

Potential risks of olfactory signaling: the effect of predators on scent marking by beavers

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Mammals scent mark their territories to advertise occupancy and ownership. However, signaling with scent for territorial defense can have a negative effect by advertising an individual's presence and location to predators. In this study, we measured responses to a simulated territorial intrusion by conspecific adult male Eurasian beavers (*Castor fiber*) either in the localized presence or in the absence of odor of a predator to test the hypothesis that the territorial defense of free-living beavers would be disrupted by the presence of predation risk in their natural environment. We predicted that beavers would significantly reduce their willingness to countermark intruder's scent in the presence of the scent of predators (wolf [*Canis lupus*] and lynx [*Lynx lynx*]), compared with a control (no odor), as responses are in general stronger to predator scent marks than nonpredator scent. Therefore, we also predicted that the effects of nonpredatory mammal scent (neophobic control) (eland [*Taurotragus oryx*] and horse [*Equus caballus*]) are to be expected somewhere in between the effects of the predator odor and a control. Our results suggest that both predator and nonpredator scents reduce beavers response to a simulated intruder's scent mounds and therefore disrupt their territorial defense. However, predator scent had a stronger effect than nonpredator scent. Beavers may therefore be at great risk on territories with predators present because of the trade-off between predator avoidance and territorial defense. Our study demonstrates the potential of predation risk as a powerful agent of counterselection on olfactory signaling behavior. *Key words:* *Castor fiber*, chemical communication, predation risk, scent marking, signals, territorial. [*Behav Ecol*]

Territories allow their owners exclusive access to critically limiting resources and are thus, in territorial species, an essential component of the owner's fitness (Davies and Houston 1984). However, fighting with conspecifics to maintain a territory is costly and can result in injury (Piechocki 1977). As a result, animals have evolved signals that carry information concerning the signalers presence and fighting ability so that potentially costly escalating conflicts can be avoided. Signals can be visual, auditory, or olfactory based, for example, mammals scent mark by depositing urine, feces, and scent from specialized glands on substrate (Eisenberg and Kleiman 1972; Brown 1979; Johnston 1983). It is widely accepted that mammals scent mark their territories to advertise their occupancy and ownership of the territory (e.g., Gosling 1982; Sillero-Zubiri and Macdonald 1998). 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; Gosling and Roberts 2001). By matching the scent of a territory owner with those of nearby scent marks, an intruder exploits the unique property of olfactory signaling that includes 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 this is to their advantage in subsequent encounters (Gosling 1982).

Signaling with scent for territorial defense can have a negative effect by advertising an individual's presence and location to predators. For instance, small mustelids find voles by using odor cues like urine and feces scent marks (Koivula and Korpimäki 2001). Scent marking can decrease fitness by increasing predation risk, and therefore, natural selection

should favor incorporating predation risk into the decision-making process of when and where to scent mark. Roberts et al. (2001) showed, in a laboratory study, that dominant male mice (*Mus musculus*) reduced scent marking in the presence of urine from a ferret (*Mustela putorius*), whereas subordinate mice did not. However, studies on response of rodents to stimuli in the laboratory may be artificial, presented in superstimulus quantities and in situations in which rodents do not have the opportunity to avoid it, making the results equivocal and unnatural (Lambin et al. 1995; Norrdahl and Korpimäki 2000; Ylönen 2001; Wolff 2003, 2004). Wolff (2004) failed to provide any evidence that voles (*Microtus ochrogaster* and *Microtus pinetorum*) decrease their frequency of scent marking in the field or in the laboratory in response to the odor of a mammalian predator (*Mustela vison*). Wolff (2004) suggested that scent marking has greater benefits, perhaps in the form of developing a presence in an area, reproductive competition, or sexual advertisement, than costs, such as increased predation risk.

To our knowledge, disruption of territory defense due to predation risk in mammals has yet to be demonstrated in the field. Recognition of and response to predator odor by prey is of adaptive significance because it reduces predation risk (Merkens et al. 1991). However, according to the threat-sensitive hypothesis (Helfman 1989), natural selection should favor individuals that take action appropriate to the magnitude of threat, which would require an accurate discrimination of predator from similar nonpredator stimuli. Several findings in the literature confirm a response to novel olfactory cues per se, but the responses are in general stronger with predator scent marks as compared with nonpredator odors (Kemble and Bolwahn 1997; Perrot-Sinal and Petersen 1997; Bramley et al. 2000). Therefore, the possibility of a neophobic effect has to be tested properly by designing experiments with predator, nonpredator, and no odors (Lambin et al. 1995; Kemble and Bolwahn 1997; Mappes et al. 1998).

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The obligate monogamous Eurasian beaver (*Castor fiber*) usually lives in family units and is strongly territorial, and aggressive encounters are common (Willson 1971; Nolet and Rosell 1994; Sharpe and Rosell 2003; Herr and Rosell 2004). Scent marking with castoreum (a mixture of secondary metabolites from urine) plays an important role in the territorial defense of the Eurasian beaver (Rosell and Sundsdal 2001), and adults of both sexes countermark where other conspecifics have marked (Rosell et al. 2000; Rosell 2002; Rosell and Steiffetten 2004). Rosell (2002) found support for the scent-matching hypothesis in Eurasian beaver.

In this study, we measured responses to a simulated territorial intrusion by conspecific adult male Eurasian beavers either in the localized presence or in the absence of predator odor to test the hypothesis that the territorial defense of free-living beavers would be disrupted by the presence of predation risk in their natural environment. We predicted that beavers significantly reduce their willingness to countermark a male intruder's scent when a predator's scent is present (the allopatric wolf [*Canis lupus*] and the sympatric lynx [*Lynx lynx*]) but not when there is a lack of odor (control; i.e., only scent from a conspecific adult male). We also predicted that the effects of nonpredator mammalian controls (neophobic controls including the nonnative eland [*Taurotragus oryx*] and the native horse [*Equus caballus*]) would fall between the 2 extremes of no treatment and predator-odor treatment.

METHODS

Study area and study animals

The study was conducted during June–August 2002 and April–August 2003 in Bø, Sauherad, and Nome municipalities in Telemark County, southeastern Norway. The beaver was absent from this area in the last part of the 19th century until the 1920s, when it reoccupied the study area (Olstad 1937). The beaver population in the area was near maximum despite annual harvesting (Rosell et al. 1998; Rosell and Hovde 2001). Beaver sites were surveyed for activity in spring prior to the bioassays. Sixty different active beaver families with 2 or more adult individuals (≥ 15 kg) were used during the study. The number of animals in each family, many of which were ear-tagged, was determined by direct counts using light-sensitive binoculars from the riverbank, a canoe, or boat at dawn and/or dusk and on many occasions before and during the field bioassay. A mean colony size of 3.8 ± 1.8 SD was found in 19 active beaver families during the autumn of 1995 in Bø municipality (Rosell et al. 2006).

We livetrapped beavers using Hancock and Bailey live traps baited with aspen twigs (Rosell and Kvinlaug 1998) or at night with landing nets (Rosell and Hovde 2001). The livetrapping was under license of the Norwegian Experimental Animal Board and the Norwegian Directorate for Nature Management. We placed all captured beavers in a cloth sack to facilitate handling and tagging. Each beaver was placed headfirst into the sack and restrained while another researcher applied eartags. This was done by maneuvering the beaver's ear out through a small hole cut in the sac. Beavers were comparatively docile, particularly when confined in the dark sack, and easily restrained (Rosell and Bjørkøyli 2002). No beavers responded aggressively, and none were visibly damaged by the procedure. Individuals were tagged with numbered plastic eartags (Dalton Continental B. V., Lichtenvoorde, The Netherlands) and/or monel metal eartags (National Band and Tag Co., Newport, KY). All beavers were weighed and assigned to age classes based on body weight: kits (< 12 months, < 10 kg), yearlings (12–24 months, 10–15 kg), and

adults (≥ 24 months, ≥ 15 kg) (Rosell and Pedersen 1999; Parker et al. 2001). We sexed the livetrapped beavers by the color and viscosity of the anal gland secretion (AGS) (Rosell and Sun 1999). After the handling, the beavers were released near the capture site.

Scent donors and collection of scent samples

We collected castoreum from 60 adult male beavers (age > 2 years, weight > 15 kg) killed by hunters within the normal hunting season during the spring (1 March to 30 April) of 1997, 1998, and 1999 in Bø municipality. Beavers were not shot expressly for the study but were a part of the local hunting quota. We opened the castor sacs with a surgical blade and scraped the castoreum from the inside surface with a metal scapula. The dead animals were sexed by checking for the presence or absence of the os penis (Osborn 1955). All castoreum samples were placed in glass vials and stored at -20 °C until use. To reduce the possibility of the test animals having had any previous contact with or being genetically related to the scent donors, only scent from individuals that were shot > 15 km from the experimental site and in different watersheds were used in a specific trial (hereafter called strangers).

Two of the most important beaver predators until the end of the 19th century were wolves and lynxes (Rosell et al. 1996; Nolet and Rosell 1998). Beavers should therefore avoid the scent of these 2 species. The horse, used as a nonpredator mammalian control odor, has been sympatric with beavers in this area for several thousand years (Børresen 2002), whereas eland (another mammalian control odor) is an African species without any evolutionary contact with beavers (Macdonald 2001). We collected fresh feces samples from lynxes ($n = 11$), wolves ($n = 9$), and elands ($n = 12$) from the Kristiansand Zoo during March 2002 (lynx, wolf, and eland) and from the University of Oslo during May 2002 (lynx). Fresh feces from horses ($n = 30$) were collected locally in May 2002. Feces were collected with latex gloves (to avoid human contact), placed in glass vials, and stored at -20 °C until use.

Experimental design

We conducted 2 types of experiments: an overnight experiment and a direct observation experiment during evenings. For the overnight experiment, we used a 3-sample choice test and constructed 3 types of experimental scent mounds (ESMs) close to the active beaver lodge (Hodgdon 1978; Müller-Schwarze and Heckman 1980). All ESMs were placed on one side of the lodge. We constructed one control ESM with castoreum from a stranger only, a second ESM with castoreum from a stranger plus predator scent (wolf or lynx), and a third ESM with castoreum from a stranger plus nonpredator scent (horse or eland). We conducted 2 different overnight trials ($n = 30$ for both): one where we used feces from wolf as a predator and horse as a nonpredator (overnight experiment 1) and another where we used feces from lynx as a predator and eland as a nonpredator (overnight experiment 2). For the direct observation experiment, we used a 2-sample choice test with one control ESM with castoreum from a stranger and another ESM with castoreum from a stranger plus feces from lynx ($n = 20$ trials). We used only lynx feces in the direct observation experiments because beavers responded strongest (i.e., showed most aversion) to their scent in the overnight experiment (see Results). The ESMs were constructed where beavers could easily walk onto land, about 10 m apart and within 50 cm of the water's edge. This made it possible to compare beaver's response to the ESMs (i.e., each beaver family was simultaneously exposed to 3 or 2 ESMs). We tried to choose experimental sites with the same amount of cover

above and around the ESMs. Placement of the ESMs were organized randomly by lot on each trial to control for side preference, and each beaver family was tested only once in each experiment. We used different families in the overnight experiment 2 (with lynx) and the direct observation experiment (also with lynx) to make sure that the beavers that responded had not had any prior experience with the lynx scent used.

For each bioassay, castoreum from 3 different strangers was used in the overnight experiments ($n = 60$ individual male odor donors; i.e., 30 males were used twice), and that from 2 different strangers was used in the direct observation experiments ($n = 40$ individual male odor donors). We used castoreum from strangers of similar characteristics for each bioassay, that is, animals of similar weight (<3 kg difference) and similar season of scent collection (<3 weeks difference). Unfortunately, we did not manage to collect enough scent samples (except for horse and beaver strangers for the direct observation experiments) to avoid pseudoreplication (Kroodsma et al. 2001), but we used the different samples equally among trials (see Haven Wiley 2003).

We wore clean plastic gloves to prevent contamination with human odor and scraped a handful of mud and debris from the bottom of the stream or from land when constructing the ESMs. We used a canoe or walked along the bank when approaching the site where the ESMs were constructed. Each ESM was approximately 15 cm wide and 10 cm high. We placed 100 g of feces in front of each ESM, except for the ESM with castoreum from a stranger only. We used a plastic bottle cap (2.5-cm top diameter, 1.2 cm high) in each ESM to hold 0.25 g of castoreum from strangers and to control the evaporation surface area (Schulte 1998; Rosell and Bjørkøyli 2002). The bottle cap was placed in the center of the ESM with the surface of the top even with the surface of the mound. For each trial, scent was set out 30–60 min before the beavers usually emerged from the lodge in the evening (1800–2100). The observation period ended when fading daylight prevented further observations. If no beavers were observed during the evening trial before it became dark, we usually terminated the trial, removed the ESMs, and tried again on another evening.

Measures of response

Overnight activity

We ranked the overnight response by checking the ESMs the following morning, a commonly used procedure (e.g., Sun and Müller-Schwarze 1998; Rosell and Bjørkøyli 2002; Rosell and Steifetten 2004). Because beavers live in family units and codefend the territory, different members of a family may respond to the ESMs sequentially at different times during the same night (Schulte 1993; Rosell and Bjørkøyli 2002; Rosell and Steifetten 2004). Rosell and Bjørkøyli (2002) observed that all responses during direct observation experiments in evenings were by adult beavers, except in 1 of 21 families where a 2 year old responded. However, previous studies have shown that beavers can discriminate castoreum samples from family, neighbor, and stranger adult males and that they show least interest in castoreum samples from family members (Schulte 1998; Rosell and Bjørkøyli 2002). Therefore, we checked and ranked the response results overnight to characterize the intensity of the collective beaver family response. This was done even if physical damage to the ESMs (pawed, flattened, or obliterated) may cause some carryover biases in the following responses by the same or other beavers (Sun and Müller-Schwarze 1997). To determine response intensity, each ESM was given a rank index value (0–6) correlated with its level of destruction, 6 indicating the strongest response.

When beavers scent marked over ESMs and/or close by on self-constructed scent mounds (which could occur independent of ESM status), we gave the respective ESM an additional index value of 1; hence, the maximum score could be 7 (for details, see Table 1 in Rosell and Bjørkøyli 2002). After measuring the response intensity at the ESMs, they were completely removed. Rosell et al. (2000) showed that beavers did not respond to ESMs without castoreum and that they responded to the smell of castoreum and not to the sight of the ESM. Therefore, we did not use an ESM without castoreum as control in this study. Activity at the ESMs that could be attributed to other mammal species, such as mink (*M. vison*), red fox (*Vulpes vulpes*), or badger (*Meles meles*), was not observed. However, we observed footprints by a swan (*Cygnus olor*) once, and it probably took 2 of the bottle cups in one trial. This trial was excluded from the analyses.

Direct observations during evenings

An observer with binoculars, located downwind on the opposite bank, recorded on a Dictaphone the duration in seconds of 2 response patterns to ESMs—1) sniffing (partly in water or on land with its back toward water and directed toward and within approximately 5 cm of the ESM) and 2) the “aggressive response”: standing on the ESM on its hind feet with the back toward inland, 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) (Rosell and Bjørkøyli 2002). 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 behavior the ESMs triggered. In our analyses, we included only the responses of the first beaver in these trials, 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. After the trial, we inspected the ESM for fresh odor. A fresh beaver scent mark is easily detectable by the human nose from a distance of 2 cm or more. We detected a new scent mark by removing the bottle cap with the original scent and sniffing the ESM area within a radius of 15 cm from the ESM or by determining whether mud/vegetation had been deposited on or within 15 cm of the ESM. If the plastic cap containing the donor scent was dislodged and moved, the ESM would then be impregnated with the donor scent. However, it was still possible to distinguish this scent from that of an overmark as the amount of scent deposited in an overmark was greater and distributed over a larger area (Rosell and Bjørkøyli 2002).

Data analysis

The data did not fit assumptions of distribution and homogeneity of variance for parametric analysis (Sokal and Rohlf 1995), and we therefore used nonparametric statistics in accordance with Siegel and Castellan (1988). We used the nonparametric Page test for ordered alternatives for within-subject effects (related samples) to compare the rank index value (overnight response and pooled overnight response) of the 3 related ESMs (Siegel and Castellan 1988). To check for differences in response between scents (predator vs. control, predator vs. nonpredator, nonpredator vs. control), we used multiple comparisons to determine which differences among conditions were significant. We calculated a critical difference value, and if the difference exceeded this value (16.5), the comparison was significant (Siegel and Castellan 1988, p 180–1). The critical difference value for the pooled results of the 2 overnight experiments was 23.3. A Cochran Q -test (k -samples) or McNemar change test (2 samples) for related samples was used to compare the results for countermarking (frequencies). A Wilcoxon signed-rank test was used to compare

the response time (sniffing and aggressive response) between lynx scent and control ESMs (Siegel and Castellan 1988). We checked for differences in response to scent for between-subject effects by using a Mann–Whitney U test for independent samples. We chose also to present mean values and their standard deviations (SDs), although all statistical tests were nonparametric, which entails comparing medians. We combined the data from both years because no significant differences in any of the measures of response were found for the different ESMs between the 2 years. It was difficult to identify the beaver eartags correctly, and many unmarked beavers also responded to the ESMs. Therefore, statistical comparisons of the sex's responses were not conducted due to small sample sizes. Tied observations were dropped from the analyses (Siegel and Castellan 1988). A probability level <0.05 was considered significant. Data analyses were performed with the statistical package SPSS version 12.0 or calculated by hand, and figures were made with Sigmaplot.

RESULTS

Overnight experiment 1

We found a significant difference in overnight response between the 3 ESMs (Page test, $Z_L = -5.8$, $P < 0.001$) (Figure 1a). Beavers responded significantly stronger to control ESMs compared with wolf ESMs (post hoc test, $P < 0.05$; critical difference value = 45) and to control ESMs compared with horse ESMs (post hoc test, $P < 0.05$; critical difference value = 33). Beavers did not respond significantly stronger to horse ESMs compared with wolf ESMs (post hoc test, $P > 0.05$; critical difference value = 12). Beavers overmarked with castoreum only 3 of the wolf ESMs and 8 of the horse ESMs, compared with 18 control ESMs. A significant difference between the 3 ESMs was found (Cochran Q -test, $Q = 21.9$, $df = 2$, $P < 0.001$).

Overnight experiment 2

We found a significant difference in overnight response between the 3 ESMs ($Z_L = -6.5$, $P < 0.001$) (Figure 1b). Beavers responded significantly stronger to control ESMs compared with lynx ESMs (post hoc test, $P < 0.05$; critical difference value = 50.5) and to control ESMs compared with eland ESMs (post hoc test, $P < 0.05$; critical difference value = 36.5). Beavers did not respond significantly stronger to eland ESMs compared with lynx ESMs (post hoc test, $P > 0.05$; critical difference value = 14). Beavers did not overmark the lynx ESMs with castoreum, but 8 of the eland ESMs and 19 of the control ESMs. A significant difference between the 3 ESMs was found (Cochran Q -test, $Q = 28.7$, $df = 2$, $P < 0.001$).

Between-overnight experiment comparison

Beavers responded significantly stronger to horse ESMs compared with lynx ESMs (Mann–Whitney test, $U = -4.4$, $P = 0.001$). However, beavers did not respond significantly stronger to eland ESMs compared with wolf ESMs ($U = 395.5$, $P = 0.275$), to wolf ESMs compared with lynx ESMs ($U = 389.0$, $P = 0.188$), or to horse ESMs compared with eland ESMs ($U = 346.5$, $P = 0.078$).

Pooled results from the 2 overnight experiments

We found a significant difference in overnight response between the 3 ESMs (predators, nonpredators, and control) ($Z_L = -37.3$, $P < 0.001$). Beavers responded significantly

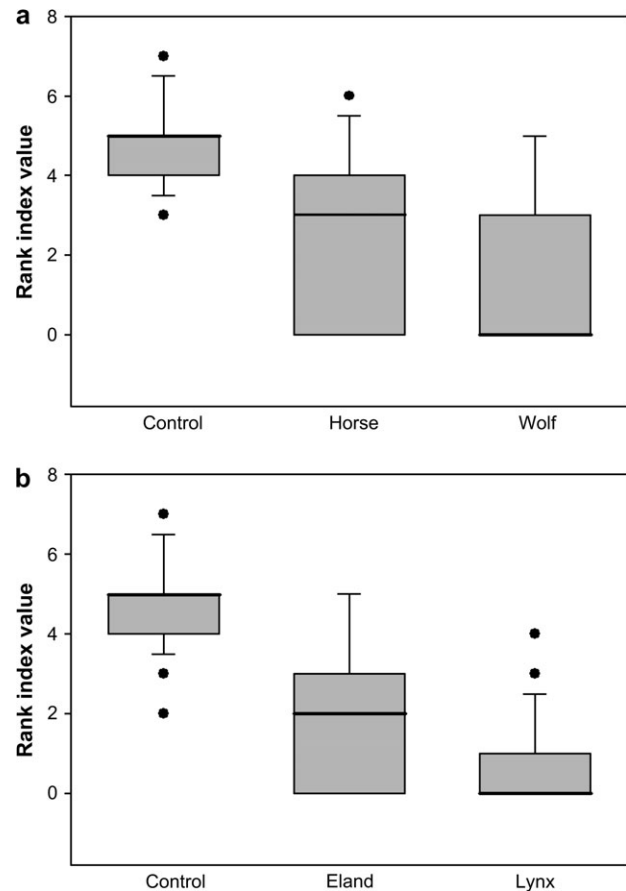


Figure 1

Box plots of the ranked level of aggression measured overnight by beavers to 3 experimentally constructed scent mounds (ESMs); that is, a control ESM with castoreum from a conspecific stranger only, a nonpredator ESM with castoreum from a conspecific stranger and feces from horse (a) or eland (b), and a predator ESM with castoreum from a conspecific stranger and feces from wolf (a) or lynx (b). The median is indicated by the horizontal bar inside the box, the first and third quartile by the box itself, and 1.5 times the interquartile range by the horizontal bars outside the box. Individual outliers are shown by filled circles.

stronger to control ESMs compared with predator (wolf and lynx) ESMs (post hoc test, $P < 0.05$; critical difference value = 94.5) and to control ESMs compared with nonpredator (horse and eland) ESMs (post hoc test, $P < 0.05$; critical difference value = 69.5). Beavers also responded significantly stronger to nonpredator ESMs compared with predator ESMs (post hoc test, $P < 0.05$; critical difference value = 26). A significant difference in overmarking between the 3 ESMs was found ($Q = 50.5$, $df = 2$, $P < 0.001$).

Direct observation experiments during evenings

Beavers spent significantly more time sniffing lynx ESMs ($\bar{X} \pm SD = 50.0 \pm 24.0$ s) than to control ESMs ($\bar{X} \pm SD = 26.7 \pm 27.0$ s) (Wilcoxon signed-ranks test, $T = -3.8$, $n = 19$, $P < 0.001$) (Figure 2). However, as predicted, beavers spent significantly more time responding aggressively to control ESMs ($\bar{X} \pm SD = 33.1 \pm 13.8$ s) than to lynx ESMs ($\bar{X} \pm SD = 10.2 \pm 14.0$ s) ($T = -3.3$, $n = 19$, $P < 0.001$) (Figure 2). Only 3 of the lynx ESMs were overmarked with castoreum compared with 19 control ESMs. A significant difference in overmarking between the 2 ESMs was found (McNemar change test, $P < 0.001$).

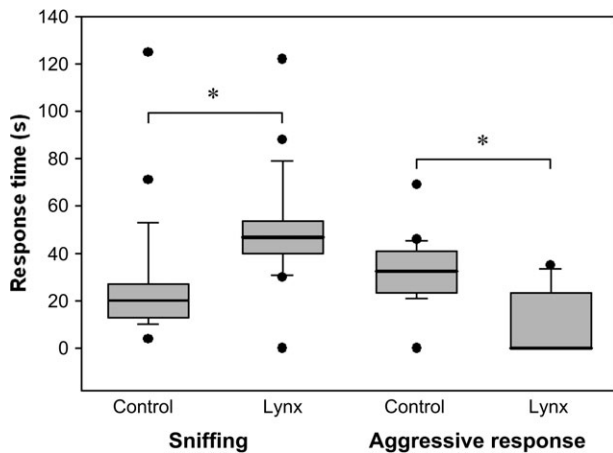


Figure 2
Box plots of responses of beavers during evenings (direct observations) to 2 experimentally constructed scent mounds (ESMs); that is, control and lynx ESMs presented as the time (in seconds) beavers sniffed and responded aggressively (straddling, pawing, and/or overmarking) (see Figure 1 for further details). * $P < 0.05$.

DISCUSSION

Our results support the hypothesis that the territorial defense of Eurasian beaver is disrupted by the presence of predation risk in the field. Overnight, beavers were less willing to countermark male intruder's scent not only in the presence of scent of predators (wolf and lynx) but also in the presence of scent of nonpredators (eland and horse) compared with the no-odor treatment (scent from a conspecific stranger only). Our direct observation experiments during evenings showed that beavers spent significantly more time sniffing lynx scent than the no-odor treatment. 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. The difference observed in sniffing could be due to the fact that beavers had to identify 2 senders on the ESM with lynx scent and stranger, whereas only 1 sender on the other ESM with stranger only. An alternative explanation may be that beavers take longer to investigate the stranger scent because of the masking properties of the predator scent. However, the important finding for our hypothesis is that beavers spent significantly more time responding aggressively to control scent than to lynx scent. When a beaver responds aggressively to a scent mound, it increases its vulnerability to predation compared with sniffing, when its back is facing inland. When the beaver has recognized the predator odor, it will spend less time countermarking the ESMs to reduce the risk of predation. Thus, the lynx scent probably elicited a "fear" response, resulting in the avoidance of the ESMs.

Significance of sympatric and allopatric predators

The effectiveness of predator odors may depend on factors such as geographic distribution of predator and prey, duration of their geographic association, and cultural transmission of predator responses among prey (Swihart 1991). An innate response by prey to a predator cue such as odor is likely to result if prey and predator have coexisted over evolutionary time (e.g., Gorman 1984; Berdoy and Macdonald 1991; Barreto and Macdonald 1999). Avoidance of a predator odor can be either species specific (Swihart 1991; Jedrzejewski et al.

1993; Nolte et al. 1993) or general (Stoddart 1982a; Weldon et al. 1993; Nolte et al. 1994). Furthermore, some prey might learn to respond only to predators that are actively dangerous (Dickman 1992; Jedrzejewski et al. 1993). Our results showed that beavers did not respond significantly different to lynx and wolf scent and responded by aversion to both predators, that is, the sympatric lynx and the currently allopatric wolf (Lande et al. 2003; Linnell et al. 2005). Presently, only approximately 20 wolves and 250 lynxes exist in Norway (Brøseth et al. 2004). The wolf has been allopatric with the beaver for the last 100 years in our study area, but wolves were the most important beaver predator until the end of the 19th century (Rosell et al. 1996; Nolet and Rosell 1998). Lynxes were common in the 19th century but were nearly extinct by 1930 (Anonymous 1996; Kvam 1997). Therefore, beavers probably show innate response to both lynx and wolf, though their response to lynx may have been refined through learning. We speculate that the past predator pressure explains the results we found for both species. The North American beaver (*Castor canadensis*) does not avoid the odors of sympatric species (river otter [*Lutra canadensis*] and coyote [*Canis latrans*]) significantly more than the odor of allopatric species (lynx [*Lynx canadensis*], wolf, and African lion [*Panthera leo*]) (Engelhart and Müller-Schwarze 1995). Rosell and Czech (2000) also found that odors from predators sympatric with the Eurasian beaver in Poland, like wolf and lynx, did not have a significantly larger effect on foraging beavers than those of originally sympatric, but now absent, species such as the brown bear (*Ursus arctos*). Responses to chemical cues from allopatric predators and failure to habituate to predator odors have been interpreted as evidence that responses to these stimuli are innate (Müller-Schwarze 1972; Stoddart 1980; Dickman and Doncaster 1984; Robinson 1990). Dickman and Doncaster (1984) suggested that similar chemicals eliciting avoidance in rodents may commonly occur in the feces and urine of carnivores; this is supported by observations that rodents often avoid the odors of carnivores with which there has been no evolutionary contact (Stoddart 1982a, 1982b). Nolte et al. (1994) postulated that to herbivores, sulfur compounds constitute a general predator cue across carnivore species.

Significance of sympatric and allopatric nonpredators

Our results indicate that beavers are able to distinguish between the odors of a predator and a nonpredator. Our results also confirm a response to novel olfactory cues per se, but the responses are stronger with predator scent as compared with nonpredator scent (see also Kemble and Bolwahn 1997; Perrot-Sinal and Petersen 1997; Bramley et al. 2000). Interestingly, feces from other herbivores are likely to represent a risk of parasitic infection as a result of the migration of helminth parasite larvae from the feces to the sward (Sykes 1978). Helminth parasites have been shown to affect the growth rate, fecundity, and probability of mortality of their hosts (Anderson 1978; Gulland 1992). There should therefore be selective pressure on the host to minimize the detrimental consequences of parasitism through fecal avoidance (Hutchings et al. 1998, 1999). Moe et al. (1999) found that reindeer (*Rangifer tarandus*) display aversion toward sheep (*Ovis aries*) feces. The study of Colman et al. (2003) suggests that reindeer have evolved a strong inter- and intraspecific feces avoidance behavior. This may drastically reduce their probability of contracting parasite and/or *Escherichia coli* infections and improve overall survival and fitness (Van der Wahl et al. 2000). Beaver may also avoid horses due to the potential cost of injuries. For example, a horse broke the leg of a beaver in the Netherlands (Rosell and Steifetten 2004).

Significance of predator odors in disrupting territory defense

Territorial animals may be under conflicting selection pressures when faced with a predator attack because responding to the predator (e.g., hiding) will decrease the chance of detecting and chasing away an intruder (Diaz-Uriarte 2001). The scent-matching hypothesis has received support by studies of scent marking in both the North American beaver (Sun and Müller-Schwarze 1998) and the Eurasian beaver (Rosell 2002; Rosell and Bjørkøyli 2002; Rosell and Steifetten 2004). For a territorial species such as the beaver, there are large benefits gained by defending a territory (Campbell et al. 2005). No other socially monogamous rodent shows the same degree of construction activities or foraging and food-storage behavior as the beaver (Busher forthcoming). Furthermore, beavers can defend large territories rather than only the immediate vicinity of the lodge, possibly as a long-term strategy for resource defense (Campbell et al. 2005). It is thus crucial that beavers maintain their scent marks in such a way that maximizes the success of matching (see Gosling 1986; Roberts and Lowen 1997; Gosling and Roberts 2001). Territorial beavers may therefore be at great risk on territories with high predator densities because of the trade-off between predator avoidance and territorial defense.

Our results are in accordance with the laboratory experiments of Roberts et al. (2001) that indicated that high-marking male laboratory mice (*M. musculus*) significantly reduced the amount of time spent overmarking the competitor's scent in the presence of predator scent (ferrets [*M. putorius*]). Therefore, the potential costs of predation cause both beavers and mice to reduce their rates of scent marking. These findings suggest that there is a unique danger inherent to counter-marking for adult beavers that typically mark at high frequencies. If predators do make use of variable densities of scent marks as a cue to likely prey densities and foraging success rates (cf. Viitala et al. 1995), then high-marking individuals will become more vulnerable to predation than those that mark their territory or range at lower frequencies (Roberts et al. 2001).

Taken together, our results suggest that both predator and nonpredator scents reduce beavers response to a simulated intruder's scent mounds and therefore disrupt their territorial defense. However, predator (lynx and wolf) scent has a stronger effect than nonpredator (eland and horse) scent. Therefore, both the findings of Roberts et al. (2001) in laboratory and our findings in the field demonstrate the potential of predation risk as a powerful agent of counterselection on olfactory signaling behavior. The results suggest that the presence of predators may influence the territorial behavior of other groups of animals as well. Further studies should examine the long-term consequences of the territorial disruption and the individual fitness consequences in particular.

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