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Source: Wildlife Biology, 6(1) : 13-21

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2000.033

Responses of foraging Eurasian beavers *Castor fiber* to predator odours

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Rosell, F. & Czech, A. 2000: Responses of foraging Eurasian beavers *Castor fiber* to predator odours. - Wildl. Biol. 6: 13-21.

The ability of Eurasian beavers *Castor fiber* to recognise different predator odours has received little research, nor has the use of predator odours to deter Eurasian beavers from damaging agricultural crops, fruit and forest trees. Recognition of and response to predator odours by prey is of adaptive significance because it reduces predation risk. We tested the hypothesis that predator odours decrease foraging and predicted that: human and wolf *Canis lupus* odour would decrease foraging more effectively than other predator odours. Our results showed that all tested predator odours (red fox *Vulpes vulpes*, river otter *Lutra lutra*, lynx *Lynx lynx*, wolf and brown bear *Ursus arctos*), except those from human and dog *Canis familaris*, significantly decreased foraging during summer. River otter, red fox, lynx, wolf and brown bear odours had the strongest effects during summer. During autumn, river otter odour was significantly more effective than the other predator odours, except those from lynx, human and red fox, in decreasing foraging. Only odour from river otter, human, lynx and red fox had a significantly stronger effect than the three controls during autumn. Overall, the river otter odour was most effective in decreasing foraging. Odours from predators sympatric with the Eurasian beaver did not have a larger effect than those of originally sympatric, but now absent species. Beavers ate more sticks with predator odour in autumn than in summer. Our results have clear practical implications, and several are suggested.

Key words: Castor fiber, Eurasian beaver, feeding repellents, foraging, odours, Poland, predators

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Received 16 April 1999, accepted 12 November 1999

Associate Editor: Tommy Asferg

The Eurasian beaver *Castor fiber* is slowly becoming re-established over much of its former range in Europe, and presently numbers are estimated at roughly half a million in Europe and Asia (Rosell & Pedersen 1999). The spread of beavers into cultural landscapes leads to conflict with man. In several countries the populations of beavers are large enough to be harvested, and hunting is again allowed. In other countries where hunting is not permitted, other measures to control the population and limit damage by beavers need to be considered (Nolet & Rosell 1998).

In Eurasia nearly all beaver-man conflicts are caused

by beavers feeding on cultivated plants such as crops and trees, or dam building (Richard 1986, Heidecke & Klenner-Fringes 1992, Rosell & Parker 1995). Dam building is by far the most important beaver damage problem although feeding damage can locally be problematic (Rosell & Parker 1995). Most of the feeding damage (>75%) is reported from within a distance of 20 m from the water's edge (Heidecke & Klenner-Fringes 1992). Nolet & Rosell (1998) suggested that restoration of at least 20 m wide zones of natural vegetation along the banks of waterways (not accessible to cattle and horses) is the best durable solution to the problem of beaver feeding damage. Alternatively, feeding damage can be reduced by chemical repellents (slaked lime, quick lime and linseed oil), fencing or by using wire around individual trees (e.g. Richard 1986).

The Eurasian beaver is territorial and usually lives in family units (Wilsson 1971, Djoshkin & Safonow 1972, Nolet & Rosell 1994). A typical family consists of a monogamous adult pair, young of the year, yearlings and sometimes two-year olds or older (e.g. Wilsson 1971, Kudrjasov 1973). The territories are scent marked with castoreum and/or anal gland secretion, which play an important role in territory defence (Rosell & Nolet 1997, Rosell & Bergan 1998, Rosell, Bergan & Parker 1998). Beavers are strict herbivores. In summer, they mainly feed on aquatic plants and various herbs, and to a lesser extent woody food (e.g. Heidecke 1988, Histøl 1989, Nolet, van der Veer, Evers & Ottenheim 1995). In autumn and winter, they mainly eat woody food, although in some areas aquatics may also be used (Simonsen 1973). Although beavers can cut down mature trees of up to 1 m in diameter, they prefer small trees with a diameter of less then 10 cm (Wilsson 1971, Simonsen 1973, Basey & Jenkins 1995, Donkor & Fryxell 1999). Most trees are cut in autumn, when the beavers are preparing their food cache. Such a cache is mainly built in climates with harsh winters (Rosell & Parker 1995).

The beaver's aquatic lifestyle and habit of constructing partially submerged dens under masses of earth and sticks (Wilsson 1971, Zurowski 1992) has seemingly limited the number of its effective predators (Rosell & Parker 1996). The main cause for the near disappearance of the beaver in the 19th century was over-hunting (Nolet & Rosell 1998). Other species known to prey on beavers in Europe are wolves *Canis lupus*, bears *Ursus arctos*, lynxes *Lynx lynx*, wolverines *Gulo gulo*, red foxes *Vulpes vulpes* and dogs *Canis familaris* (Dezhkin & Safonov 1966, Tyurnin 1984, Zurowski 1989, Kile, Nakken, Rosell & Espeland 1996, Rosell, Parker & Kile 1996). Humans and wolves are regarded as the beaver's main predators in Europe. Humans have preyed upon Eurasian beavers both in historic and presumably prehistoric time, and human predation was the major cause for the near extirpation of the beaver in Europe (Nolet 1996, Nolet & Rosell 1998, Rosell et al. 1996). In Isle Royale National Park wolf predation is so common that it is considered to regulate the local North American beaver *C. canadensis* population (Shelton & Peterson 1983). Recently, Andersone (1998) reported that beavers appeared to be the most important food item for wolves in Latvia during summer, and concluded that wolves switched to beavers when ungulates were few. Substantial predation by the black bear *U. americanus* on beaver has only been reported from an island in Lake Superior (Smith, Trauba & Anderson 1994). The lynx, wolverine, red fox and dog are rarely reported as predators on beavers and probably have minor effects on beaver populations. The river otter *Lutra lutra* and pine marten *Martes martes* are also suspected to prey on the Eurasian beaver in some areas (see references in Tyurnin 1984, Rosell & Hovde 1998). However, in many areas where the Eurasian beaver and the river otter are sympatric beaver remains have not been found in otter excrements (see references in Tyurnin 1984). Also, North American beavers are rare in the diet of the river otter *Lontra canadensis*. In a northeast Alberta area with high beaver and otter densities, Reid (1984) found that only 5 of 1,140 (0.4%) otter scats contained beaver remains. However, the otter may have fed on beaver carcasses. No beaver remains were found in seven other studies of otter droppings, cited by Reid (1984). Studies on the otter diet, undertaken in beaver lodges in Canada, also showed that otters did not prey on young beavers (Tumilson & Karnes 1987). The mink *Mustela vison* is probably not a predator of Eurasian beaver. Brzezinski & Zurowski (1992) found that young beavers were not eaten by mink during spring in northern Poland. Beaver kits were probably sufficiently guarded by their parents and mink were not able to enter the beaver lodges without exposing themselves to attacks by adults.

In North America, predator odours, especially of the coyote *C. latrans*, lynx *L. canadensis* and river otter, are promising as feeding repellents for the North American beaver (Engelhart & Müller-Schwarze 1995). Although mammals respond to scent from allopatric predators and often are repelled by them, chemical cues from sympatric species are generally more effec-

tive (Mason, Epple & Nolte 1993). Predator odours also have the potential to reduce feeding in many other genera of rodents (e.g. Vernet-Maury, Polak & Demael 1984, Robinson 1990, Sullivan, Crump, Wieser & Dixon 1990, Merkens, Harestad & Sullivan 1991, Swihart 1991, Nolte, Mason, Epple, Aronov & Campbell 1994, Borowski 1998). Recognition of and response to predator odours by prey is of adaptive significance because it reduces predation risk (Merkens et al. 1991).

The Eurasian beaver's ability to recognise different predator odours has apparently received no attention, nor has the use of predator odours to deter Eurasian beaver from damaging agricultural crops, fruit and forest trees. Therefore, we designed a study to test the hypothesis that predator odours decrease beaver foraging by investigating the effects of such scents on food consumption in the field. The following prediction was tested: human and wolf odour would be more effective in reducing beaver foraging than the other predator odours.

Material and methods

Our study was conducted in Suwalki Lakeland in northeastern Poland (53°50'N, 23°15'E). Gently rolling hills up to 220 m a.s.l., intersected by lakes and rivers form the landscape. Approximately 3.4% of the area is covered by water (Zurowski & Kasperczyk 1986). The natural vegetation on the banks of the watersheds consists mostly of shrubs of willow *Salix* spp. and aspen *Populus tremula*. Suwalki Lakeland is densely forested and human population is relatively low (about 10 inhabitants/km^2; Rocznik Statystyczny 1997). World War II, and a resulting shift of national boundaries, caused the complete extirpation of Eurasian beavers from Poland by 1945, and the species is now strictly protected (Dzieciolowski & Gozdziewski 1999). The mean density of sites on the entire beaver range in the Suwalki Lakeland in 1984/85 was 15.3/100 km^2 (Zurowski & Kasperczyk 1986). The population in Suwalki Lakeland was about 4,500 in 1994 (Dzieciolowski 1996). In our study area, river otter (Brzezinski, Romanowski, Cygan & Pabin 1996), wolves (Okarma 1993), red foxes (Buchalczyk 1981, 1983, Pielowski 1982) and lynxes (Kamieniarz & Panek 1996) are present, while the brown bear occur only in the Carpathian Mountains in southern Poland (Jakubiec & Buchalczyk 1987). Information on monthly average rainfall was supplied by the closest meteorological station located about 40 km from the centre of the research area (Rocznik Statystyczny 1998). There was only a small difference in monthly average rainfall between the summer (51.5 mm) and autumn (63.5 mm) trials.

To compare our results from the Eurasian beaver with those from the North American beaver, we used the methods of Engelhart & Müller-Schwarze (1995). Predator odour samples were prepared from excrements (see Table 1). All faeces, except those from dogs, were collected from animals in Zoo Lodz, Zoo Poznan and Zoo Warsaw during April-June 1997. The dog samples were collected from pets. We assume that the faeces from the zoo animals were similar enough to those of wild animals because the zoo animals were fed with the same type of food as the animals eat in the wild. The river otters were fed with fish and frogs, the red foxes and the lynxes with rabbit meat, and the wolves and the brown bears with beef and pork. For all samples, one part faeces (by weight) was suspended in two parts pure methanol for two hours and then filtered with a vacuum filter. The filtrate was used for the experiment. The odour samples were stored in glass jars with alcohol-proof plastic lids in a refrigerator until use.

Aspen sticks cut from aspen saplings in the study area were used as carriers for the odours. Stems with a diameter of 1-2 cm and with as few lateral twigs as possible, were selected. The sticks were cut fresh on the first day of each trial, pruned, and cut into 30 cm long sections. The bark of all sticks, except the 'intact' control, was perforated by rolling them on a nailboard, to facilitate uptake of the methanol solutions. The sticks were dried at room temperature for two hours before being scented by dipping two thirds of their length into the extracts for two seconds (except those left intact). One stick was perforated and untreated (blank), and one unperforated and untreated (intact). In addition, sticks were soaked in a deer repellent based on human sweat named HUKINOL and produced by KIEFERLE GmbH, Germany. This repellent is used to protect forest plantations (P. Janiszewski, pers. comm.). We also soaked sticks in pure methanol as a solvent control. The sticks were dried for two hours at room temperature before further handling.

For each trial we used 10 randomly selected beaver colonies. We used different colonies for each of five consecutive trials, i.e. 50 colonies per season. The colonies used in the summer trials (16 July - 9 August 1997) were used again in the autumn trials (11 Octo-

ber - 4 November 1997). A trial consisted of 10 sticks placed in a row on the ground, 30 cm apart, at the bank of each pond parallel to the water's edge, near feeding places that were frequently visited by beavers. Each stick carried one of the seven predator odours, and the remaining three sticks were controls. The sticks were placed in a random order, determined by lot, and the same pattern was used for all colonies during one trial. A trial lasted for five days and nights, i.e. five beaver activity periods, without replacing any missing or altered sticks. New sticks were always used on a new trial. We used a total number of 1,000 sticks during the summer and autumn trials.

We recorded the results of nocturnal beaver activity each day between 7 and 9 a.m., and classified the sticks into: 1) eaten, i.e. completely or peeled ≥80%, or missing sticks, and 2) not eaten, i.e. peeled <80%, left intact and in place or left intact and moved. Beavers sample sticks and often discard partially peeled sticks (Engelhart & Müller-Schwarze 1995). Sticks that were not eaten after five activity periods were regarded as rejected.

We used χ^2-tests to test for overall significance in the differences between odours in number of sticks eaten after five activity periods during both summer and autumn trials (Sokal & Rohlf 1995). Thereafter we tested for which odours were significantly different using Tukeys T-method for multiple comparisons (approximate) (Berenson & Levine 1989). Sign tests were used to test if the median number of sticks eaten during the summer were less than the median number of sticks eaten during the autumn. All probabilities presented are one-tailed unless otherwise indicated (Sokal & Rohlf 1995).

Results

Summer

The number of experimental sticks eaten by the beaver (Fig. 1) differed significantly between odours ($\chi^2 = 257.6$, $P < 0.0001$). After five activity periods, it ranged from 0% for river otter and red fox odours to 90% for blank and intact aspen sticks. After river otter and red fox, the most repellent odours were lynx (6% eaten), wolf (8% eaten), and brown bear (10% eaten). Among the responses of beavers to the different samples, significant differences were found in the following comparisons: all odours except blank vs intact, and all odours, except human and dog vs methanol control (Table 1). Generally, there were no significant differences between the single predator odours. All predator odours, except human and dog odours, had a significantly stronger effect on beaver foraging than the three controls.

Autumn

In the autumn, the number of experimental sticks eaten by the beaver (see Fig. 1) also differed significantly between odours ($\chi^2 = 139.7$, $P < 0.0001$). As in summer, river otter odour was avoided most, but not quite as pronounced as in summer (0% vs 18% eaten). The most frequently eaten samples were blank and intact (98% each). Generally, river otter odour was significantly different from all other predator odours, except human odours (26% eaten), lynx (42% eaten) and red fox (46% eaten) (see Table 1).

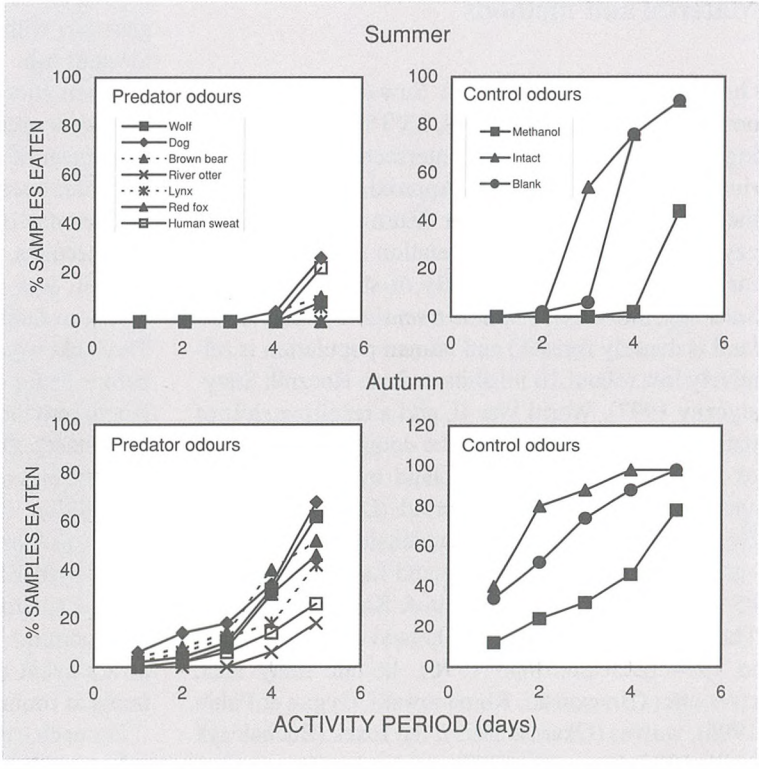

Figure 1. Responses by beaver (% samples completely eaten or peeled ≥80%, and/or missing) to different odours and predator odours at Suwalki Lakeland in Poland during summer and autumn, 1997. The activity period lasted for five consecutive days and nights (1-5), without replacing any missing or altered sticks.

Table 1. Difference in beaver responses to odour samples after five activity periods for summer and autumn trials during 1997.

Odour	RO[a]	Lynx	Wolf	BB[a]	Dog	HS[a]	M[a]	I[a]	B[a]
Summer trials									
Red fox	-	-	-	-	-	-	*	*	*
River otter		-	-	-	-	-	*	*	*
Lynx			-	-	-	-	*	*	*
Wolf				-	-	-	*	*	*
Brown bear					-	-	*	*	*
Dog						-	-	*	*
Human sweat						-	-	*	*
Methanol control								*	*
Intact									-
Autumn trials									
Red fox	-	-	-	-	-	-	*	*	*
River otter		-	*	*	*	-	*	*	*
Lynx			-	-	-	-	*	*	*
Wolf				-	-	*	-	*	*
Brown bear					-		-	*	*
Dog						*	-	-	-
Human sweat							*	*	*
Methanol control								-	-
Intact									-

[a] Abbreviations for odours: RO: river otter; BB: brown bear; HS: human sweat; M: methanol control; I: intact; B: blank.
* and - state if the comparison is significant or not by Tukey's T-method for multiple comparisons (approximate) at total significance level 5%.

Seasonal variation

Only 10.3% of sticks with predator odours were eaten in summer, compared with 44.9% in autumn. This difference was significant (two-tailed, S = 7 positive differences, P = 0.0156, N = 7). In summer trials, 23.3% of all sticks were consumed, compared with 49.0% in autumn. This difference is also significant (two-tailed, S = 10 positive differences, P = 0.002, N = 10). Only sticks with human odour were eaten in similar amount during the summer and autumn trials (22 and 26%, respectively).

Discussion

Significance of predator odours in influencing foraging

Our results supported the hypothesis that predator odours on aspen sticks decrease foraging by the Eurasian beaver. The results also showed that Eurasian beavers are able to distinguish between different odour treatments of food. We predicted that human and wolf odours would be most effective. However, the results showed that during summer all predator odours, except those of human and dog, significantly decreased beaver foraging. River otter, red fox, lynx, wolf and brown bear odours had the strongest effects during summer. During autumn, river otter odour was significantly more effective than the other predator odours, except those of human, lynx and red fox, in decreasing beaver foraging. Only river otter, lynx, human and red fox odours had a significantly stronger effect than the three controls during autumn. Similar results were found by Engelhart & Müller-Schwarze (1995) for the North American beaver. They showed that coyote, lynx and river otter odours had the strongest effects and concluded that predator odours were promising as feeding repellents.

The effectiveness of predator odours as natural repellents 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 odour is likely to result if prey and predator have coexisted over evolutionary time (e.g. Gorman 1984, Berdoy & Macdonald 1991, Ward, Macdonald & Doncaster 1997). However, research done with house mice *Mus musculus* conducted on an island without any mammalian predators showed that reaction to predator odour (cat *Felis catus* and red fox) may disappear after a certain number of generations (Dickman 1992), and therefore is not passed on genetically. Avoidance of a predator odour can be either species-specific (Swihart 1991, Jedrzejewski, Rychlik & Jedrzejewska 1993, Nolte, Farley, Campbell, Mason & Epple 1993) or general (Stoddart 1982a, Weldon, Graham & Mears 1993, Nolte et al. 1994). Furthermore, some prey learn to respond only to predators that are actively

dangerous (Dickman 1992). The dog had the weakest effect during both summer and autumn trials. This finding may be due to the novelty of the pet dogs' odour. Indeed, no wild dogs are present in our study area. Interactions between beaver and humans have occurred in Poland for a very long time before the protection. Fossils of Eurasian beavers appear in early Pliocene deposits (12 million years ago) in Europe (Novak 1987). The duration of the geographic association between the different predators and the Eurasian beaver in our area, and/or the past or present predator pressure probably explains the results we found. Engelhart & Müller-Schwarze (1995) found that the slightly more avoided odours were those of predator species that were sympatric with the respective North American beaver populations. Beavers avoided the odours of sympatric predators such as river otter and coyote that actually occur within the range of the tested beaver slightly more than those of originally sympatric, but now absent, species such as the wolf. However, the North American beaver did not avoid the odours of sympatric species significantly more than the odour of the allopatric species, i.e. African lion *Panthera leo* (Engelhart & Müller-Schwarze 1995). Our results did not show that odours from predators sympatric with the Eurasian beaver, like wolf and lynx, had a significantly larger effect than those of originally sympatric, but now absent, species such as the brown bear. Responses to chemical cues from allopatric predators and failure to habituate to predator odours have been interpreted as evidence that responses to these stimuli are innate (Müller-Schwarze 1972, Stoddart 1980, Dickman & Doncaster 1984, Robinson 1990). Dickman & Doncaster (1984) suggested that similar chemicals eliciting avoidance in rodents may commonly occur in the faeces and urine of carnivores; this is supported by observations that rodents often avoid the odours of carnivores with which there has been no evolutionary contact (Stoddart 1982a, b).

Beavers showed the strongest response to the scent of river otters, a predator species not only sympatric but actually often living together with the beaver in the same habitats, indeed in the same lodges built by beavers apparently without preying upon them (Reid 1984, Brzezinski et al. 1996, V.E. Sidorovich, pers. comm.). From an ecological point of view, it is an extremely interesting and novel finding. It does not match the classical interpretation of 'repellents' as the river otter does not appear to be a predator on beaver. A plausible interpretation may be that river otter excrement inhibited feeding by beavers more than the other predator excrements because it simply tastes or smells foul, and not because of predator recognition. Indeed, the beavers ate other sticks close by the otter sticks.

Seasonal variation

Beavers in our study ate more sticks with predator odours in autumn than in summer trials. We also found that beavers ate significantly more of all sticks during autumn than in summer. Engelhart & Müller-Schwarze (1995) also found a similar seasonal difference, and concluded that this was most likely correlated with reduced abundance of palatable food. In summer, beavers feed very little on tree bark and prefer to eat leaves and chew the bark of a twig only after all leaves are consumed. They also eat grass and herbs. This might explain less interest in the aspen sticks during summer. In late autumn, the growing season is over and beavers depend almost exclusively on bark for food. The beaver become less selective and the aspen samples might become more attractive (Engelhart & Müller-Schwarze 1995).

Predator odours may also become less effective after heavy rains (Sullivan, Nordstrom & Sullivan 1985, Engelhart & Müller-Schwarze 1995), and this might vary for each predator odour. In our study area there was only a small difference in monthly average of rainfall between the two field trials, so we assume rainfall did not affect our results. However, rain may have had an effect on the total result. The biggest problem in the work with odours as repellents has not been to find substances that animals will avoid, but to find substances that will have a long-term effect, i.e. substances that beavers do not habituate to, that does not wash away with rainfall or evaporate too fast (Sullivan et al. 1985, Engelhart & Müller-Schwarze 1995).

Management implications

Our results may have several practical implications. One implication is that predator odours could reduce damage by free-ranging Eurasian beaver to agricultural crops, fruit and forest trees, and be a humane, environmentally acceptable chemical that can be used to manage wild Eurasian beaver populations. In a few species predator odour has been a successful means to reduce feeding damage in field trials by 60-100% for time periods ranging from 1 to 5 months (Sullivan & Crump 1984, Sullivan 1986, Sullivan, Crump & Sullivan 1988a, Swihart 1991). Woodchucks *Marmota*

monax, for example, avoid marking fruit trees sprayed with bobcats' *L. rufus* urine for as long as 93 days, and continue to avoid bobcats' urine even when exposed to the odour in consecutive years (Swihart 1991). Trees are long-lived, and rodent damage is difficult to prevent completely. No repellent is likely to provide total protection. Nevertheless, predator odours, and in particular river otter odour, could reduce damage by beavers during periods when trees are most vulnerable, e.g. during early spring and late autumn. A component of the weasel's *M. nivalis* scent has successfully suppressed feeding damage to seedlings by hares *Lepus americanus* for a six-week period in a field bioassay trial (Sullivan & Crump 1984). This period covered the early spring when conifer seedlings were susceptible to hare damage, just after snow-melt and prior to hares switching to preferred summer herbaceous foods.

Because other rodents avoid burrows treated with predator odours (e.g. Sullivan, Crump & Sullivan 1988b), it is also conceivable that Eurasian beavers might avoid treated burrows, lodges and/or dens. Indeed, adult pocket gophers *Thomomys talpoides* were deterred from colonising an area treated with sulphur compounds from the anal glands of the stoat *M. erminea* (Sullivan & Crump 1986, Sullivan et al. 1990).

Attempts to prevent Eurasian beavers from repairing destroyed dams and plugging culverts may also be possible at least for a short period when it is most necessary. Guenther (1956) reported that the North American beavers temporarily avoided dams with bear *Ursus* sp. and cougar *F. concolor* scent, but resumed repair when the scent dissipated. However, Buech (1985) tried wolf faeces as deterrents to plugged culverts with no success.

Further clarification of the role and utility of predator odours as repellents of the Eurasian beaver is warranted. Also, testing of the organic components, specially of the river otter, and particularly the volatile components, may enable identification of the compounds responsible for the response we observed. This may explain several of the results reported her.

Acknowledgements - we thank Per Christian Hagen for statistical advice, Göran Hartman, Thrine M. Heggberget, Jan Heggenes, Arild Landa, Howard Parker, Bruce Schulte, Geir A. Sonerud and Lixing Sun, and two anonymous reviewers for their constructive comments on earlier drafts of this paper. We also thank the board of National Forests in Suwalki region and students of the Biology Department at Jagiellonian University for help in field works and Dr. Andrzej Górecki, Director of Institute of Environmental Biology at Jagiellonian University for administrative support. This research was founded by grant no. 97/1/A/4 obtained from Castor Research Society, Poland.

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