)?

Jeg viste at duftmarkeringer spiller en signifikant, indirekte rolle i forsvaret av territoriet hos den eurasiatiske beveren. Antall duftmarkeringer var tetthetsavhengig. Bever med mange nære naboer (høyt utfordret) trenger sannsynligvis å duftmarkere oftere for å bli utvetydig gjenkjent som eier av territoriet. Plasser med høy tetthet er imidlertid kanskje også av bedre kvalitet, noe som gir eierne av territoriet mer energi å bruke på forsvaret, og flere grunner for å forsvare. Det var en signifikant positiv korrelasjon mellom antall duftmarkeringer og varigheten av okkupasjonen av territoriet samt lengden av banker med trær. Bofaste ser derfor ut til å investere mer i duftmarkeringer i territorier med god kvalitet og når et territorium har vært okkupert for relativ lang tid. Teoretisk, jo store potensiell verdi territoriet har for de bofaste, i kontrast til inntrengere, desto hardere bør eieren slåss for å beholde det territoriet.

Territoriet ble duftmarkert signifikant oftere om våren når spredningen av 2-åringer normalt skjer, og duftmarkeringene ble konsentrert nær grensene til territoriet, tilsynelatende for å maksimere signaleffektiviteten til potensielle inntrengere før de entrer territoriet. Signifikant flere duftmarkeringer ble konstruert oppstrøms i forhold til nedstrøms av hytta, sannsynligvis fordi bevegelsen av individer på vandring hovedsakelig er nedstrøms. Disse resultatene støtter hypotesen om grenseoppretholdelse.

Castoreum ble nesten utelukkende avsatt på duftmarkeringer fra januar til ut mars og ser ut til å være hovedlukten brukt i forsvar av eurasiatiske beverterritorier. AKS ble sjelden avsatt og har muligens en annen funksjon.

Den eurasiatiske beveren viste territorial atferd når en "inntrenger", i form av kunstig konstruerte eksperimentelle duftmarkeringshauger (EDH'er) med castoreum fra fremmede voksne hanner, ble plassert inne i territoriet. De ødela EDH'ene og overmarkerte med sin egen lukt i 80% av forsøkene. Overmarkeringen ser ut til å ha vært et forsøk på å maskere duften fra de fremmede voksne hannene med sin egen duft. Disse resultatene gir dermed noe støtte til duftmaskeringhypotesen. Duftmarkeringer kan derfor sørge for en troverdig annonsering av et individs evne til å dominere eller forsvare et område, siden bare de som suksessfullt dominerer et område kan sikre at deres markeringer både dominerer og er nyligere avsatt enn de fra en utfordrende konkurrent. Overmarkeringen annonserer derfor muligens at territoriet er opptatt og signaliserer kostnaden av konkurransen hvis trusselen ignoreres. Jeg observerte at beverne ofte startet å patruljere territoriet etter å ha besøkt EDH'ene. En mangel på respons på EDH'er uten castoreum indikerer at beveren reagerte på duften av castoreum og ikke på synet av duftmarkeringshaugen.

De eurasiatiske beverne snuste på castoreum og AKS fra en fremmed, signifikant lenger enn fra en nabo. De reagerte aggressivt, signifikant lenger på castoreum, men ikke på AKS, fra en fremmed enn fra en nabo. Når EDH'ene forble ute over natta og responsen ble målt den påfølgende morgenen, reagerte beverne signifikant sterkere på både castoreum og AKS fra en fremmed enn fra en nabo. Disse resultatene indikerer at den eurasiatiske beveren kan bruke duft for å diskriminere mellom naboer og fremmede, og gir dermed støtte til tilstedeværelsen av "kjære fiende" fenomenet (reduert aggresjon mot kjente okkupanter på naboterritoriene).

De eurasiatiske beverne tilbrakte signifikant lenger tid på å reagere aggressivt på artsfrenders enn ikke-artsfrenders (nordamerikanske bevere) EDH'er. De reagerte også signifikant mer aggressivt på artsfrenders enn ikke-artsfrenders EDH'er over natt. Sammenligninger av castoreum gasskromatogram viste at forskjeller mellom artene forklarte 34% av den totale variasjonen i forbindelsene oppdaget, mens forskjeller mellom kjønnene forklarte 13%. For AKS, var henholdsvis 49% og 46% av denne variasjonen forklart av forskjeller mellom arter og kjønn. Disse resultatene bekrefter hypotesen at den eurasiatiske beveren diskriminerer mellom duftmarkeringer fra de to artene, med andre ord utøver arts diskrimineringsevner. Dette indikerer at den eurasiatiske beveren vil anse påtrengende duftmarkeringer fra den nordamerikanske beveren å utgjøre en mindre territoriell trussel enn fra en artsfrende, og vil derfor mindre sannsynlig bruke tid og energi på å overmarkere disse duftmarkeringene.

Jeg konkluderer med at mitt studium har bidratt til en bedre forståelse av funksjonen

av duftmarkering i territoriet til den eurasiatiske beveren ved å demonstrere deres evne til å overføre duftbeskjeder effektivt, både i tid og rom, og deres evne til å overmarkere og diskriminere EDH'er fra inntrengere som utgjør ulik grad av trussel. Mine resultater gav støtte til ideen at funksjonen for duftmarkering av territoriet hos eurasiatisk bever er å annonsere dominans status, og dermed sørge for muligheter for inntrengere til å vurdere tilstedeværelsen av eieren som vil redusere kostnadene av de agonistiske konfliktene for både eier og inntrenger (statusannonseringshypotesen). Mine resultater støtter også den generelle duftssammenligningshypotesen, med andre ord dens prediksjoner 1 (duftmarker hvor inntrengere er mest sannsynlig å møte disse), 3 (gjør seg tilgjengelig for duftssammenligning av inntrenger) og 4 (fjern eller erstatt duftmarkeringer av andre) ble alle støttet. Prediksjon 2 (duftmarker seg selv med duften brukt til å markere territoriet) trenger imidlertid å klargjøres. Det er fortsatt uklart om beveren smører castoreum på pelsen, og/eller markerer seg selv med AKS for å gjøre pelsen vanntett og dermed fungere samtidig som en "levende duftmarkering". Det neste steget bør være å redegjøre for disse spørsmålene. Funksjonen til duftmarkering som er foreslått her er imidlertid nødvendigvis ikke den eneste funksjonelle mekanismen, siden en funksjon ikke trenger å utelukke andre. To andre hovedfunksjoner for duftmarkering hos eurasiatisk bever som ikke helt kan utelukkes er at duftmarkeringer kan bli brukt til å merke og dermed forsvare ressurser innen territoriet (hypotesen om ressurs merking), og at duftmarkeringen er relatert til reproduksjonen (for eksempel ved å annonsere reproduktiv status og bevoktning av maken i løpet av paringstiden). Mitt arbeid har lagt vekt på kommunikasjonen mellom familiegrupper. Mer arbeid trengs imidlertid for å klargjøre duftmarkeringens rolle i kommunikasjonen innen familiegrupper.

Abstract

This thesis examines how scent marking in Eurasian beaver (*Castor fiber*) functions in territorial defence. Beavers usually deposit scent (castoreum and/or anal gland secretion (AGS)) onto small piles of mud and debris, and all age classes and both sexes participate in marking. I hypothesized that scent marking plays an important role in territory defence of free-ranging Eurasian beavers and investigated the following issues. (1) Which factors affect scent-marking behaviour? (2) How are scent marks distributed temporally and spatially during an annual cycle? (3) Is castoreum and/or AGS used in territorial defence? (4) How does this species respond to simulated territorial intruders? (5) Can the Eurasian beaver discriminate between scent from neighbours and strangers, and between scent from its own species and that of the North American beaver (*C. canadensis*)?

I show that scent marking plays a significant indirect role in territorial defence by the Eurasian beaver. The number of scent marks was density dependent. Beavers with many close neighbours (highly challenged) may need to scent mark more often to be unambiguously recognised as territory owners. However, high-density sites may also be of better quality, providing territory holders with more energy to spend in defence and more reasons to defend. There was a significant positive correlation between the number of scent marks and both the duration of territory occupancy and length of wooded banks. Therefore, residents appear to invest more in scent marking in good quality territories, and when a territory has been occupied for a relatively long time. Theoretically, the greater potential value of the territory for residents, in contrast to intruders, makes it worth fighting harder for.

Territories were scent marked significantly more often in spring when dispersal of 2-years-olds normally occurs and scent marks were concentrated near territorial borders, apparently to maximize the signal effect to potential trespassers on or before entering the territory. Significantly more scent marks were constructed upstream than downstream of the lodge, probably because the movement of dispersing individuals is predominantly downstream. These results support the border maintenance hypothesis.

From January through March castoreum was almost exclusively deposited on scent marks and appears therefore to be the main scent signal used in the defence of Eurasian beaver territories. AGS was rarely deposited and appears to have another function.

Eurasian beaver showed territorial behaviour when an "intruder", in the form of artificially-constructed experimental scent mounds (ESMs) containing castoreum from alien

adult males, was placed inside the territory. They destroyed the ESMs and overmarked with their own scent in 80% of the trials. Countermarking appears to have been an attempt to mask the odour of alien adult male conspecifics with their own odours. This result therefore gives some support to the scent-masking hypothesis. Scent marks could thus provide a reliable advertisement of an individual's ability to dominate or defend the area, since only those successfully dominating the area can ensure that their marks both predominate and are more recently deposited than those of any challenging competitors. The countermarking may therefore advertise that the territory is occupied and signal the costs of competition if the threat is ignored. I frequently observed that beavers, after visiting the ESMs, started to patrol the territory. A lack of response to ESMs without castoreum indicated that beavers were responding to the smell of castoreum and not to the sight of the scent mound itself.

Eurasian beavers sniffed both castoreum and AGS from a stranger significantly longer than those from a neighbour. They responded aggressively significantly longer to castoreum, but not to AGS, from a stranger than from a neighbour. When ESMs were allowed to remain overnight and the response measured the following morning, beavers responded significantly stronger to both castoreum and AGS from a stranger than from a neighbour. These findings indicate that Eurasian beavers can use scent to discriminate between neighbours and strangers, thereby supporting existence of the "dear enemy" phenomenon (reduced aggression towards familiar occupants of neighbouring territories).

Eurasian beavers spent significantly longer time responding aggressively to conspecific than to heterospecific (North American beavers) ESMs. They also responded significantly more aggressively to conspecific than to heterospecific ESMs overnight. Gas chromatographic comparisons of castoreum showed that differences between species accounted for 34% of the total variation in compounds detected, while differences between sexes accounted for 13%. For AGS, 49% and 46% of this variation was explained by differences between species and sex, respectively. The results confirm the hypothesis that the Eurasian beaver discriminates between scent marks of the two species, i.e. exhibits species discrimination abilities. This indicates that the Eurasian beaver would regard intrusive scent marks from the North American beaver as a lesser territorial threat than from a conspecific, and would therefore be less likely to spend time and energy countermarking these scent marks.

In conclusion, my study has contributed to a better understanding of the function of territorial scent marking in the Eurasian beaver by demonstrating their capability of transmitting odorous messages efficiently, both temporally and spatially, and their ability to

countermark and discriminate ESMs from intruders of different degrees of threat. My results lend support to the idea that the function of territorial scent marking in the Eurasian beaver is to advertise related dominance status, thereby providing opportunities for intruders to assess the presence of the owner, and thus reducing the costs of agonistic conflicts for both the owner and intruder (the status advertisement hypothesis). My results also support the general scent-matching hypothesis, i.e. its predictions 1 (mark where intruders are most likely to encounter marks), 3 (make themselves available for scent matching by intruders) and 4 (remove or replace marks of others) were all supported. However, prediction 2 (mark themselves with the substances used to mark the territory) needs to be clarified. It's still unclear whether beavers smear castoreum on their pelage, and/or mark themselves with AGS in order to waterproof the fur, and thereby simultaneously function as a "living-scent mark". The next step should be to clarify these issues. However, the function of scent marking suggested here is not necessarily the only functional mechanism, as one function need not necessarily exclude others. Two other main functions for scent marking in Eurasian beavers that cannot be entirely ruled out are that scent marks may be used to label and thereby defend resources within the territory (the labelling resources hypothesis), and that marking is related to reproduction (e.g. by advertising reproductive status and guarding the mate during the breeding period). My work has emphasized intergroup communication. However, more work is needed to clarify the role of scent marks in intragroup communication.

Introduction

Territoriality has been defined in many ways. Maher & Lott (1995) proposed the following definition of territory: “a fixed space from which an individual or group of mutually tolerant individuals actively excludes competitors from a specific resource or resources”. Territoriality may be expected to evolve when the benefits gained from exclusive access to limited resources exceed the costs of defence (Brown 1964, Stamps 1994). Costs of territoriality can be minimized if resident animals advertise their occupation of an area in order to deter intrusion and avoid escalated encounters with conspecifics. Advertisement will only be effective, however, when ownership signals are reliable indicators of an animal’s ability to control the resources contained within defended areas (Parker 1974, Zahavi 1975). Although examples of visual and auditory signals functioning as territorial advertisement are common (e.g. Hailman 1977, Catchpole 1982), it has been argued that chemical signals are especially effective in this regard (Gosling 1986). If an animal has scent marked an area comprehensively, it must have inhabited it at least long enough to do so (Gosling 1982). Additionally, the signal remains active even when its author is absent from an area.

Mammalian scent marking is often associated with territorial defence (e.g. Gosling 1990). It is widely accepted that mammals scent mark their territories to advertise their occupancy and ownership of the territory (e.g. Peters & Mech 1975, Macdonald 1980, Erlinge et al. 1982, Gosling 1982, Gorman & Mills 1984, Smith et al. 1989, Sillero-Zubiri & 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). Alternative hypotheses, however, have been proposed for scent marking in mammals: identification of species, subspecies, group, or individuals, signalling social and reproductive status or mood, promoting synchronisation of reproductive cycles, attracting members of the opposite sex, labelling resources, and reassurance/confidence (see for example, reviews by Eisenberg & Kleiman 1972, Johnson 1973, Müller-Schwarze 1974, Thiessen & Rice 1976, Henry 1977, Brown 1979, Brown & Macdonald 1985, Kruuk 1992, Branch 1993, Lazaro-Perea et al. 1999). Scent marks therefore might serve several functions, which may change or vary with the time of year or the location of the mark. However, these alternative hypotheses will not be the main focus here.

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). The

intimidation hypothesis states that intruders may interpret scent marks as a threat with immediate physical attack if they are encountered by the resident (Hediger 1949, Richardson 1991, 1993). Scent marks would serve to delimit the territory and to deter intruders from entering the interior for prolonged visits in the absence of the signaller. 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 trespassed, and hence indirectly protect 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, 1990, Richardson 1993). As there is typically a delay between signal emission and reception in olfactory signalling, the main mechanism involved is thought to be “scent-matching”, in which competitors or mates match the odour from scent marks with the odour of conspecifics they encounter (Gosling 1982, Gosling & McKay 1990). It is therefore critical that signallers maintain their scent in such a way that maximizes the success of matching (Gosling 1986, Roberts & Lowen 1997, Gosling & Roberts 2001). This is achieved both by replenishing their own scent marks on a regular basis and by countermarking any scent deposited by competitors within their territory or area of dominance (Roberts 1998, Rich & Hurst 1999).

Numerous systematic investigations of chemical communication have been conducted with small mammals amenable to laboratory experimentation. However, similar studies are notably lacking for large species (Swaisgood et al. 1999). Additionally, better designed field studies are needed in order to better understand the significance of scent for territorial communication in general. Therefore, I chose the Eurasian beaver (*Castor fiber*, 2n=48) as a model to further elucidate this topic.

Both the Eurasian and the North American beavers (*C. canadensis*, 2n=40) are strongly territorial and aggressive encounters are not uncommon (e.g. Lavrov & Orlov 1973, Piechocki 1977, Svendsen 1989, Nolet & Rosell 1994). Beavers usually deposit scent (castoreum and anal gland secretion (AGS), see below) onto small piles of mud and debris close to the water's edge (e.g. Wilsson 1971, Svendsen 1980a). All age-classes, except kits younger than 5 months, and both sexes defend their territories by scent marking (Wilsson 1971, Buech 1995). A variety of functions have also been assumed for scent marks in the beaver (see Dugmore 1914, Green 1936, Aleksuk 1968, Butler & Butler 1979, Müller-Schwarze & Heckman 1980, Svendsen 1980a, Rosell & Bergan 1998). However, by testing alternative hypotheses, Houlihan (1989) confirmed the territorial function of North American beaver scent marks and rejected other interpretations (see also Hodgdon 1978, Müller-

Schwarze & Heckman 1980, Svendsen 1980a, Houlihan 1989, Welsh & Müller-Schwarze 1989, Schulte 1998). To-date, only anecdotal observations exist for the functions of scent marking in territorial defence by Eurasian beavers. Studies of scent marking in the Eurasian beaver typically have focused on the behaviour of only a few animals or of captive/semi captive individuals (Wilsson 1971, Anderson & Westerling 1984, Nolet & Rosell 1994). Understanding the functions of scent marking in Eurasian beaver territorial defence may contribute important findings for a better understanding of this species' communication system and olfactory communication in general. Also, comparative studies are essential to understand evolutionary pathways.

Factors affecting the number and distribution (temporal and spatial) of scent marks

The number of scent marks varies spatially and temporally in populations of most species of mammals and may be correlated with breeding activity, food availability, levels of dominance and density (Ralls 1971, Johnson 1973, Gosling 1990). Social odours are a limited resource whether the animal use faeces, urine, or secretion from skin glands (sebaceous and sweat glands (apocrine and eccrine glands)) (Müller-Schwarze 1983, Gorman 1984a). Scent marking can also involve a significant investment in terms of time and energy (Gosling 1986) including the cost of reduced growth rate and body size (Gosling et al. 2000). Given these constraints, scent marks should not be deployed at random, but instead in an organised pattern that maximises 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 the border of a territory (Gosling 1982, Gorman 1990). This hypothesis (the border maintenance hypothesis) predicts that animals should mark where neighbours are most likely to encounter marks (Gosling 1986, Smith et al. 1989), and preferentially along borders adjacent to the most threatening rivals (Johansson & Liberg 1996).

If scent-marking activity is correlated with population density (highly challenged), a positive correlation between number of neighbouring territories (or number of neighbouring individuals) and number of scent marks should be expected. Scent marks may serve as an economical means of preventing neighbours from gradually expanding their territories. For instance, when a potential threat emerged in the form of a neighbouring blind mole rat (*Spalax ehrenbergi*) adjacent to an animal's territory, the territory owner shifted its urination and defecation site to the border adjacent to the potential invader (Zuri et al. 1997). Brashares & Arcese (1999) found that territorial oribi males (*Ourebia ourebi*) marked at common

boundaries in relation to the number of male helpers in neighbouring territories, but not in relation to numbers of females. If an animal lives in flowing water, the upstream edge of the territory might be predicted to be the more 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 & Mckay 1990). In an important empirical demonstration, Stenström (1998) showed that in fallow deer (*Dama dama*), resource-holding stags scent-marked more frequently when their defended resources were challenged, but that those that scent-marked at higher frequencies were subjected to fewer agonistic encounters than those marking at lower rates (i.e. the status advertisement hypothesis was supported (Gosling 1990)). However, many species place scent marks throughout their territories, sometimes at a higher density near more frequently used trails, dens, lodges, or sleeping sites (Müller-Schwarze 1983, Gosling & Roberts 2001). Labelling of resources by scent marking has been thought to be related to either signalling ownership of the resource or to signal depletion of it (e.g. foxes (*Vulpes vulpes*): Henry 1977, otters (*Lutra lutra*): Kruuk 1992).

Many species of mammals produce or discharge scents only at certain times of the year, which is usually, but not always, the breeding season. If a primary function of scent marking in beaver is territorial defence, 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 2-years-olds normally occurs (Beer 1955, Bergerud & Miller 1977, Molini et al. 1980, Svendsen 1980a). The North American beaver scent marks occur most often during May and June following birth and the dispersal of 2-year-olds (Müller-Schwarze & Heckman 1980, Svendsen 1980a, Sun et al. 2000). Scent marks are therefore assumed to signal occupancy to potential intruders, notably dispersing 2-year-olds (e.g. Aleksiuik 1968, Svendsen 1980a).

Organs (odorants) used in territorial defence

The production of behaviourally significant odours by mammals occurs in many organs that pass chemicals to the external environment. The major sources of odours used in territory defence are the skin glands (e.g. Müller-Schwarze 1983, Flood 1985), but metabolic by-products/excretions such as faeces and urine also may be used. Urine and faeces may be ideal substances for scent marking because they have a minimal energetic cost to the signaller (e.g. Gosling 1981, 1985, Brashares & Arcese 1999).

Recent studies have demonstrated that scent types can carry different information and

thus have different functions (Johnston et al. 1993). For instance, the study by Gorman et al. (1978) on otters showed that deposits of spraints and urine might be used in the maintenance of otter territories, while the deposits of AGS sometimes found at latrines appear to have another function. The primary roles of skin glands of carnivores are the maintenance of the pelage and thermoregulation (Gorman & Trowbridge 1989). The same scent may also code for different information and thus serve multiple functions (e.g. Quay & Müller-Schwarze 1971, Epple et al. 1979, Johnston 1985), while several different scents may carry the same information (Baldwin & Meese 1977, Roeder 1980, Martin & Beauchamp 1982).

Beaver possess two pairs of scent producing organs, castor sacs and anal glands (Svendsen 1978, Walro & Svendsen 1982, Valeur 1988), and both are suspected to be used during scent marking activity to defend territories (e.g. Rosell & Bergan 1998). They are located in two cavities between the pelvis and base of the tail (Walro & Svendsen 1982, Valeur 1988). The anal gland is a holocrine secretory gland, but the castor sac is simply a pocket lined with a layer of nonsecretory epithelium. They both open into the uro-genital pouch (cloaca) (Svendsen 1978). The castor sac is used to store what is believed to be a mixture of secondary metabolites from urine, collectively called castoreum (Walro & Svendsen 1982). Copious amounts of castoreum deposited on scent mounds result from a process not dissimilar to urination, except that the urine flushes through the contents of the castor sacs. This material can be deposited on the scent mound without the animal contacting the substrate with the cloacal region. The anal gland papillae however must be rubbed on the substratum in order to deposit the exudates (Wilsson 1971, Svendsen 1978). It is suspected that castoreum is the most frequently used of the two during the scent-marking of territories (e.g. Schulte et al. 1994, Bergan 1996). Castoreum may be an ideal substance for scent marking the territory because it has a minimal energetic cost to the signaller. Selection for effective signal-sending behaviour harnesses odours that are already available at no extra cost (Müller-Schwarze 1999). The large number of phenolics and terpenes in castoreum (Tang et al. 1993, 1995), most likely diet-derived, may therefore constitute an honest signal, advertising the nutritional quality available to the individual and indirectly, the food supply in the territory (Müller-Schwarze 1999). However, it is presently not known if beavers deposit castoreum and AGS together, or alone when scent marking their territories. Neither is it known how often beavers deposit castoreum compared to AGS.

Social recognition and discrimination

The special features of behaviour that involve recognition will in some way always affect the lifetime success of any animal. Depending upon the nature of the objects being discriminated, different forms of recognition can be defined (Sherman et al. 1997). Mammalian pheromones can code for a wealth of information including species, subspecies, social group, individuality, sex, age, social status and reproductive condition (e.g. Müller-Schwarze 1974, Brown 1979, Müller-Schwarze 1983, Feoktistova 1995). The ability to discriminate odours from different individuals has been documented for several mammalian species (reviewed in Halpin 1980, 1986). However, whether the Eurasian beaver can recognise an intruder (i.e. is this a potential intruder?) and discriminate a neighbour from a stranger or a conspecific from a heterospecific (i.e. which of these potential intruders should be most aggressively responded to?) is unknown.

Territory intruders

When an animal finds a fresh scent mound in its territory it should be aware of the threat transmitted. In order to maintain its territory, the resident should add its own mark as a counter threat (Richardson 1991), a pattern of behaviour called countermarking (see also below). Scent countermarking is a common phenomenon among mammals and numerous functions have been proposed for it (e.g. Ewer 1968, Ralls 1971, Johnston et al. 1994, Wilcox & Johnston 1995, Roberts 1998, Sliwa & Richardson 1998, Ferkin 1999, Roberts & Dunbar 2000). In addition, overmarking and destroying a scent mound may mask information from other individuals. By covering a previously deposited scent with its own scent, an animal may prevent access by other individuals to chemicals from the underlying scent, thus making it difficult or impossible to perceive individual signatures in it. However, it is unlikely that countermarks will completely cover the competitor's scent (see Johnston et al. 1995, Hurst & Rich 1999). A masking hypothesis has been proposed for many species that scent mark in situations that suggest territorial or home area defence and/or advertisement of dominance (Mertl 1977, Macdonald 1979, Hurst 1987, 1990). Johnston et al. (1994) suggested that in golden hamsters (*Mesocricetus auratus*) countermarking might have competitive functions, because after test males investigated the marks of two individuals, one covering that of the other, they remembered the top, but not the bottom scent. A possible explanation is that the top scent physically masked the bottom scent by preventing the chemicals in the bottom scent from vaporising and thus being perceived by a hamster. These results suggest that one individual could gain an advantage over another in advertising for a mate, defending a burrow, etc., by marking over the scent of competitors and masking the evidence of their

presence in the area. Such behaviour could be an effective competitive strategy (Johnston et al. 1995).

Observing intruding beavers scent marking, and particularly the interactions between intruders and residents under field conditions is difficult. Artificially constructed experimental scent mounds (ESMs) with fluid or secretion applied to them could, however, mimic the presence of intruders. ESMs with castoreum from a non-territorial floater (strangers) usually elicit territorial responses in North American beaver (e.g. Schulte et al. 1994, Schulte et al. 1995a), but not castoreum from a member of the same family (Schulte 1998). As North American beavers tend to minimise their time on land, and since these behavioural responses to unfamiliar castoreum even take precedence over feeding (Müller-Schwarze et al. 1983, Müller-Schwarze 1992), they appear to have a vital function in territorial defence. Responses vary from lying in the water near the scent mound with nose raised to actually marking over an intruder's scent mound (e.g. Sun & Müller-Schwarze 1997, Schulte 1998). However, no extensive studies have yet been conducted on the response of Eurasian beavers to ESMs introduced into the territory, and it is not known if they respond in a similar way (see however Anderson & Westerling 1984).

The “dear enemy” phenomenon

One mechanism by which individuals may reduce defence costs is to reduce aggression towards familiar occupants of neighbouring territories, known as the dear enemy phenomenon (Fisher 1954, Krebs 1982, Ydenberg et al. 1988, Temeles 1994). Once territorial boundaries have been established, a territorial neighbour poses less threat to an individual's territory and an aggressive response to its display would add unnecessary costs to territorial defence. Strangers, however, pose a greater threat and a heightened aggressive response might well be worth the cost of time and energy expended (Jaeger 1981, Temeles 1994).

Other than increased visitation to ESMs marked with stranger castoreum, Schulte (1993, 1998) found little support for the dear enemy phenomenon in the North American beaver and concluded that further work is needed to clarify this issue. However, in Schulte's study area the distance between neighbouring sites averaged $0.95 \text{ km} \pm 0.47 \text{ SD}$ ($N=12$) and there was always an unoccupied stretch of stream between territories. Consequently, in Schulte's study neighbours may have been regarded as strangers since the contact between neighbours and their scent marks may have been relatively rare. It may be more important and easier to discriminate neighbours from strangers in areas where territories are located close together, and where frequent contact between neighbours occurs, than in areas were relatively

large distances between territories exist. Therefore, beavers living in areas with adjacent territories should show a more pronounced dear enemy phenomenon. A criterion in Temeles' (1994) review of the dear enemy phenomenon was to only include studies where neighbouring territories directly abut each other. The role of neighbour interactions in the territorial behaviour of monogamous, crepuscular and nocturnal mammals is not well known. The long-term occupancy of a territory by beavers implies that neighbour recognition and tolerance are beneficial to maintaining territorial claims.

Species discrimination

Hurst & Rich (1999) have argued that when territory owners or dominant individuals are challenged by a competitor, through attempting to deposit competing scent marks in their scent-marked territory or area of dominance, countermarking of the competitor's scent marks would prove that they have overcome the challenge and successfully excluded the competitor, or otherwise inhibited further challenges. Countermarking also ensures that own scent marks always remain the most recently deposited. Such behaviour is readily seen among conspecifics (e.g. Roper et al. 1993, Gosling & Wright 1994, Ramsay & Giller 1996), but few studies have examined the prevalence of countermarking between heterospecifics (see however Paquet 1991, Fornasieri & Roeder 1992).

Interspecific territoriality might evolve when species with overlapping ecological requirements interact (Simmons 1951). The greater the degree of overlap between species, the greater the competition for limited resources (Schoener 1983). Responses to heterospecific scent marks should therefore be profitable in the sense of excluding potential competitors, and by gaining exclusive access to these resources. The ability to adequately respond to heterospecific scent marks should thus be most prevalent among species coexisting within the same area, or in areas of narrow sympatry (Murray 1971). Among allopatric species the incentive of responding to heterospecific scent marks is thus not present, and Johnston & Robinson (1993) also argued that allopatric species have not been under any selective pressure to respond to heterospecific signals or to recognize particular individuals of another species. However, mammals often respond to scent from allopatric predators and are often repelled by them (e.g. Rosell & Czech, 1999). Dickman & Doncaster (1984) suggested that similar chemicals eliciting avoidance in rodents may commonly occur in the faeces and urine of carnivores (see also Bininda-Emonds et al. 2001). This is supported by observations that rodents often avoid the odours of carnivores with which there has been no evolutionary contact (Stoddart 1982a,b, Nolte et al. 1994, see also Roberts et al. 2001). Gorman (1984b)

showed that the Orkney race of common voles (*Microtus arvalis orcadensis*) that had been isolated from mammalian predators for at least 5000 years, strongly avoided stoat (*Mustela erminea*) odour, suggesting an innate rather than learned response. Bowers & Alexander (1967) argued that genetically similar species often share the same olfactory range. Therefore, the response to olfactory signals may also be strong among allopatric congenetics.

No study has so far investigated how the Eurasian beaver reacts to scent marks from the North American beaver (or vice versa), and whether it exhibits species discrimination abilities. It is important to examine how chemical signals and behavioural response to the signals have diverged along with the speciation process. Also, this is of particular interest in the wake of introductions of the North American beaver to Eurasia and the impending range concurrence of the two species (Lahti 1995).

Main aims of the study

I hypothesize that scent marking plays an important role in territory defence of free-ranging Eurasian beavers (Figure 1). Based on the main issues outlined above, I investigated the following issues (listed as papers **I-VI**).

In **paper I**, I examined which factors (density of animals, reproduction, duration of territory occupancy, season, location, colony size and age) affect scent-marking behaviour.

In **paper II**, I examined the temporal and spatial distribution of number scent marks during an annual cycle.

In **paper III**, I hypothesised that castoreum would be the main scent signal used in the defence of beaver territories during winter and predicted it would be deposited more often than AGS.

Based on the findings of **papers I and II**, **paper IV** is specifically devoted to discovering how the Eurasian beaver responds to simulated territorial intruders (field bioassay with use of ESMs). I hypothesised that territory owners would show one or more forms of territorial behaviour when an intruder has scent marked inside the territory and predicted that owners would show a stronger response to ESMs with castoreum than to ESMs without.

Paper V tested the idea that the Eurasian beaver exhibits the dear enemy phenomenon. I hypothesised that Eurasian beavers would show a longer and stronger response to scent (castoreum and AGS) from wandering strangers compared to scent from territorial neighbours.

In the last **paper (VI)**, I tested the hypothesis that the Eurasian beaver, being allopatric

to the North American beaver, would discriminate between scent marks of the two species, i.e. that it would exhibit species discrimination abilities. I predicted that the Eurasian beaver would show a more aggressive territorial response toward conspecific than to heterospecific scent marks.

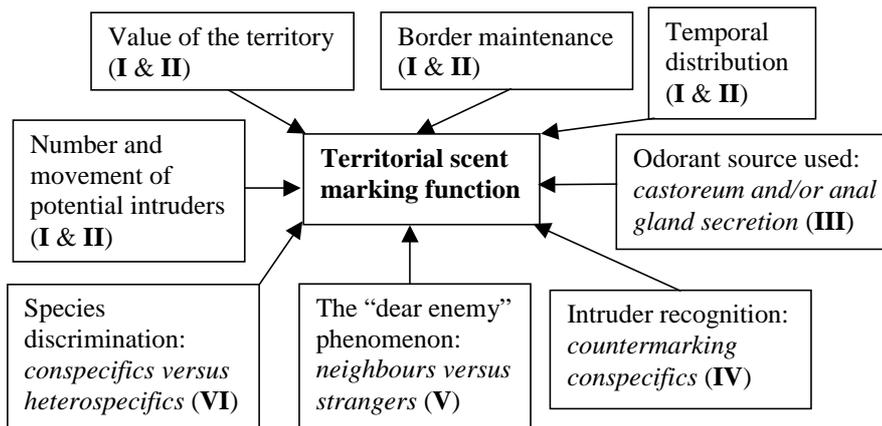


Figure 1. Main factors and hypotheses investigated in this study that are related to the function of scent marking in Eurasian beaver (*Castor fiber*) territoriality. The numbers in brackets refers to the specific paper(s) in the thesis.

Study areas and main methods

Study areas

The first study (**paper I**) was conducted in the Biesbosch region (about 100 km²) in the freshwater estuary of the rivers Rhine and Meuse in the Netherlands (51°45'N, 4°50'E). Beavers were re-introduced here in 1988-1991, and the population is still growing. During these years, a total of 42 Eurasian beavers were sequentially released (Nolet 1995). The remaining studies (**papers II-VI**) were conducted in Telemark County, southeastern Norway, primarily on the rivers Bø, Lunde, Gvarv and Saua. Beavers have occupied this area since the 1920s (Olstad 1937). Hunting and trapping pressure during the study was light and population density seemingly unaffected by harvesting.

Main methods

Recording of scent marks and collection of scent samples

I recorded the number and location of scent marks inside 13 and 7 territories in **papers I** and **II**, respectively. Binoculars were used to spot the scent marks from a canoe or boat and all scent marks found were registered on a map.

I collected castoreum and AGS samples (Rosell & Sun 1999) from beavers either shot by hunters (Parker & Rosell 2001) or live-trapped in landing nets (Rosell & Hovde 2001) or in Hancock- or Bailey live-traps (**papers III-VI**). Live-trapped beavers were individually marked (ear tagged and implanted with microchips). All beavers (both shot and live-trapped) were sexed (Rosell & Sun 1999), weighed and assigned to age classes based on body weight (Hartman 1992, Rosell & Pedersen 1999, Parker et al. 2001) (**papers III-VI**). However, in **paper III** the age of dead beavers was determined by examining tooth root closure and cementum annuli layers of the first molar (van Nostrand & Stephenson 1964).

In **paper III** I collected a total of 96 scent marks on snow and 14 control samples of secretion-free snow. All samples were analysed using gas chromatography and mass spectrometry (GC-MS). In order to obtain a control material I chemically analysed AGS and castoreum from 60 dead beavers. I compared the compounds found in the dead beavers with compounds found in the scent marks to elucidate whether animals used the castor sacs and/or the anal glands in territory defence.

The ESM experiments

In **paper IV** I constructed ESMs with castoreum from stranger adult males. During the first evening of observation the ESM was untreated (i.e. without castoreum) followed by one successive evening with castoreum. In **papers V** and **VI** I presented beaver families with a two-way choice between two pairs of ESMs (see Sun & Müller-Schwarze 1997). This method was chosen to signal an asymmetry between the two scent marks (see Ferkin 1999, Rich & Hurst 1999). In addition, environmental factors were the same for both ESMs compared with experiments using only one ESM (see Schulte 1998). Pilot experiments did not suggest that one odour influenced the other since beavers focused on one ESM at the time. Here I constructed ESMs with both castoreum and AGS. In **paper V** I presented ESMs with AGS from a neighbour and from strange adult male in one pair, and ESMs with castoreum from a neighbour and from a strange adult male in the other pair (see Figure 1, **paper V**). In **paper VI** I presented ESMs with AGS from the Eurasian beaver and the North American beaver in

one pair, and ESMs with castoreum from the Eurasian beaver and the North American beaver in the other pair. In **paper VI** I used samples from both males and females. In an attempt to discover any chemical correlates of behavioural response, gas chromatographic analyses of AGS and castoreum from both species were also performed. In order to test whether the gas chromatograms (GC) from the two species (both males and females) differed in the composition of compounds detected, GC samples were compared using Partial Least Squares (PLS2) regression (Wold et al. 1983).

Direct observations

An observer with binoculars placed downwind and on the opposite bank recorded quietly on a dictaphone (beavers appeared to not react to the human voice) the duration in seconds of three response patterns to ESMs: 1) the first land visit to the ESM, i.e. from the moment the beaver walked onto land within a radius of approximately 0.5 m from the ESMs to when it returned to the water, 2) sniffing (on land, and directed towards and within approximately 5 cm of the ESM) and 3) the ‘aggressive response’, i.e. standing on the ESM on hind feet, pawing and/or overmarking (putting a pile of mud either at the side or on top of the ESM and then marking it with castoreum and/or AGS) (Sun & Müller-Schwarze 1997). Sniff duration was used as a measure of the time required by beavers to identify the scents. The ‘aggressive response’ duration indicated how strong an agonistic behaviour the ESMs triggered (**papers V & VI**).

In **paper IV** I recorded whether or not one or more beavers swam past the ESM, sniffed from the water (directed towards and within 5 m of an ESM), walked onto land (land visit) and performed some form of activity at the ESM (e.g. Sun & Müller-Schwarze 1997, Schulte 1998). When beavers were present, but did not react to the odour stimulus (i.e. swam past the ESM within 5 m of it), the response was defined as “no response”. One or more activities falling into the other three categories were defined as a “response”. I included only the responses of the first beaver in my analyses because physical damage to the scent mounds (pawed, flattened or obliterated) may cause some carry-over biases in the following responses by the same or other beavers (Sun & Müller-Schwarze 1997). I also separated the responses into four categories with the following index values: value 0, beaver observed but did not respond to the ESM; value 1, the only response was sniffing (when on land and at the ESM); value 2, beaver sniffed and straddled the ESM and value 3, beaver sniffed, straddled, pawed and (or) overmarked the ESM.

Overnight activity

Because beavers usually live in family units, different members of a family may respond to ESMs sequentially at different times during the same night (Schulte 1993, Sun & Müller-Schwarze 1998a). Therefore, a response result is a descriptor of the territoriality of a family rather than of an individual (Schulte 1993) (**papers IV-VI**). I checked and ranked the response result overnight (i.e. the response measured the following morning) to characterize the intensity of the collective beaver family response (see Table 1 **paper V**). When beavers scent marked over ESMs and/or close by on self-constructed scent mounds (which could occur independent of ESM status), I gave the respective ESM an additional index value of 1, i.e. the maximum score could be 7 (**papers V & VI**). In **paper IV** I separated the overnight response into two categories: response or no response. A response involved either overmarking (depositing fresh odour) the ESM without destroying it, destroying it (partly or completely) without depositing fresh odour (determined by the human nose), or destroying it (partly or completely) and depositing fresh odour. If a beaver left no trace of its presence on or near the ESM this was recorded as no response, even if a beaver had visited the ESM during the observational period the previous evening. This maintained the independence of the observed and overnight measures of land-visit response. After having recorded the overnight activity, the ESM was obliterated. A new ESM was constructed on the successive evening and provided with castoreum before the second evening's experiment started (**paper IV**).

Main results of the individual papers

Factors affecting the number and distribution (temporal and spatial) of scent marks

The results from **paper I** showed that beaver colonies with close neighbours scent-marked more often than isolated ones, and that the number of scent marks increased significantly with the number of neighbouring territories and individuals, the mean distance to all other territories, duration of territory occupancy (2-5 years) and length of wooded banks within the territory. The results from **paper I** showed that there was a peak in number of scent marks in the last week in April and the first week in May.

The results from **paper II** showed that: (1) the number of scent marks in territories was significantly higher in spring (beginning of April-end of May) when dispersal of

subadults normally occurs (see Figure 1, **paper II**), (2) the number of scent marks was clumped near territorial borders (see Figure 2, **paper II**) and (3) the number of scent marks was significantly greater upstream than downstream of the lodge.

Organs (odorants) used in territorial defence

The main results showed that all the collected scent marks (n=96) contained compounds from castoreum (see Figure 1, **paper III**) and that compounds from AGS were found in only 4 scent marks (**paper III**).

Social recognition and discrimination

Territory intruders

During the first evening, when ESMs were presented without castoreum, no response to the ESM was observed. Likewise, no overnight response was recorded. However, during the second evening and night, when ESMs with castoreum were presented, beavers responded strongly. In 55% of the trials, beavers made a land visit to the ESM often preceded by a sniff. In 27% of the trials, they were observed to sniff the ESM from the water but did not make a land visit. I frequently observed that beavers, after visiting the ESMs, started to patrol the territory. The overnight response showed that the beavers overmarked or destroyed the ESM without depositing fresh odour in 5% of the trials and that they destroyed the ESM and deposited fresh odour in 80% of the trials. The proportion of trials with observed and overnight responses was significantly lower during the first evening-overnight compared with the second evening-overnight (**paper IV**).

The “dear enemy” phenomenon

Direct observations of the families during evenings showed that: (1) beavers sniffed both castoreum and AGS from a stranger significantly longer than from a neighbour (**paper V**) and (2) beavers aggressively responded significantly longer to castoreum, but not to AGS, from a stranger than from a neighbour (**paper V**). When ESMs were allowed to remain overnight and the response measured the following morning, beavers responded significantly stronger to both castoreum and AGS from a stranger (**paper V**).

Species discrimination

Results showed that beavers (1) did not spend significantly longer time sniffing conspecific over heterospecific ESMs (see Figure 1a, **paper VI**), (2) spent significantly longer time responding aggressively to conspecific over heterospecific ESMs (see Figure 1b, **paper VI**) and (3) responded significantly more aggressive to conspecific over heterospecific ESMs overnight (see Figure 1c, **paper VI**). Gas chromatographic comparisons of castoreum showed that differences between species accounted for 34% of the total variation in compounds detected, while differences between sexes accounted for 13% (see Figure 2a, **paper VI**). For AGS, 49% and 46% of this variation was explained by differences between species and sex, respectively (see Figure 2b, **paper VI**).

Discussion and prospects for future studies

Factors affecting the number and distribution (temporal and spatial) of scent marks

Beaver colonies in the central part of my study area (Biesbosch) scent-marked significantly more than did colonies at the periphery. The number of scent marks increased significantly with the number of neighbouring territories and individuals. I also found that the number of scent marks decreased with increasing mean distance to all other territories. This may be regarded as a measure of how central a territory is situated. That the number of scent marks is population density dependent has previously been shown for both the North American beaver (Butler & Butler 1979, Müller-Schwarze & Heckman 1980, Houlihan 1989) and the Eurasian beaver (Anderson & Westerling 1984). Thus when beavers have many close neighbours (highly challenged) they apparently need to scent mark more often to be unambiguously recognised as territory owners (**paper I**). These results lend support to the idea that investment in scent marking reduces the costs of directly defending territories, i.e. reduced costs of agonistic encounters (the status advertisement hypothesis, Gosling 1990, Stenström 1998). Whether scent marking subjects beavers to fewer agonistic encounters needs to be clarified. However, high-density sites may also be of “better quality”, providing territory holders with more excess energy to spend in their defence, and more reasons to defend. Another alternative explanation is that the frequency of scent marking is condition-dependent such that better quality animals defending better territories are able to scent-mark more.

Nolet et al. (1995) found that, in contrast to other food studies on beavers, in the

Biesbosch they ate woody plants almost exclusively all year round. Wooded banks within the territory were therefore clearly an important resource. Beavers released in unoccupied habitat spent considerable time exploring their surroundings, especially during the first two years of the reintroduction (Nolet & Rosell 1994). Thus, once established, these (large) territories were presumably well worth defending. Theoretically, the greater potential value of the territory for residents, in contrast to intruders, makes it worth fighting harder for (e.g. Gosling et al. 2000, Gosling & Roberts 2001). Thus intruders should retreat (Maynard Smith 1976). Nolet & Rosell (1994) found that the earliest arrivals claimed larger territories, and also territories of better quality, than later arrivals. I found a significant positive correlation between both the number of scent marks and the duration of territory occupancy (<5 years) and length of wooded banks as did Hodgdon (1978). It appears that residents invest more in scent marking in good quality territories, and when a territory has been occupied for a relatively long time, as a means of defending it better (**paper I**).

The number of scent marks was highest in spring (April-May) (**papers I & II**). This is in agreement with earlier studies for both species of beavers (e.g. Butler & Butler 1979, Müller-Schwarze & Heckman 1980, Svendsen 1980a, Nitsche 1985a,b). The results suggest that the high frequency of scent marking in spring probably is primarily associated with a peak in dispersal of subadults at this time (e.g. Molini et al. 1980, Svendsen 1980b).

If the primary function of beaver scent marking is territory defence, then markings might be expected to be clustered near territorial boundaries. Hediger (1949) commented that many species deposit scent where they meet or expect rivals, e.g. near territory borders. Peters & Mech (1975) reported that wolves (*Canis lupus*) concentrated scent marks at the periphery of the territory. The same pattern was also found for the Eurasian beaver (this study, **paper I & II**), and for many other mammals (Aleksiuk 1968, Kruuk 1978, Kruuk et al. 1984, Smith et al. 1989, Richardson 1991, Sun et al. 1994, Gese & Ruff 1997, Sillero-Zubiri & Macdonald 1998, Brashares & Arcese 1999). 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 (**paper II**). The continually ice-free state of the Bø River (Telemark County) allows dispersion throughout the entire year (**paper II**). Nearly the same situation exists in the Biesbosch (usually ice-bound for less than 2-3 weeks) (Nolet & Rosell 1994) (**paper I**). However, low water temperatures make prolonged swimming a very costly activity (e.g. MacArthur 1989, MacArthur & Dyck 1990, Nolet & Rosell 1994) and therefore may influence the frequency and distribution of scent marking during winter. Indeed, from October to December, when marking activity was minimal, almost all marking occurred at

territorial borders. In this manner, beaver presumably maximise the effect of the scent marking process at a time of the year when time and energy are mainly allocated to preparation for winter (**paper II**). This supports the hypothesis that mark density communicates to intruders the potential of an encounter with the owners (Gorman & 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 & Richardson 1998).

More scent marks were located upstream than downstream of the lodge. This was the case regardless of the location (upstream or downstream) of the nearest neighbour. 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 beavers. Whether marking activity is concentrated upstream 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. Indeed, Sun et al. (2000) recently showed that the majority (74%) of dispersing North American beavers (n=46) initiated dispersal in a downstream direction after ice-out. However, I do not know the main direction of dispersal in my study area, and beavers have been shown to disperse both upstream and downstream (Leege 1968, Van Deelen & 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 beavers keep their nostrils at the water level, thus enabling them to sense chemical messages from neighbouring beavers concentrated within the surface film (Grønneberg & Lie 1984) (**paper II**) (see also below).

Organs (odorants) used in territorial defence

My results in **paper III** supported the prediction that castoreum was most frequently deposited on scent marks (96 of 96) and appears therefore to be the main scent signal used in the defence of Eurasian beaver territories during January-March. Scent marking with castoreum may provide a volatile alerting signal for attracting attention (Müller-Schwarze

1999). Alerting signals contain no information about an individual, or even a species (Müller-Schwarze 1999). Responses to single compounds support the hypothesis that castoreum is used for signalling territorial occupancy, which requires only one bit of information in the signal for making a decision by receivers, i.e. whether the territory is occupied or not (Müller-Schwarze & Houlihan 1991, Schulte et al. 1994, Sun & Müller-Schwarze 1999). It may be that the lighter, more volatile compounds in the castoreum direct receivers toward the less volatile but potentially more informative chemical components still present at the scent mark. This is supported by the fact that 94% of the compounds had a molecular weight below 300.

In contrast, AGS was deposited on only 4 of 96 scent marks, and may therefore have another function. AGS may act as a chemical messenger in the water territory (Grønneberg & Lie 1984) sensed at close range or through contact with the animal. The latter is supported by the fact that only 12.5% and 32.5% of the compounds detected in AGS of females and males, respectively, had a molecular weight below 300. It could be advantageous for a swimming mammal such as the beaver to present chemical signals in the form of lipid substances that would concentrate at the air-water interface (Albone 1984). By lubricating the fur with AGS, which would be released into the water, beavers could also act as a "living scent mark". As AGS is insoluble in water (Svendsen 1978), beavers downstream would receive a concentrated flow of chemical scent information in the surface film from upstream territories (**paper II**). The recently discovered vomeronasal organ in Eurasian beavers may play a significant role at the air-water interface but its importance for chemical communication in beavers is not known (Døving et al. 1993, Rosell & Pedersen 1999). However, the design of the beaver's nose enables this amphibious animal to sample the chemical composition of its environment. Above water the beaver can inhale air and expose its olfactory organ to volatile substances, and in water the vomeronasal organ can sample water-borne substances. Further, anal glands, which are located in the anus (Svendsen 1978), may add AGS to the faeces when beavers defecate in the water. For instance, the large complex of sebaceous and apocrine glands located in and around the anus of many species of antelope may add individual-specific secretion to faeces (Barrette 1977, Mainoya 1980, Gosling 1982). However, further studies are needed to clarify whether beavers use AGS on scent marks at other times of the year. Indeed, several researchers have seen Eurasian beavers protrude their anal gland papillas during spring and summer scent marking (Rosell & Bergan 1998, Rosell unpublished) (**paper III**).

Social recognition and discrimination

Territory intruders

Eurasian beavers showed territorial behaviour when an “intruder” (experimenter) had scent marked with castoreum inside the territory (**paper IV**). They destroyed the ESM with castoreum and deposited fresh odour in 80% of the trials, which indicated that they countermarked and probably tried to mask the odour of alien adult male conspecifics with their own odours. That is, they responded in a way similar to the over-marking shown by many other species (e.g. Hurst 1987, 1990, 1993, Johnston et al. 1994, 1995, Roberts 1998, Bel et al. 1999, Ferkin 1999). Also, the lack of a response to ESMs without castoreum indicated that beavers were responding to the smell of castoreum and not to the sight of the scent mound. Studies of North American beavers have also shown no significant response to blank ESMs (Müller-Schwarze et al. 1986, Müller-Schwarze & Houlihan 1991, Schulte 1998). Since scent marks and countermarks remain in the environment and, even in the absence of their authors, provide a continuous record of competitive challenges between conspecifics attempting to advertise their presence and dominance in the area. Scent marks could thus provide a reliable advertisement of an individual’s ability to dominate or defend an area, since only those successfully dominating the area can ensure that their marks both predominate (Gosling 1982) and are more recently deposited than those of any challenging competitors (Hurst 1993, Hurst & Rich 1999). The countermarking may therefore advertise that the territory is occupied and signal the costs of competition if the threat is ignored (e.g. Gosling 1990, Roberts & Dunbar 2000).

Distinguishing among multiple scent marks is essential for the animal if it is to identify potential mates, competitors, and territory owners (Johnston et al. 1995, 1997a,b, Wilcox & Johnston 1995, Johnston & Bhorade 1998, Ferkin 1999, Kohli & Ferkin 1999). Johnston et al. (1994) outlined three hypotheses to explain what happens when scent marks of two conspecifics overlap. The first hypothesis, called scent-blending, states that the two scents will mix together, forming a new unique scent. The second hypothesis, the scent-bulletin-board, states that the scents of each individual remain distinct from one another. The third hypothesis, the scent masking, states that the top scent will physically mask the presence of the bottom scent. Studies on golden hamsters, meadow voles (*M. pennsylvanicus*) and prairie voles (*M. ochrogaster*) have shown that animals exposed first to an overmark, respond preferentially and display a better memory for the odour of the top-scent donor than that of the bottom-scent donor (Johnston et al. 1994, 1995, 1997a,b, Wilcox & Johnston 1995,

Johnston & Borade 1998, Ferkin et al. 1999, Woodward et al. 1999). This preference for the top scent suggests that these animals treat the odour of the top-scent donor as being more important or having greater value than that of the bottom-scent donor, i.e. supports the scent-masking hypothesis (Ferkin 1999). However, the mating system involved may affect the manner in which animals respond to conspecific over-marks (Woodward et al. 2000). It may be more costly for monogamous prairie voles than for promiscuous meadow voles to be the bottom-scent donor of an over-mark (Ferkin 1999, Woodward et al. 1999). For meadow voles, Woodward et al. (2000) suggested that over-marking an opposite-sex conspecific's mark may be akin to an advertisement used in courtship to attract multiple mates. In contrast, for prairie voles, devaluation of an opposite-sex conspecific's scent mark may represent a form of mate guarding (Woodward et al. 2000). By over-marking the scent marks of same-sex intruders, a male and a female prairie vole may indicate to its mate and to conspecifics that the pair bond is intact and the territory is occupied (Woodward et al. 1999). At present, it is not known whether beavers can distinguish between individual over-marks and respond to them later when encountered individually. Further studies should therefore investigate these issues for male and female beavers.

The “dear enemy” phenomenon

The main results of **paper V** indicated that Eurasian beavers responded significantly longer and stronger both to castoreum and AGS from strangers than from neighbours. These findings indicate that neighbour scent was more familiar to the territorial beavers, and that beavers showed a stronger agonistic behaviour to scent from strangers. This supports the hypothesis that beavers exhibit the dear enemy phenomenon, and is consistent with the general hypothesis that on multi-purpose breeding territories, a territorial owner's potential losses to strangers is higher than to neighbours (Temeles 1994). Because of some spatio-temporal overlap between territorial neighbours, social conflict by repeated physical aggression would be costly in time and energy and should be avoided (Maynard Smith & Parker 1976). The dear enemy phenomenon should be particularly prevalent among species that can inflict serious injuries during escalated contests, injuries that could significantly lower the future fitness of one or both contestants (Jaeger 1981). Beavers are highly aggressive and contests may lead to serious injuries or even death (Novak 1987).

The most efficient behaviour for a monogamous species occupying a territory for many years is to recognise neighbours and to tolerate their close proximity, but to be less tolerant to strangers. Animals that associate regularly and are equally likely to win or lose in a

conflict can have stable, long-term relationships based on mutual avoidance (Randall 1989). The dear enemy phenomenon in beavers is most likely an evolutionary response to the high cost and low payoff of escalated aggression between territorial neighbours (see also Jaeger 1981). Beavers in our study area presumably learn the identity of their neighbours by repeated exposure to them and their scent marks at the edges of territories (see Rosell & Bergan 1998, **paper II**). Schulte (1998) found weak evidence of the dear enemy phenomenon in the North American beaver. However, on that study area there were always unoccupied stretches of stream between territories indicating less contact between neighbours and a reduced potential for learning their identity. Consequently, in Schulte's study, neighbours may have been regarded as strangers since the contact between neighbours and their scent marks may have been relatively rare. Indeed, a criterion in Temeles' (1994) review of the dear enemy phenomenon was to only include studies where neighbouring territories directly abut each other.

Sun & Müller-Schwarze (1997) concluded that North American beavers use AGS to discriminate between unfamiliar sibling and unfamiliar non-relatives, but not castoreum. However, Schulte (1998) found that North American beavers discriminated among castoreum from family and non-family adult males. Therefore, both Schulte's (1998) and my findings suggest that castoreum, as well as AGS, contains information about familiarity, though no chemical analyses, as yet, have documented this.

Another possible explanation for why territory residents are less aggressive toward neighbours compared to strangers is that they might be exhibiting kin recognition. Sun et al. (2000) showed that two- and three-year-old female and male beavers dispersed on average 10 km and 3.5 km, respectively, from their natal families, in a high-density population of North American beavers. This indicates that beavers, especially males, may disperse shorter distances and establish territories at the nearest available site. In this manner beavers may decrease their future defence costs by settling next to their natal area (Sun et al. 2000). In a study of the Eurasian beaver, Nolet & Rosell (1994) found that information about vacant territories was apparently rapidly available to nearby individuals. As a consequence, not only the familiarity but also the genealogical relationships between neighbours must be taken into account when trying to explain the dear enemy phenomenon in beavers.

Several authors have reported that if bird songs recorded from a neighbour are broadcast to a resident from the territory boundary opposite the shared boundary, the residents treat neighbours and strangers equally aggressively (Wiley & Wiley 1977, Falls 1978, Trivers 1985). Therefore, animals living on adjacent territories should show a clearer dear enemy

phenomenon than animals on territories with undefended space between. Caley & Boutin (1987) found that amicable behaviour of muskrats (*Ondatra zibethicus*) decreased significantly with increasing distance between captures, and therefore with decreasing familiarity. Emlen (1971) played back the songs of indigo buntings (*Passerina cyanea*) from increasingly distant territories to selected territory holders and found that more aggression was displayed to the playbacks of songs of more distant males. Vestal & Hellack (1978) found that there were marked differences between neighbour and stranger interactions of two related species of deer mice (*Peromyscus*). Their neighbour and strange males of *P. maniculatus* did not differ in any measures, which is in contrast to data from *P. leucopus*. The difference between the two species appears to lie in *P. maniculatus* neighbours having a less well-developed social relationship than *P. leucopus*. However, most of the aspects of beaver morphology, behaviour and ecology differ very little between the two species (Wilsson 1971, Novak 1987, Rosell & Pedersen 1999). I therefore speculate that the discrepancy in results from Schulte's (1998) and my study is not due to species differences, but to the presence of undefended space between territory borders shown in that study that may interfere with mechanisms responsible for neighbour-stranger discrimination. However, Schulte's (1998) design was different from mine. In that study, ESMs from neighbours and strangers were presented separately on consecutive nights whereas in my study the two were presented simultaneously during one night. In fact, one of his measures (land visitation rate) supported the dear enemy phenomenon. Therefore, another explanation may be that the discrepancy is due to the experimental design. The next step should be to clarify if beavers are more aggressive to scent from more distant individuals.

ESMs deposited close to a resident's lodge, as in my study, may provoke a greater aggressiveness and desire to identify the marker. Resident aardwolves (*Proteles cristatus*) sniffed neighbour's marks significantly longer when found inside of their territories than at the borders (the 'centre-edge effect', Falls 1982, Sliwa & Richardson 1998). Further studies should clarify this issue for beavers.

Species discrimination

The results in **paper VI** confirm my hypothesis that Eurasian beavers discriminate between scent marks of the two species. This is supported by the significantly longer time spent responding aggressively, and stronger aggression exerted upon conspecific than heterospecific scent marks. This indicates that the Eurasian beaver does not recognize the scent marks of the North American beaver to be an equally potential threat as those of conspecifics. Although

beavers were indiscriminate when sniffing the ESMs, sniffing can be defined as only the investigation stage within a complete set of multiple responses. The main purpose of a beaver's investigation of an ESM is to identify the sender, and then, based on the information obtained, decide what appropriate actions to take (i.e. signal detection theory, see Bradbury & Vehrencamp 1998). Thus, similar sniffing durations, or a lack of preference, does not indicate inability to discriminate (Brown 1979, Johnston 1993, Gouat et al. 1998), but can be interpreted as a process of decision-making. A similar behaviour has also been described for tree shrews (*Tupaia belangeri*) where the presentation of heterospecific scent marks elicited intense olfactory investigation, but no equivalent increase in scent marking activity (Holst & Buerger-Goodwin 1975). If the chemical signal present in castoreum and AGS of each species to some extent matches the chemical template of the other species, this might have led to the undifferentiated sniffing duration because beavers found it difficult to distinguish the two species. As such, sniffing duration is more likely to be a measure of olfactory similarities between the two species than an actual measure of discriminatory abilities.

When congenetic species are separated for any length of time, they may diverge in such a manner that neither species is distinguishable to the other with regard to chemical signals. Although some chemical constituents may persist in both species, they may not provide adequate information to evoke a territorial response of similar strength as to a conspecific. As such, Eurasian beavers would regard intrusive scent marks of the North American beaver as a lesser territorial threat than conspecific scent marks, and would therefore be less likely to spend time and energy countermarking these scent marks. I can however not rule out the possibility that beavers do recognize some of the chemical constituents of heterospecific scent marks, but without frequent contact they do not respond as aggressively as to conspecific scent marks. Murray (1971) pointed out that interspecific territoriality is a characteristic that is not adaptive and has not been selected for, but might evolve when two species compete for some material resource when they occur in the same habitat (see also e.g. Catchpole 1978, Greenberg et al. 1996, Griffis & Jaeger 1998). This implies that a territorial response toward heterospecific scent marks should be based on individual experiences only, and not on autonomically controlled (Paquet 1991) or innate mechanisms. Thus, the reduced aggression observed toward scent marks of the North American beaver might be explained by a lack of stimulation, i.e. both chemical and visual stimulus are needed to evoke a territorial response. Studies of interactions between temporally displaced signals indicate that the first cue (in this case chemical) functions to alert the receiver to the presence of the second cue (visual), increasing the probability of its detection

and recognition (Endler 1992, 1993, Wiley 1994).

The corresponding results of the two types of aggressive responses measured (i.e. direct and overnight responses) indicate that discrimination of heterospecific scent marks is not a specific feature related to the first beaver responding, but is common behaviour among most individuals. The fact that beavers live in family units enhances the possibility of more than one family member responding to the same scent marks during the night. This was readily seen during observation trials where several family members successively responded to the same pair of ESMS. Although successive visits would probably increase the cumulative probability of recognition errors, the results in this study show that misdirected territorial aggression is rare, implying that the chemical constituents present in the North American beaver scent marks are insufficient to evoke a territorial response. The GC comparisons of castoreum show that between-sex variation within the same species (13%) is less pronounced than between-species variation (34%). This demonstrates that the composition of compounds present in castoreum differs between the two species, and that the reduced aggression observed toward castoreum of the North American beaver may be attributed to this difference. Since castoreum is a mixture of secondary metabolites most likely originating from the beaver's diet (Svendsen 1978, Müller-Schwarze 1992, 1999), the most obvious explanation to account for the difference in chemical composition would be the differences in the diet between the two species. This would also explain the less pronounced variation found between males and females of the same species, because food types are more similar in the same habitat than in different habitat. However, the two species inhabit similar vegetation types (see Nordiska ministerrådet 1984 for comparison) and probably forage on many of the same plants. Thus, other factors than diet may be in part responsible for the observed difference (e.g. bacterial flora: Albone et al. 1977, Walro & Svendsen 1982, genetically based components: see Halpin 1986).

The suggestion that a reduced aggressive response toward scent marks of the North American beaver is based on chemical differences between the two species is to a greater extent supported by AGS in which between-species variation accounted for 49%. A possible interpretation for this major difference would be that one of the primary functions of AGS is to signal species identity in order to maintain reproductive isolation. Tinbergen (1953) stated that although closely related species are very often similar in behaviour and morphology, there are always some striking differences between mating cues. However, since both species have been separated since bisection, the development of species-specific mating cues has not been required, and therefore has probably also not been selected for. A more plausible

interpretation would be that the difference in chemical constituents of AGS has gradually evolved as a consequence of genetic drift and/or adaptation to the local environment, following Mayr's (1963) geographic isolation speciation model. Ovaska (1989) found that in two separated populations of the salamander (*Plethodon vehiculum*), pheromonal divergence could not be explained by premating isolation mechanisms evolved through reinforcement, but suggested that it was brought about by pleiotropic effects associated with other changes evolved in isolation (see also Passmore 1985, Verrel & Arnold 1989, Dempster et al. 1993, Andersson 1994). On the other hand, the profound difference between male and female AGS within the same species (46%) suggests that AGS is used to signal sexual identity (see Schulte et al. 1995b, Rosell & Sun 1999, Sun & Müller-Schwarze 1999). Its function in territory maintenance, however, is unclear. Compared to castoreum, AGS is probably more costly to produce. I found in **paper III** that out of 96 scent marks on snow only four contained compounds from the anal glands. Although no equivalent study has been performed during the ice-free seasons, this indicates that the primary function of AGS is probably not to act as a territory defence signal. Sun & Müller-Schwarze (1998a) recently documented that related North American beaver individuals shared more features in the chemical AGS profile than did unrelated individuals. Sun & Müller-Schwarze (1998b) further demonstrated that it is possible to use some AGS compounds to classify different families. As such, these studies indicate that AGS is probably used in kin and family recognition.

Future research should focus on the responsive behaviours and territorial interactions between the two species in areas of sympatry. By performing similar experiments in Eurasia where North American beavers have been introduced it will be possible to establish whether or not Eurasian beavers recognize North American beavers as potential competitors, and determine the validity of the belief that the North American beaver has out competed the Eurasian beaver in parts of Finland (Lathi 1995). It will also be interesting to know how the North American beaver reacts to scent marks from the Eurasian beaver (under investigation, A.M. Schipper, L. Sun & F. Rosell unpublished). Ignorance of the importance of olfactory communication between animals may seriously compromise the existence of endemic species when introducing ecologically similar species (e.g. European mink (*M. lutreola*), Maran et al. 1998, red squirrels (*Sciurus vulgaris*), Wauters et al. 2000).

Conclusion and alternative hypotheses of scent marking

The results presented in this thesis supported my main hypothesis that scent marking plays an important role in territory defence of free-ranging Eurasian beavers. My study has contributed to a better understanding of the function of territorial scent marking in the Eurasian beaver by demonstrating their capability of transmitting odorous messages efficiently, both temporally and spatially, and their ability to countermark and discriminate ESMs from intruders of different degrees of threat.

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, 1985, 1990). By matching the scent of a territory owner with those of nearby scent marks, an intruder employs the unique property of olfactory signalling that includes the provision of both a historical and a spatial record of a territorial individual's behaviour. 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). If the hypothesis was true, one would expect owners to (1) mark where intruders are most likely to encounter marks; (2) mark themselves with the substances used to mark the territory; (3) make themselves available for scent matching by intruders; and (4) remove or replace marks of others (Gosling 1982, 1985, 1986, Gorman 1984a). The scent-matching hypothesis has received support by studies of scent marking in several species, e.g. ferret (*M. furo*) (Clapperton et al. 1988), house mice (*Mus domesticus*) (Gosling & McKay 1990), suni antelope (*Neotragus moschatus*) (Somers et al. 1990), yellow mongoose (*Cynictus penicillata*) (Wenhold & Rasa 1994), and North American beaver (Sun & Müller-Schwarze 1998c). My results also support this hypothesis, i.e. predictions 1 (**papers I & II**), 3 (**paper IV**) and 4 (**papers IV, V & VI**) were all supported. However, prediction 2 needs to be clarified. I showed in **paper III** that the main scent signal used in territorial defence was castoreum. It's still unclear whether beavers smear castoreum on their pelage, and/or mark themselves with AGS to waterproof the fur, and thereby function as a "living-scent mark". The next step should be to clarify these issues.

The function of scent marking suggested here is not necessarily the only functional mechanism, as one function need not necessarily exclude others. For instance, Rosell & Bergan (2000) found support for the hypothesis that Eurasian beavers emphasize scent-marking behaviour during the breeding season (January-March) in watersheds that are ice-free year-round. Eurasian beavers scent marked significantly higher during the breeding versus the nonbreeding (October-December) portion of winter. They speculated that a female might need an effective method to advertise her reproductive status (see also Roberts & Dunbar 2000),

even if she mates with her lodge-mate, because in some places the adult male and female maintain two or more winter lodges and may be found in separate lodges. Females may deposit castoreum (volatiles with low molecular weight) at scent marks to signal to males that ovulation has occurred and to attract them from a distance. In contrast, AGS (high molecular weight) may give detailed information at the individual level and therefore induce mating when at a close-range. In contrast, males may increase their scent marking activity during the breeding season to keep other males away from their territory (i.e. mate guarding, see also Roberts & Dunbar 2000, Woodward et al. 2000) containing a receptive female, probably by using both castoreum and AGS. Further studies are needed to clarify how information in scent marks are coded and transmitted during the breeding season.

Due to the diversity of information that can be coded in a signal, chemical signals can often serve different functions at the same time. Most of the possible functions are not mutually exclusive, and the meaning of a signal often depends on the content of the signal, the identity of the sender, the identity of the receiver, and their relationship. Therefore, more information is needed about frequency of marking by different group members (age, social status and sex), behavioural context in which the signal is deposited, and variability in frequency and pattern among groups of different social composition. Another possible main function for scent marking in beavers that cannot be entirely ruled out is that marking is related to use or defence of resources within the territory (the labelling resources hypothesis, Henry 1977, Kruuk 1992, Branch 1993). My work has emphasized intergroup communication. However, more work is needed to clarify the role of scent marks in intragroup communication.

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