

Territorial scent marking behaviour in the Eurasian beaver (*Castor fiber* L.)

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Abstract

This paper reviews 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. Scent marking plays a significant indirect role in territorial defence by the Eurasian beaver. Resident beavers appear to invest more in scent marking in good quality territories, and when a territory has been occupied for a relatively long time. Territories are scent marked significantly more often in spring when dispersal of 2-years-olds normally occurs and scent marks are concentrated near territorial borders, apparently to maximize the signal effect to potential trespassers on or before entering the territory. These results support the border maintenance hypothesis. During winter castoreum is almost exclusively deposited on scent marks and appears therefore to be the main scent signal used in the defence of Eurasian beavers territories. AGS is rarely deposited and appears to have another function. Eurasian beaver show territorial behaviour when an "intruder", in the form of artificially-constructed experimental scent mounds (ESMs) containing castoreum from alien adult males, is placed inside the territory. They destroy the ESMs and overmark with their own scent. Countermarking appears to be an attempt to mask the odour of alien adult male conspecifics with their own odours. Scent marks can 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. 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 can discriminate between scent marks of the two species, i.e. exhibits species discrimination abilities. This indicates that the Eurasian beaver will regard intrusive scent marks from the North American beaver (*C. canadensis*) as a lesser territorial threat than from a conspecific, and would therefore be less likely to spend time and energy countermarking these scent marks. These findings show that Eurasian beavers are capable of transmitting odorous messages efficiently, both temporally and spatially, and to countermark and discriminate ESMs from intruders of different degrees of threat. 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). Scent marking by Eurasian beaver supports also the general scent-matching hypothesis. However, the function of scent marking suggested here is not necessarily the only functional mechanism, as one function need not necessarily exclude others.

Key words: Eurasian beaver, *Castor fiber*, Territory defence, scent marks, discrimination, North American beaver

Zusammenfassung

Das Verhalten der Revierabgrenzung mittels geruchlicher Stoffe beim Eurasischen Biber (*Castor fiber* L.)

In dieser Arbeit wird überprüft, welche Funktionen Geruchsmarkierung bei der territorialen Abgrenzung beim Eurasischen Biber (*Castor fiber*) hat. Normalerweise deponieren Biber Geruchsstoffe (Castoreum und/oder Analdrüsensekret (AGS)) auf kleinen Haufen aus Schlamm und Sand, wobei sich alle Altersklassen und beide Geschlechter beim Markieren beteiligen. Geruchsmarkierung spielt beim Eurasischen Biber eine signifikante indirekte Rolle bei der Revierverteidigung. Es scheint, dass sesshafte Biber in optimalen und relativ lang besetzten Revieren stärker geruchlich markieren. Im Frühling werden die Reviere öfter mit Geruchsmarkierungen versehen, wenn normal dispergierende 2-jährige Biber vorkommen. Die Markierungen sind an den Reviergrenzen häufiger, offenbar um ungebetene Eindringlinge an, bzw. vor dem Eindringen in das besetzte Revier abzuschrecken. Dieses Ergebnis unterstützt die Hypothese von der Instandhaltung der Reviergrenze. Während des Winters wird ausschließlich mit Castoreum markiert und es scheint so, dass es beim Eurasischen Biber der Hauptgeruchsstoff in der Revierabgrenzung ist. AGS wird seltener abgesetzt und es hat offenbar andere Funktionen.

Eurasische Biber zeigen Territorialverhalten, wenn ein „Eindringling“ in Form eines künstlich hergestellten Geruchs-Markierungshügels (ESMs), das Castoreum eines fremden adulten Männchens enthält, ins Revier eingebracht wird. Die Revierinhaber zerstören den ESMs und markieren mit ihrem eigenen Geruch. Es sieht so aus, dass durch die eigene Markierung der fremde Duft überlagert werden soll.

Geruchsmarken können zuverlässige Aussagen über die Fähigkeit eines Individuums, das Revier zu halten oder zu verteidigen, vermitteln, wenn nur die erfolgreichen, dominanten Tiere des Gebietes sicher sein können, dass sie ihre Markierungen überwiegend und häufiger als die herausfordernden Gegner anbringen.

Diese Gegenmarkierung bestätigt, dass

das Revier besetzt ist und signalisiert, dass es zum Kampf kommt, sollte die Drohung nicht beachtet werden. Eurasische Biber können Geruchsstoffe verwenden, um zwischen Nachbarn und Fremden zu unterscheiden, was sich durch das Phänomen „dear enemy“ (geliebter Feind) erklären lässt (reduzierte Aggressivität zwischen Familienangehörigen benachbarter Territorien).

Eurasische Biber können Gerüche der beiden Arten unterscheiden, wobei die Arten dazu aber unterschiedliche Fähigkeiten zeigen.

Das deutet daraufhin, dass der Eurasische Biber mit aufdringlicheren Geruchsmarken sich vom Nordamerikanischen Biber (*C. canadensis*), der weniger solcher territorialen Drohungen setzt und auch weniger Zeit und Energie darauf verwendet, andere Marken mit seinem eigenen Geruch zu überdecken.

Diese Erkenntnis zeigt, dass Eurasische Biber in der Lage sind, effektiv geruchliche Nachrichten, sowohl zeitlich als auch räumlich, zu übermitteln und ESMs von Eindringlingen hinsichtlich ihrer Bedrohung einzuschätzen und geruchlich zu überlagern.

Die Funktion der geruchlichen Reviermarkierung beim Eurasischen Biber ist die Vermittlung des Status, dadurch haben Eindringlinge die Möglichkeit, die Anwesenheit des Revierinhabers einzuschätzen. Dadurch reduziert sich für beide, sowohl für Revierinhaber als auch für den Eindringling, das Risiko und der Aufwand einer kämpferischen Auseinandersetzung (Hypothese vom angekündigten Status).

Die Geruchsmarkierung beim Eurasischen Biber untermauert also die Hypothese, dass sich der Duft, passend zur Situation, anpassen lässt.

Wie auch immer, die Funktion der Geruchsmarkierung lässt darauf schließen, dass es sich nicht unbedingt um den einzigen Mechanismus handelt, ist aber auch nicht auszuschließen.

Introduction

Eurasian beavers (*Castor fiber*) are strongly territorial and aggressive encoun-

ters are not uncommon (e.g. LAVROV & ORLOV 1973, 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 waters edge (e.g. WILSSON 1971). All age-classes, except kids younger than 5 months, and both sexes defend their territories by scent marking (WILSSON 1971). 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.

The main aim of this review is to sum up the most important findings from the authors doctoral dissertation (ROSELL 2002a) and show that scent marking plays an important role in territory defence of free-ranging Eurasian beavers. I will elucidate: 1) how different factors affect the number and distribution (temporal and spatial) of scent marks; 2) which organs (odorants) beavers use in territorial defence; and 3) whether they can recognize an intruder (i.e. is this a potential intruder?) and discriminate a neighbour from a stranger (the "dear enemy" phenomenon; reduced aggression towards familiar occupants of neighbouring territories) or a conspecific from a heterospecific (i.e. which of these potential intruders should be most aggressively responded to?).

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

ROSELL & NOLET (1997) found that beaver colonies in the central part of Biesbosch, the Netherlands, scent-marked significantly more than did colonies at the pe-

riphery. The number of scent marks increased significantly with the number of neighbouring territories and individuals. They 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 (*C. canadensis*) (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 (ROSELL & NOLET 1997). 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 territo-

ries, and also territories of better quality, than later arrivals. ROSELL & NOLET (1997) 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 (ROSELL & NOLET 1997).

The number of scent marks is highest in spring (April–May) (ROSELL & NOLET 1997, ROSELL et al. 1998). This is in agreement with earlier studies for both species of beavers (e.g. BUTLER & BUTLER 1979, MÜLLER-SCHWARZE & HECKMAN 1980, SVENDSEN 1980a, NITSCHKE 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 is also found for the Eurasian beaver (ROSELL & NOLET 1997, ROSELL et al. 1998), and for many other mammals (ALEKSIUK 1968, KRUK 1978, KRUK 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 is maintained throughout the year (ROSELL et al. 1998). The continually ice-free state of the Bø River (Telemark County, Norway) allows dispersion throughout the entire year (ROSELL et al. 1998). Nearly the same situation exists in the Biesbosch (usually ice-bound for less than 2–3 weeks) (NOLET & ROSELL 1994, ROSELL & NOLET 1997). 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 is minimal, almost all marking occurs 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 (ROSELL et al. 1998). 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 are located upstream than downstream of the lodge. This is 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 North American 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, 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, ROSELL et al. 1998) (see also below).

Organs (odorants) used in territorial defence

ROSELL & SUNDS DAL (2001) found that castoreum is 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 castoreum compounds has a molecular weight below 300.

In contrast, ROSELL & SUNDS DAL (2001) found that 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, has 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 concen-

trate 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" (see however ROSELL 2002b). 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 (ROSELL et al. 1998). 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).

Social recognition and discrimination

Territory intruders

Eurasian beavers show territorial behaviour when an "intruder" (experimenter) scent mark with castoreum inside the territory (ROSELL et al. 2000). ROSELL et al. (2000) showed that beavers 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 & BHORADE 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

ROSELL & BJØRKØYLI (2002) results 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 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, Rosell et al. 1998). 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-fam-

ily adult males. Therefore, both SCHULTE (1998) and ROSELL & BJØRKØYLI (2002) 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 7 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 interac-

tions 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). The discrepancy in results from SCHULTE's (1998) and ROSELL & BJØRKØYLI (2002) studies may not be due to species differences, but to the presence of undefended space between territory borders shown in SCHULTE's study that may interfere with mechanisms responsible for neighbour-stranger discrimination. However, SCHULTE's design was different from ROSELL & BJØRKØYLI. In SCHULTE's study, ESMs from neighbours and strangers were presented separately on consecutive nights whereas in ROSELL & BJØRKØYLI's study the two were presented simultaneously during one night. In fact, one of SCHULTE's 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 ROSELL & BJØRKØYLI's 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

STEIFETTEN & ROSELL (unpublished) results confirm the 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 & VEHRNCAMP 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 & BUERGEL-GOODWIN 1975). If the chemical signal present in castoreum and ACS 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 counter-marking these scent marks. We 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 is readily seen during observation trials where several family members successively respond to the same pair of ESMs. Although successive visits would probably increase the cumulative probability of recognition errors, the results in STEIFETTEN & ROSELL's 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 PASS-

MORE 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. 1995a, 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. ROSELL & SUNDS-DAL (2001) found 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 ROSELL (2002a) supported the main hypothesis that scent marking plays an important role in territory defence of free-ranging Eurasian beavers. This work 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 1984). 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). ROSELL (2002a) results also support this hypothesis, i.e. predictions 1 (ROSELL & NOLET 1997, ROSELL et al. 1998), 3 (ROSELL et al. 2000) and 4 (ROSELL et al. 2000, ROSELL & BJØRKØYLI 2002, STEIFETTEN & ROSELL unpublished) were all supported. However, prediction 2 needs to

be further clarified (see however ROSELL 2002b).

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 func-

tion 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, KRUK 1992, BRANCH 1993). This work has emphasized intergroup communication. However, more work is needed to clarify the role of scent marks in intragroup communication.

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