Eurasian beavers (*Castor fiber*) behavioral response to simulated territorial intruders

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Abstract: The Eurasian beaver (*Castor fiber*) lives in family groups which defend territories against other conspecifics. Part of the territory defence is to construct scent mounds near the stream bank within territories and mark them with castoreum, a urine-based fluid from the castor sacs, and/or anal-gland secretion. The aim of this study was to test the hypothesis that Eurasian beaver show one or more forms of territorial behavior when an intruder, simulated in the form of experimental scent mounds (ESM's), has scent marked inside the territory. We predicted that beavers would show a stronger response to ESM's with castoreum than to ESM's without. Results showed that 85% of all beaver families (N=20) made one or more behavioral responses to ESM's marked with castoreum from foreign adult males, whereas no ESM's presented without castoreum received a response. We therefore conclude that a main function of territorial marking in beaver is to advertise spatially related dominance status, thereby providing opportunities for intruders to assess the presence of the owner and reducing the cost and risks of agonistic conflict for both the owner and intruders. Additionally, it appears to be the scent emitted from an ESM and not the sight of it that beaver respond to.

Introduction

In order to have a territorial function, certain behavioral patterns should be evident by both the territory holder and the intruder (Gosling 1982; Gorman 1984). Animals marking inside another territory may demonstrate their intent to take over the territory, or at least to increase the size of their present territory, and are expected to be prepared for physical escalation if the resident is encountered (Richardson 1993). Animals often scent mark where other conspecifics have marked, a pattern of behavior called counter marking. Scent counter marking is a common phenomenon among mammals and numerous functions have been proposed for it (Ewer 1968; Ralls 1971). 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). In addition, over marking 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. 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 hamsters (*Mesocricetus auratus*) counter marking 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 behavior could be an effective competitive

strategy (Johnston et al. 1995).

The Eurasian beaver (*Castor fiber*) lives in family groups, which defend territories against other conspecifics (e.g. Djoshkin and Safonow 1972; Nolet and Rosell 1994). The basic social unit consists of a monogamous adult pair, young of the year, yearlings and sometimes two-year olds or older (Wilsson 1971). A part of the territory defence behavior is to construct small piles of mud and debris usually < 1 m from the stream bank and mark them with castoreum, a urine-based fluid from the castor sacs, and/or anal-gland secretion (AGS) (e.g. Rosell and Nolet 1997; Rosell and Bergan 1998; Rosell et al. 1998). Castoreum is thought to be a more likely source of territorial-odor signal than AGS in North American beaver (*C. canadensis*) (e.g. Schulte et al. 1994; Schulte et al. 1995). Scent marks are assumed to signal occupancy to potential intruders, notably dispersing 2-year-olds, and are most frequent at the borders during the entire year (Rosell et al. 1998). All age classes of Eurasian beavers and both sexes participate in marking the territory at scent mounds (Wilsson 1971).

Observing intruding beavers scent marking, and interactions between the intruders and the residents may be quite difficult. Experimental scent mounds (ESM's) with secretion applied to them could, however, mimic the presence of intruders. ESM's with castoreum from strangers usually elicit territorial responses in North American beaver (e.g. Schulte et al. 1994; Schulte et al. 1995), 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 behavioral 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 intruders scent mound (e.g. Sun and Müller-Schwarze 1997; Schulte 1998). However, no extensive studies have yet been conducted on the response

of Eurasian beavers to ESM's introduced into the territory, and it is not know if they respond in a similar way. Anderson and Westerling (1984) constructed ESM's (with castoreum from one adult male) in one Eurasian beaver territory, but only reported the overnight activity (number of new scent mounds constructed during the night). They did not observe the actual behavior during scent mound construction and scent marking.

The aim of this study was to test the hypothesis that Eurasian beavers show one or more forms of territorial behavior when an intruder has scent marked inside the territory. We expected castoreum to be the main functional element of a scent mound and not the human-constructed mound itself. Thus, we predicted that beavers would show stronger responses toward ESM's with castoreum than toward ESM's without, and that they would counter mark where another conspecific had marked.

Materials and methods

Study area and study animals

The study was conducted between 21 April and 21 September 1997 in Bø municipality (266 km^2) (59°25`N, 09°03`E), Telemark County, Norway. Colony density in the municipality was believed to be close to saturation. The density of beaver on the study area was 0.76 colonies and 3.0 animals km^{-1} stream length (Rosell et al. 1998). The population was believed to be near saturation as beaver had returned to the area 70 years previous (Olstad 1937; Hartman 1994) and hunting pressure was light. All twenty colonies used in this study were surveyed for fresh activity during spring 1997 prior to field experimentation. Each recipient family contained at least two large individuals assumed to be adults based on numerous dawn and dusk counts using binoculars (Zeiss 8 x 56). The territorial boundaries were drawn on the basis of the location of scent mound concentrations (Rosell and Nolet 1997; Rosell et al. 1998) and from regular sight observations of animals moving up- and

downstream of the lodge throughout the study period (Rosell et al. 1998).

Collection of scent

Two adult male beavers (20.0 and 22.0 kg) living >10 km from the closest experimental site, and in an another watershed, were shot with a rifle on 8 April 1997. We assumed that these two donors and the members of each recipient family were unlikely to have had previous contact. We also assumed that the quality of castoreum from both adult male donors was equal, and therefore that the behavioral responses elicited were independent of which male was used. Only scent from males was used because they are thought to be the primary markers and responders to scent marks (Buech 1985; Schulte 1998). We sexed beavers by the presence of os penis (Osborn 1955). The castor sacs were cut open with a surgical blade and the castoreum scraped from the inside surface with a metal scapula. The castoreum was placed in a glass vial and stored frozen (-20° C) until use.

Experimental procedure

To study territorial responses of resident beavers, we constructed one ESM on each of the twenty different territories to mimic the presence of an intruder. The ESM was a handful of mud and debris grabbed from the bottom of the stream by the experimenter wearing clean gloves to avoid transmittal of human odor. The ESM (approximately 20 cm diameter and 10 cm high) was constructed within 20 m of the lodge, and located approximately 50 cm from the water's edge. The ESM's were intended to mimic a real scent mound. The site chosen for placement of the ESM was along the stream bank where beavers usually passed within 10 m during daily travel, and at a place where beavers were able to exit from the water. When ESM's were marked with castoreum, approximately 1g (Müller-Schwarze et al. 1983) was placed in a plastic bottle cap (2.5 cm top diameter, 1.2 cm high) and the bottle cap placed in

the centre of the ESM with the surface of the top even with the surface of the mound. In untreated ESM's, no castoreum was placed in the bottle cap.

During the first evening of observation the ESM was untreated (i.e. without castoreum) followed by one successive evening with castoreum (from one of the two adult male donors). Use of blank ESM's (no castoreum added) permitted us to examine if the human-made mound itself was eliciting responses. Blank ESM's were always presented first, as the opposite sequence would have been difficult to conduct since the smell from a castoreum ESM can be expected to linger for an unknown number of days. Also, the beavers' scent experience (memory) from the previous day could cause carry-over bias to the next day. The site chosen for placement of the ESM's was the same for both nights, within 1-2 m distance. Beaver conceivably could show new object avoidance or indifference and therefore would require a night to get used to new objects in their territories before responding overtly. However, several studies on the North American beaver have recorded an overt response to ESM's with castoreum during the first evening (Müller-Schwarze et al. 1983; Schulte et al. 1994; Schulte et al. 1995; Schulte 1998), and we assumed a similar response here. In all trials the ESM was constructed approximately one hour before the beavers emerged from their lodges (usually between 1800 hours to 2000 hours) and observations continued until dark. Each observation period lasted about 4 hours.

Measures of response

During the observation periods an observer sat 30 to 50 m away on the opposite bank and down wind, watching the area through binoculars. Each evening we 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 and Müller-Schwarze 1997; Schulte 1998). When beavers were present but

did not react to the odor stimulus (swam past the ESM within 5 m) the response was defined as “no response”. One or more of the three other categories were defined as a “response”.

In a sniff response, beavers orient toward the ESM and noticeably sniff by raising their lower jaw slightly out of the water. The number of land visits was recorded and a dictaphone was used to record the duration (in seconds) of the first land visit. Land visits to the ESM are indicative of greater territorial activity than oriented sniffing from the water alone (e.g. Schulte et al. 1994). Land visits occurred when a beaver left the water and moved directly to the ESM. The land visit ended when the beaver re-entered the water (e.g. Schulte et al. 1994).

A complete beaver response to an ESM can be sequentially separated into sniffing (on land, and directed towards and within approximately 15 cm of the ESM), straddling (standing on the ESM on hind feet), pawing, and over marking (marking it with castoreum and/or anal gland secretion) (e.g. Sun and Müller-Schwarze 1997). Weaker responses, however, consist of only the earlier parts of the sequence. We thus used response completeness (the number of different behavioral patterns in a response) to measure response intensity. We included only the response of the first beaver in our observational analyses because physical damage to the scent mound might lead to carry-over biases in the following responses (Sun and Müller-Schwarze 1997). We 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, stranded, pawed and/or over marked the ESM.

In addition to evening observations, ESM’s were checked the following morning for signs of visitation during the night (overnight response) and separated into two categories: “response” or “no response”. A response involved either over marking the ESM without destroying it, destroying it (partly or completely) without depositing fresh odor, or destroying it (partly or completely) and depositing fresh odor. 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. Fresh odor was detected by removing the bottle cap with or without scent and sniffing the ESM area within a 50-cm radius of its centre. Only scent detectable by the human nose at 2 cm or more, was recorded (Rosell et al. 1998). If an ESM did not have a smell detectable by the human nose, it was classified as unmarked (see, however, Bollinger 1980; Schulte 1993, Rosell and Nolet 1997). Because beavers usually live in family units, different members of a family may respond to scent mounds at different times during the same night. Therefore, a response result is a descriptor of the territoriality of a family instead of an individual (Schulte 1993). 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.

Statistical Methods

We used nonparametric statistics in accordance with Siegel and Castellan (1988) and Sokal and Rohlf (1995). We assumed independence of trials for statistical analysis. Because of small sample size in each category we pooled the categories for the evening observations, and also the categories for the overnight responses. For analysis of the duration of land visits, we included only trials with land visits (i.e. only non-zero values were used). However, we used all trials, in which beavers were observed, to compare number of land visits. We used the Fisher Exact test as a conservative measure for testing the null hypothesis that the groups within a set did not differ (response versus non-response). Probability values are one-tailed and 5% was used as the level of significance. Mean values are presented with standard errors.

Results

During the first evening when ESM's were presented without castoreum no response to the ESM was observed (Table 1). Likewise, no overnight response was recorded (Table 1). However, during the second evening and night when ESM's were presented with castoreum beavers responded strongly (Table 1). 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. The mean number of land visits was 1.36 ± 0.51 (N=11), the mean duration of the first land visit was 50.67 ± 13.35 seconds (N=6) and the mean response completeness was 1.18 ± 0.40 (N=11). We frequently observed that beavers, after visiting the ESM's, started to patrol the territory. The overnight response showed that the beavers over marked or destroyed the ESM without depositing fresh odor in 5.0% of the trials, and that they destroyed the ESM and deposited fresh odor in 80.0% 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 (Fisher Exact test, $P<0.0001$ for both, Table 1).

Discussion

The result that beaver in 82-85% of all families responded to ESM's with castoreum supported our hypothesis that Eurasian beaver showed territorial behavior when an intruder had scent marked inside the territory. They destroyed the ESM and deposited fresh odor in 80% of the trials, which indicated that they counter marked and tried to mask the odor of alien adult male conspecifics with their own odors. That is, they responded in a way similar to the over marking shown by many other species (e.g. Leyhausen 1965; Johnson 1973; Müller-Schwarze et al. 1973; Rasa 1973; Butler and Butler 1979; Biben 1980; Hurst 1987; Johnston et al. 1994; Johnston et al. 1995). Also, the lack of a response to ESM's without castoreum

indicated that beaver were responding to the smell of castoreum and not to the sight of the scent mound. Though we attempted to leave as little human scent as possible at experimental sites, it is conceivable that this could have affected our results. E.g., more ESM's with castoreum might have received a response, and possibly even some blank ESM's, had no human odor been present.

Studies of North American beaver have also shown no significant response to blank ESM's (Müller-Schwarze et al. 1986; Müller-Schwarze and Houlihan 1991; Schulte 1998). Eurasian beavers responded to ESM's (sniffed, straddled, pawed and/or over marked) in a manner similar to North American beaver. However, while the North American beaver usually carries mud in their front paws while walking bipedally to construct a scent mound, the Eurasian beaver has never been observed doing this. The Eurasian beaver simply scrape together a mound from mud and debris found on site (Wilsson 1971).

Sun and Müller-Schwarze (1998) provided strong evidence for a generalised scent-matching hypothesis, rather than a specific scent-fence alternative. Their results demonstrated that the response of resident North American beaver families (territory owners) to repeatedly occurring scent materials (castoreum and anal gland secretion on ESM's) from strangers (adult males ≥2 years old) did not increase over time. For responses to castoreum, all but two behavioral categories showed a significantly descending trend. The descending trend in response to the same signal without matching the signaller demonstrates a declining importance of the signal alone over time (Sun and Müller-Schwarze 1998). The scent-matching hypothesis predicts among other things that: 1) the territory owner should make itself available for scent matching by the intruder, and 2) the owner should remove or replace marks in the territory that do not match its own odor (Gosling 1982). Our results supported the first prediction because we frequently observed that beavers, after visiting the ESM's, immediately began to patrol the territory probably looking for the intruder. By matching the

scent of a territory owner with those of nearby scent marks, an intruder employs the unique property of olfactory signalling that included the provision of both a historical and a spatial record of a territorial individual's behavior. Territory owners can thus signal their status to intruders in a way that cannot be mimicked and that is to their advantage in subsequent encounters (Gosling 1982). The second prediction was not supported by Sun and Müller-Schwarze's (1998) study on the North American beaver. They concluded that further studies are needed to clarify why over marking is rare in the North American beaver. In contrast, our results showed that territory owners removed ESM's with castoreum during the night in 85% of all cases, thus supporting the second predictions as well. Schulte (1998) also found that the North American beaver regularly walked over or overmarked the ESM with castor fluid from adult male intruders (strangers).

We conclude that the main function of territorial marking in beaver is to advertise spatially related dominance status, thereby providing opportunities for intruders to assess the presence of the owner, thus reducing the cost and risks of agonistic conflicts for both the owner and intruders (Erlinge et al. 1982; Gosling 1982; Gorman 1984).

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Table 1. Number of beaver families showing a behavioral response to experimental scent mounds constructed within territories the first evening/night, without castoreum, and the following evening/night, with castoreum. Responses were measured both by direct observation[a] in the evening prior to darkness and as an overnight response[a] the following morning.

	Observed response			Overnight response		
		Proportion showing:			Proportion showing:	
	N[b]	Response	No response	N	Response	No response
First evening/night: without castoreum	14	0%	100%	20	0%	100%
Following evening/ night: with castoreum	11	82%	18%	20	85%	15%

[a] See "Material and methods" for complete explanation of categories.

[b] Only families where beavers were observed are included.