A test of the dear enemy phenomenon in the Eurasian beaver

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We tested the hypothesis that Eurasian beavers (*Castor fiber*) exhibit the dear enemy phenomenon, i.e. respond less aggressively to intrusions by their territorial neighbours than intrusions by non-territorial floaters (strangers). This ability could be advantageous in facilitating differential treatment of wandering strangers versus established neighbours. Territorial beavers were presented with scent from neighbouring and stranger adult males. Thirty-nine different active beaver families, 18 in 1998 and 21 in 1999, were presented with a two-way choice between two pairs of experimental scent mounds (ESMs); mounds with castoreum from a neighbour and a stranger, and mounds with anal gland secretion (AGS) from a neighbour and a stranger. Direct observations of the families during evenings showed that: (1) beavers sniffed both castoreum and AGS from a stranger significantly longer than from a neighbour, and (2) beavers aggressively responded (time standing on the mound on hind feet, pawing and/or overmarking) significantly longer to castoreum, but not to AGS, from a stranger than from a neighbour. When ESMs were allowed to remain overnight and the response measured the following morning, beavers responded significantly stronger to both castoreum and AGS from a stranger. These findings indicate that Eurasian beavers can use scent to discriminate between neighbours and strangers, thereby supporting existence of the dear enemy phenomenon in this species.

A territory is an area defended by a group or individual (Davies & Houston 1984). Territoriality is observed when the benefits gained from exclusive access to limited resources exceed the costs of defence (Brown 1964). One mechanism by which individuals may reduce defence costs is to reduce aggression towards familiar occupants of neighbouring territories, known as the dear enemy phenomenon (Fisher 1954; Temeles 1994). Once territorial boundaries have been established, a territorial neighbour poses less threat to an individual's territory and an aggressive response to its display adds costs to territorial defence. Non-territorial floaters (strangers), however, would pose a greater threat and a heightened aggressive response might be worth the cost of time and energy expended (Jaeger 1981; Temeles 1994).

Both the Eurasian (*Castor fiber*) and North American beaver (*C. canadensis*) are strongly territorial and aggressive encounters are not uncommon (Novak 1987; Nolet & Rosell 1994). Beavers usually live in families consisting of an adult pair, kits, yearlings and sometimes 2-year-olds, and mark their territories by depositing castoreum and/or anal gland secretion (AGS) on small piles of mud, sticks and grass (scent mounds) close to the water's edge (Wilsson 1971; Novak 1987; Rosell & Bergan 1998). They are monogamous, which is rare among Rodentia, non-dimorphic and a family can occupy the same lodge for many years (Wilsson 1971; Novak 1987).

In a review of neighbour-stranger discrimination studies in a variety of taxa (mammals, birds, reptiles, amphibians and insects) Temeles (1994) found that the dear enemy phenomenon occurred primarily in species with territories that contain both the breeding site and food supply ('multi-purpose/breeding' territory), but rarely in species with feeding territories or very small breeding territories. Beavers typically occupy this 'multi-purpose/breeding' territory. However, only 10 of 55 species reviewed by Temeles (1994) were mammals and only two (3.3%) of the studies used olfactory stimuli (Mertl 1977; Ferkin 1988). For five (50%) of the mammal species the tests where conducted on neutral arenas. Fox & Baird (1992) concluded that neutral arenas do not replicate the cost-benefit relationship that favours territory defence and that this design does not adequately test for the dear enemy phenomenon. Therefore, further work with mammals should employ tests performed in the field or at least under conditions that closely reflect the field because these are the conditions under which territoriality is adaptive.

Other than increased visitation to experimental scent mounds (ESMs) marked with stranger castoreum, Schulte (1993, 1998) found little support for the dear enemy phenomenon in the North American beaver and concluded that further work is needed to clarify this issue. However, in Schulte's study area the distance between neighbouring sites averaged 0.95 km ± 0.47 SD (N=12) and there was always a unoccupied stretch of stream between territories. It may be more important and easier to discriminate neighbours from strangers in areas where territories are located close together, and where frequent contact between neighbours occurs, than in areas were relatively large distances between territories exist. Therefore, beavers living in areas with adjacent territories should show a clear dear enemy phenomenon. The role of neighbour interactions in the territorial behaviour of monogamous, crepuscular and nocturnal mammals is not well known. The long-term occupancy of a territory by beavers implies that neighbour recognition and tolerance are beneficial to maintaining territorial claims.

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

METHODS

Study Area and Study Animals

The study was conducted in 1998 (25 March-31 August), and in 1999 (10 April-23 September) at the Bø, Lunde, and Saua rivers (59° 17´-25´N, 09° 04´-17´E) in southeastern Norway. The rivers have been inhabited by beavers since the 1920s (Olstad 1937) and despite annual harvesting colony density was believed to be near maximum. Colony density in 1998 on the Bø, Lunde and Saua rivers was 0.64, 1.4 and 0.53 colonies/km stream respectively (Rosell & Hovde 2001, Rosell & Sundsdal 2001). Beaver sites were surveyed for activity in spring prior to the bioassays. Thirty-nine different active beaver families (18 in 1998 and 21 in 1999) with two or more adult individuals (≥15 kg) were used during the study. The number of animals in each family, many of which were eartagged, was determined by direct counts using light-sensitive binoculars from the riverbank, a canoe, or boat at dawn and dusk, and on many occasions before and during the field bioassay. Mean family size was $\overline{X}$ ±SD=3.6±2.1 (N=18, Range=2-9) in 1998 and $\overline{X}$ ±SD=3.8±1.7 (N=21, Range=2-8) in 1999. The territorial boundaries were drawn on the basis of the location of scent mound concentrations (Rosell & 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). Two families used in this study had three immediate neighbours (two upstream and one downstream), and two had only one close neighbour downstream. The rest of the families had two neighbours, one upstream and one downstream. All territories were adjacent, with no unoccupied stretches of stream separating them.

We live-trapped beavers using Hancock and Bailey live-traps baited with aspen twigs, or at night with landing nets (Rosell & Hovde 2001). The live-trapping was under licence of the Norwegian Experimental Animal Board and the Norwegian Directorate for Nature Management. All captured beavers were handled in a cloth sack with no sedative. Their ears were tagged with numbered plastic eartags (Dalton Continental B. V., the Netherlands) and/or monel metal tags (National Band and Tag Co., Kentucky, USA). 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 & Pedersen 1999; Parker et al. 2001).

Scent donors and collection of Scent Samples

We collected scent samples from 42 adult males ($\overline{X}_{\text{weight}}$±SD=20.3±2.6kg, Range=15.2-26.0kg). We designated samples collected from animals in territories next to the experimental animals as territorial neighbours, and animals from other watersheds located > 20 km away as wandering strangers. We assumed that the strangers were unknown to the territorial beavers and not closely genetically related to the families used in the field experiments.

We collected scent from animals killed by hunters between 10 April and 9 May 1998 (n = 8) and 24 March and 26 April 1999 (n = 5). We opened the castor sacs with a surgical blade and scraped the castoreum from the inside surface with a metal scapula. AGS was collected from the glands by cutting off the last 2-3 mm of the papillae and squeezing out the secretion (Rosell & Sun 1999; Rosell et al. 2000). The dead animals were sexed by checking for the presence or absence of the os penis (Osborn 1955).

We live-trapped the remaining 29 scent donors between 25 March and 15 August 1998 (n = 15) and 31 March and 23 September 1999 (n= 14). Of the 29 beavers live captured and used as donors, 26 (89.7%) were observed in their respective territories on one or several of the capture trips or during direct observations. Before collecting the scent samples, the rectum was evacuated and the cloaca area rinsed with distilled water. The papillae of the anal gland were pushed out separately and the AGS squeezed out. To collect the castoreum the abdominal region was first massaged by hand. A gentle rolling motion oriented downward from the urinary bladder towards the cloaca and over the castor sacs released castoreum (Schulte 1998). We sexed the live-trapped beavers by the colour and viscosity of AGS (Rosell & Sun 1999). After the sample collection, the beavers were released near the capture site.

All samples were placed in glass vials and stored at -20^{o}C until use. For each bioassay, castoreum and AGS from the same individual were used. We used scent from neighbours and strangers of similar characteristics for each bioassay, i.e. animals of similar weight (<three kg difference), similar time from collection to freezing of scent samples (>five h or <five h) and similar season of scent collection (<one month difference).

Experimental Design

Four types of ESMs, castoreum from a neighbour (C-N) and a stranger (C-S) and AGS from a neighbour (A-N) and a stranger (A-S) were constructed inside each territory. A C-N/C-S pair was placed on one side of the lodge and an A-N/A-S pair on the other. The ESMs of each pair were placed 30 cm apart, and within 50 cm of the water's edge (Fig. 1). The ESMs were constructed where the beavers easily could make a land visit (walk onto land). This made it possible to compare beaver's response to C-N versus C-S and A-N versus A-S, i.e. each family was simultaneously exposed to two different two-sample choice tests (see also Sun & Müller-Schwarze 1997). Placement of the ESMs (C-N, C-S, A-N, A-S) were organised randomly by lot on each trial to control for side preference, and each beaver family was tested only once.

Figure 1 near here

We wore clean plastic gloves to prevent contamination with human odour 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 to the site where the ESMs were constructed. Each ESM was approximately 15 cm wide and 10 cm high. The 30 cm distance between the two scent mounds was to ensure that once a beaver responded to one of them, it would also have an equal opportunity to respond to the other, hence between-treatment effect could be compared (Sun & Müller-Schwarze 1997).

We used a plastic bottle cap (2.5 cm top diameter, 1.2 cm high) in each ESM to hold 0.25 ml of scent material and to control the evaporation surface area (Schulte 1998). The bottle cap was placed in the centre 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 (1800-2000 hours). 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 (only done in 1999).

Measures of Response

Direct Observations

An observer with binoculars down-wind on the opposite bank recorded on a dictaphone the duration in seconds of three response patterns to ESMs (to C-N and C-S and/or to A-N and A-S): 1) the first land visit to the ESM, i.e. from the moment the beaver walked onto land within a radius of approximately 0.5 m from the ESMs to when it returned to the water, 2) sniffing (on land, and directed towards and within approximately 5 cm of the ESM) and 3) the 'aggressive response', i.e. standing on the ESM on its hind feet, pawing and/or overmarking (putting a pile of mud either at the side or on top of the ESM and then marking it with castoreum and/or AGS) (Sun & Müller-Schwarze 1997; Rosell et al. 2000). Sniff duration was used as a measure of the time required by beavers to identify the scents. The 'aggressive response' duration indicated how strong an agonistic behaviour the ESMs triggered. We included only the responses of the first beaver in our analyses because physical damage to the scent mounds (pawed, flattened or obliterated) may cause some carry-over biases in the following responses by the same or other beavers (Sun & Müller-Schwarze 1997).

Overnight Activity

We also ranked the overnight response by checking the ESMs the following morning (Table 1). Since beavers live in family units, different members of a family may respond to ESMs sequentially at different times during the same night (Schulte 1993, Sun & Müller-Schwarze 1998). Therefore we checked and ranked the response result overnight to characterize the intensity of the collective beaver family response (Table 1). 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, i.e. the maximum score could be 7 (Table 1). After measuring the response intensity of the ESMs the following morning they were completely removed. Activity at the ESMs that could be attributed to other mammal species such as mink (*Mustela vison*) was not observed.

Table 1 near here

Data Analysis

The data did not fit assumptions of distribution and homogeneity of variance for parametric analysis (Sokal & Rohlf 1995) and we therefore used nonparametric statistics in accordance with Siegel & Castellan (1988). We used Wilcoxon signed-ranks test for matched samples to compare the response time (sniffing and aggressive response) and rank index value (overnight response) between neighbour and stranger ESMs. We checked for differences in response to scent for between-subject effects (castoreum versus AGS) by using a Mann-Whitney U-test for independent samples. We chose to present mean values and their standard deviations (SD), although all statistical tests were nonparametric, which entails comparing medians. The data from the two years were combined because no significant differences in any of the measures of response were found for the different ESMs between the two years. We also combined the data from the dead and live captured beavers because no significant differences were found between the results for the two groups. Tied observations were dropped from the analysis (Siegel & Castellan 1988). Since our hypothesis predicted that beavers would show reduced territorial behaviour to neighbours compared to strangers, these tests were one-tailed (Siegel & Castellan 1988). All other tests were two-tailed and a probability level Ò0.05 was considered significant. Data analyses were performed with the statistical package SPSS version 10.0.

RESULTS

Responses to Neighbours versus Strangers

Beavers spent significantly more time sniffing C-S compared to C-N (Z=-2.4, N=17, P=0.001) and A-S compared to A-N (Z=-2.3, N=21, P=0.010) (Table 2). Beavers aggressively responded significantly longer to C-S than to C-N (Z=-2.3, N=16, P=0.010). However, no significant difference in aggressive response duration was found between A-S and A-N (Z=-1.0, N=19, P=0.172). Overnight, beavers responded significantly stronger to C-S compared to C-N (Z=-1.7, N=21, P=0.044), and A-S compared to A-N (Z=-3.1, N=28, P=0.001).

Table 2 near here

Responses to Castoreum versus AGS

Land visits to the two castoreum ESMs (C-S and C-N) had an average duration of 72.1 seconds (N=16, SD=44.9), which was not significantly longer than to AGS ESMs ($\overline{X}$ ±SD=49.3±30.6, N=19) (Z=-1.6, P=0.117). Beavers made the first land visits to castoreum between 1950hour and 2336hour, and between 1954hour and 2343hour for AGS. On average they did not visit the ESMs with castoreum significantly earlier than those with AGS ($\overline{X}$ ±SD=21.32h±71min; $\overline{X}$ ±SD=22.00h±64min, respectively) (Z=-1.3, P=0.182).

No significant difference in sniffing time was found between C-N and A-N (Z=-0.7, P=0.490), or C-S and A-S (Z=-1.0, P=0.317). Beavers did not aggressively respond longer to C-N than to A-N (Z=-0.3, P=0.804) or to C-S compared to A-S (Z=-1.3, P=0.204). Beavers responded significantly stronger to C-N overnight compared to A-N (Z=-3.4, P=0.001) but not significantly stronger to C-S compared to A-S overnight (Z=-1.4, P=0.168).

Responses of Different Age-Classes and Sexes

All responses during the evening observations were by adult beavers, except in one family where a two year-old responded to the ESMs with AGS (sniffed 27s on A-N and 16s on A-S, and responded aggressively only to A-N (10s)). It was difficult to identify the beaver eartags correctly and many unmarked beavers also responded to the ESMs. We therefore managed to determine the sex of only 15 beavers (N=8 males, N=7 females) in 13 families. No clear sex difference was observed, though further statistical comparisons were not conducted due to small sample sizes.

DISCUSSION

The results indicate that Eurasian beavers respond significantly longer and stronger both to castoreum and AGS from strangers than from neighbours. These findings indicate that the neighbour scent was more familiar to the territorial beavers, and that beavers showed a stronger agonistic behaviour to scent from strangers. This strongly 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 tolerate their presence in closer proximity, but to be less tolerant to strangers. Animals that associate regularly and are equally likely to win or lose in a conflict can have stable, long-term relationships based on mutual avoidance (Randall 1989). The dear enemy phenomenon in beavers is most likely an evolutionary response to the high cost and low payoff of escalated aggression between territorial neighbours (see also Jaeger 1981). Beavers in our study area presumably learn the identity of their neighbours by repeated exposure to them and their scent marks at the edges of territories (see Rosell & Bergan 1998; 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-family adult males. Therefore, both Schulte's (1998) and our 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.

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Table 1. Rank system of increasing intensity used to measure the overnight response by beaver families to experimental scent mounds (ESMs)

ESM status	Description	Rank index value
Intact	No clear sign of beaver response	0
Prints/scratch marks	Beaver footprints or scratch marks on ESM	1
Bottle cap disturbed	Bottle cap disturbed, but still on the ESM	2
Bottle cap dug out	Bottle cap removed and found away from ESM	3
ESM removed	ESM material partially removed	4
ESM flattened	ESM flattened with material at least partially present	5
ESM obliterated	ESM completely removed and no material left in the original place	6
Scent marking over the ESM or close by[a]	A new scent marking was detected by removing the bottle cap with or without[b] the original scent and sniffing the ESM area within a radius of 15 cm from the ESM[c], or mud/vegetation had been deposited on or within 15 cm of the ESM	+1

[a]The ESM status rank could be increased by +1 for all status categories except the first, i.e. “Intact”.

[b]If the plastic cap containing the donor scent (0.25 ml) was dislodged and moved, the ESM was 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.

[c]A fresh beaver scent mark is easily detectable by the human nose from a distance of 2 cm or more.

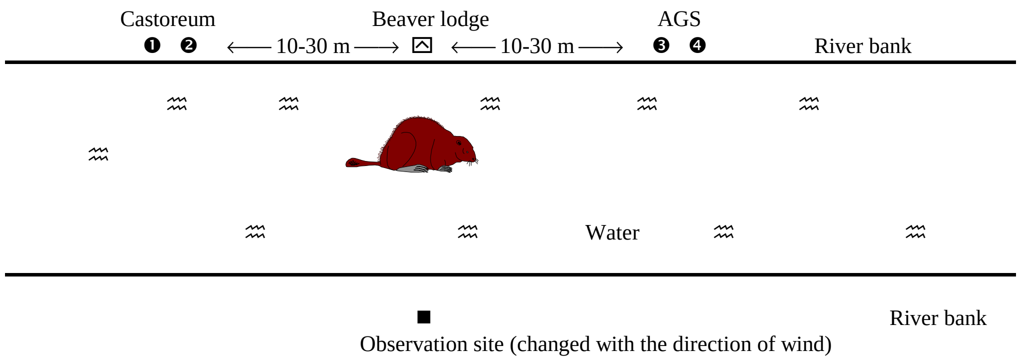
Table 2. Mean beaver response (±SD) to four types of experimental scent mounds (castoreum from a stranger (C-S) and a neighbour (C-N) and anal gland secretion from a stranger (A-S) and a neighbour (A-N)). N=sample size

Response	C-S	C-N	N	A-S	A-N	N
Sniffing (s)	26.4±21.5	11.7±14.7	17	18.1±13.1	7.6±10.0	21
Aggressive (s)	10.9±7.2	3.4±4.8	16	9.4±10.5	4.6±7.4	19
Overnight (rank)	5.3±1.9	4.7±1.6	21	4.6±2.1	2.1±2.3	28

FIGURE LEGENDS

Figure 1. The experimental design of the field bioassay. The side of the lodge where the experimental scent mounds (ESMs) containing castoreum or anal gland secretion (AGS) where placed, and the position of neighbour vs. stranger scent within each pair of scent mounds (1 and 2, and 3 and 4) were chosen randomly by lot for each trial to control for side preference. The ESMs of each pair were placed 30 cm apart, and within 50 cm of the water's edge. Note that the observation site changed depending on wind direction.

Figure 1


Castoreum
Beaver lodge
AGS
❶ ❷ ←— 10-30 m —→ ←— 10-30 m —→ ❸ ❹
River bank
Water
River bank
Observation site (changed with the direction of wind)