

Resident beavers (*Castor canadensis*) do not discriminate between castoreum scent marks from simulated adult and subadult male intruders

J. Herr, D. Müller-Schwarze, and F. Rosell

Abstract: Subadult intruding beavers (*Castor* spp.) could be expected to pose a higher threat than adults to territory holders because, unlike adults who usually own a territory, subadults need to acquire a territory and a mate to reproduce successfully. We tested the responses of territorial beavers (*Castor canadensis* Kuhl, 1820) to simulated intrusions by adult and subadult males. Territorial intrusion was simulated through scent playback experiments that exposed residents to castoreum from adult and subadult strangers simultaneously. We obtained responses from 13 resident beavers. Neither sniffing response nor physical or total responses differed between castoreum from adults and subadults. This was true for both sexes combined and separate. There was also no significant correlation between the mass of the scent donor and the response intensity. We found no evidence that territorial beavers responded differentially to castoreum scent marks from intruders of different ages. Either beavers consider all strange intruders as posing a high threat and hence do not treat them differentially or castoreum does not contain sufficient information to allow beavers to discriminate between age classes. We suggest that rather than directly assessing intruders by means of intrinsic information contained in the scent mark, beavers assess their competitors through scent matching.

Résumé : L'intrusion des castors (*Castor* spp.) subadultes devrait poser une plus grande menace aux détenteurs de territoire que celle des adultes, parce que, contrairement aux adultes qui ont déjà un territoire, les subadultes doivent se trouver un territoire et s'accoupler afin d'assurer leur reproduction. Nous avons évalué les réactions de castors (*Castor canadensis* Kuhl, 1820) à des intrusions simulées de mâles adultes et subadultes. Nous avons simulé les intrusions territoriales par des expériences de recapitulation d'odeurs dans lesquelles les résidents sont exposés simultanément au castoréum d'étrangers adultes et subadultes. Nous avons enregistré les réactions de 13 résidents. Les réactions de reniflement, les réactions physiques et les réactions globales ne diffèrent pas en présence du castoréum des adultes et celui des subadultes. Cela vaut pour les deux sexes combinés ou considérés séparément. Il n'y a pas non plus de corrélation significative entre la masse du donneur d'odeur et l'intensité de la réaction. Il n'y a pas d'indication que les castors territoriaux réagissent différemment aux marques d'odeur de castoréum des intrus d'âges différents. Ou bien les castors considèrent tous les intrus comme posant une forte menace et ainsi ne les traitent pas de manière différentielle, ou bien le castoréum ne contient pas suffisamment d'information pour permettre aux castors de distinguer les classes d'âge. Nous croyons que les castors évaluent leurs compétiteurs par l'association des odeurs, plutôt que par une évaluation directe des intrus au moyen des informations intrinsèques contenues dans les marques d'odeur.

[Traduit par la Rédaction]

Introduction

The benefits of owning a territory include exclusive access to resources such as food, mates, and nest sites, while the main costs are generally time and energy spent on excluding competitors as well as increased risk of injury during potential conflicts with intruders (Bradbury and Vehrencamp 1998). Standoffs between territory owners and intruders rarely escalate because the intruder withdraws in

the majority of cases (Gorman 1990). One way of avoiding costly encounters would be to assess the threat level posed by the opponent and scale the contest level accordingly (Parker 1974).

Fighting ability is often linked to body size, and hence larger individuals tend to have an advantage over smaller ones. This results in encounters being settled rapidly between unequal competitors, while contests among similar-sized individuals last longer and are of a higher intensity (Archer 1988). Encounters between territorial neighbours also tend to be shorter ("dear enemy phenomenon"; Fisher 1954). This is due to either the higher familiarity between the two competitors and an associated reduction in role mistakes (Ydenberg et al. 1988) or a reduced threat level posed by a neighbour as opposed to a stranger (Temeles 1994). In fact, unlike neighbours, strangers generally do not own a territory or a mate and hence are more likely to compete with a resident (Temeles 1994). The information used to assess competitors is often transmitted through territorial signals that can be visual (e.g., Hurd and Enquist 2001), auditory

Received 14 October 2005. Accepted 13 February 2006.
Published on the NRC Research Press Web site at
<http://cjz.nrc.ca> on 28 April 2006.

J. Herr¹ and **D. Müller-Schwarze**. Faculty of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY 13210, USA.
F. Rosell. Faculty of Arts and Sciences, Department of Environmental and Health Studies, Telemark University College, N-3800, Bø i Telemark, Norway.

¹Corresponding author (e-mail: janherr_lux@yahoo.com).

(e.g., Godard and Wiley 1994), or olfactory (e.g., Gorman 1990). In order for this system to work, natural selection should have selected for honest signals, which accurately represent each rival's competitive ability (Zahavi 1993).

North American (*Castor canadensis* Kuhl, 1820) and Eurasian beavers (*Castor fiber* L., 1758) are highly territorial, and each colony maintains an all-purpose territory that it scent marks (Schulte 1993; Rosell 2002). Scent marks consist of small piles of mud and vegetation on which scent is deposited (scent mounds) (Aleksiuk 1968; Rosell and Nolet 1997). These scent mounds are placed along the shoreline, often near trails, feeding beds, and resting sites (Müller-Schwarze and Heckman 1980; Rosell and Nolet 1997). The seasonal peak of scent-mounding activity occurs in spring (Svendsen 1980) during the main dispersal period (Sun et al. 2000). However, resident beavers still react strongly to strange scent marks later in the year (Müller-Schwarze et al. 1983).

Beavers use two types of scent material, anal gland secretion (AGS) and castoreum, which are produced by the anal glands and castor sacs, respectively. Both structures are located in subcutaneous cavities between the pelvis and the base of the tail (Walro and Svendsen 1982). AGS contains information on kinship, family membership, and sex (Sun and Müller-Schwarze 1999). The castor sacs are epithelial pockets that have no secretory ability. When beavers scent mark, the mixing of urine with the contents of the castor sacs (i.e., castoreum) results in castor fluid. Castoreum is based on urine and contains many compounds that are believed to be dietary derivatives (Müller-Schwarze 1992). Several of these compounds have been shown experimentally to elicit territorial behaviour, although they are generally not as active as whole castoreum (Müller-Schwarze and Houlihan 1991; Schulte et al. 1995b). Based on this evidence and evidence from the Eurasian beaver, castoreum is considered to be the beaver's main territorial signal (Rosell and Sundsdal 2001).

A variety of studies have shown not only that mammalian urine can encode information on breeding condition (e.g., Whittle et al. 2000), dominance (e.g., Harvey et al. 1989; Novotny et al. 1990; Miller et al. 1998), and age (e.g., Ma et al. 1999; Osada et al. 2003), but also that such information can be successfully transmitted to conspecifics (e.g., Hurst et al. 2001; Osada et al. 2003; White et al. 2003). Furthermore, differences in chemical profiles between adult and subadult, dominant and subordinate, or breeding and non-breeding individuals usually depend on the presence and concentrations of hormonal metabolites. This suggests that these signals constitute honest representations of an animal's physiological state (Schulte and Rasmussen 1999).

Beavers live in family groups where subadult individuals are subordinate to their parents and reproductively inactive until after dispersal (Müller-Schwarze and Schulte 1999). These age differences and the associated differences in size, dominance, and readiness to acquire a mate and territory might be reflected in castoreum. Although fights do occur and are potentially very costly, occasionally resulting in death (Piechocki 1977; Novak 1987), beavers defend their territories against intruders mainly through scent marking. In this study we used a behavioural field bioassay to test whether territory owners scale their territorial responses according to the age of the scent (castoreum) donor.

While Schulte (1998) had, in an earlier study, carried out experiments to investigate this problem, he found no significant differences in the responses of beavers to scent from adult and subadult strangers. He scored only the duration and the number of land visits while ignoring individual behaviours typically displayed by beavers in response to scent stimuli. However, these behaviours have subsequently proven very valuable in discrimination bioassays (Sun and Müller-Schwarze 1997; Rosell and Bjørkøyli 2002; for a review see Herr 2005). Other studies have also shown that results may be strongly dependent on the methods used (compare Peterson et al. 2005 with Rosell and Steifetten 2004). We thus used a different experimental setup with different response categories to test the hypothesis that subadult beavers pose a higher threat than adults to residents because subadults need to acquire a territory and a mate to be able to reproduce successfully. We predicted that residents would show a stronger response towards subadult scent.

Methods

Study area and study animals

The study was conducted at Huntington Wildlife Forest (HWF), a 6000-ha property located in the central Adirondacks, New York (44°00'N, 74°13'W) and owned by the State University of New York College of Environmental Science and Forestry. The elevation at HWF ranges from 457 to 825 m. The property has five natural lakes, one man-made lake, and many streams and ponds. The area has been inhabited by North American beavers since at least the early 1920s (Johnson 1927) and the beaver population is unexploited. Between 1986 and 2002, beaver population density averaged 0.46 ± 0.01 (SE) colonies/km² (Herr 2005). We determined colony size by live-trapping and tagging beavers at 10 colonies and by subsequently observing the animals at their colony sites in the evenings on at least four occasions between May and July 2004. Mean colony size was 3.5 ± 0.5 beavers, excluding kits, as these had not yet left the lodge at the time of the study.

We live-trapped 61 beavers (22 males, 28 females, 11 unknown) using Hancock live-traps baited with aspen (*Populus tremuloides* Michx.) during spring and summer 2003 and spring 2004. Beavers of unknown sex were mostly yearlings, which are more difficult to sex (Williams et al. 2004). The trapping was carried out under licenses "to collect or possess wildlife" (Nos. LCP03-319 and LCP04-313) issued by the New York State Department of Environmental Conservation. We set the traps before dark and checked them between 0600 and 0700 the following morning. We placed each caught individual head-first in an animal feed bag so we could handle and tag it without having to use an anaesthetic (see Rosell and Bjørkøyli 2002). We pierced holes in the corner of the bag where the beaver's nose was located to facilitate breathing. Once a beaver was confined in the bag it was relatively docile and easily handled. We assigned each beaver to an age class based on its mass (yearling ≤ 9.1 kg; 9.1 kg $<$ 2-year-old ≤ 14.5 kg; 14.5 kg $<$ adult; Schulte 1993). Beavers were sexed by opening the end of the bag and palpating the cloacal region to determine the presence or absence of the baculum (Osborn 1955). These results were validated using the colour of the anal gland se-

cretion (Schulte et al. 1995a). Each beaver was ear-tagged with coloured plastic (Dalton I.D. Systems, Oxon, UK) or aluminum tags (National Band and Tag Co., Newport, Kentucky) to facilitate age (subadult or adult) and sex recognition. This was done by manoeuvring the beaver's ear through a hole in the bag. Beavers were released at the site of capture after approximately 20 min. None of the animals were visibly harmed by the handling procedure, as they swam or dove away normally after being released and performed normal behaviour the following evening.

Scent donors and experimental design

We obtained castor sacs from 31 dead male beavers that were harvested by fur trappers in central New York (>150 km from HWF) during the regular trapping season (November 2003 – April 2004). We assumed all adults to be territorial residents, as trapping usually occurs in established colonies known to the trapper. Thus it seems unlikely that floater adults would have been represented in the sample. All castor sacs were frozen immediately after being removed from the dead beavers and were labeled with date of harvest, site of harvest, and mass of the beaver. We subsequently dissected the castor sacs with a surgical blade and scraped the castoreum (yellow–brown paste) out with a spatula. Each castoreum sample was preserved singly in a vial and kept frozen (–16 °C) until it was used in the experiments. Freezing and thawing is not expected to affect the potency of castoreum (Schulte 1998). We divided the 31 beavers into two groups: those obtained between November and January, before the breeding season, and those trapped in March and April, after the breeding season (Müller-Schwarze and Sun 2003). Because subadults are reproductively inactive, none of them would have been in breeding condition. To control for possible seasonal changes in castoreum composition (although castor sac size does not change seasonally; Bollinger et al. 1983; Rosell and Schulte 2004), we randomly formed adult (17.7–23.6 kg) – subadult (4.1–14.5 kg) pairs ($n = 13$) only within each of these two groups. Each pair consisted of two beavers that were obtained from two different colonies.

We used these castoreum samples in scent playback experiments to test the territory owners' abilities to discriminate between simulated adult and subadult intruders. The experiment was based on a two-sample choice test (Sun and Müller-Schwarze 1997). Wearing latex gloves, we constructed two experimental scent mounds (ESMs) consisting of mud and vegetation scraped from the pond or stream for each playback experiment. The ESMs were placed 30 cm from the water's edge and 40 cm apart (for an illustration see Sun and Müller-Schwarze 1997). We treated one ESM with 1 g (Müller-Schwarze et al. 1983) of castoreum from an adult male and the other ESM with 1 g of castoreum from a subadult male. The castoreum was placed inside a plastic bottle cap, which was inserted into the ESM, its open side level with the surface of the ESM (Rosell and Bjørkøyli 2002). We selected left and right positions at random to control for side preferences (White et al. 2003). Because beavers never respond to untreated mud piles, we did not include a blank control in the experimental design (Schulte et al. 1995b; Rosell et al. 2000). Since it is impossible to control which colony member will respond to an ESM,

we felt that it was more appropriate to test a given individual's response to both types of scent using a two-sample choice test as opposed to exposing different beavers sequentially to single ESMs (see Schulte 1998).

We set up the ESMs usually between 1600 and 1630, about 30–60 min before the beavers' late-afternoon activity period started, and ended the playbacks after a response was obtained or when fading daylight made observations impossible. The same observer (J.H.) carried out all observations from a position 10–15 m downwind to avoid being smelled by the beavers. We avoided pseudoreplication by allowing only one response towards each pair of castoreum samples and only one response per beaver (Kroodsma et al. 2001). To avoid having more than one beaver exposed to introduced scent per trial, we removed the ESMs as soon as one beaver had responded. This allowed us to obtain a response from a second beaver at the same colony during a subsequent observation period. All playbacks were carried out between June and August 2004, after the mating season (Müller-Schwarze and Sun 2003) and the seasonal peak in scent-mounding activity.

Response measures

Whenever a beaver detected the ESMs, we recorded the response using a digital camcorder (Optura Xi systems, Canon USA Inc., Lake Success, New York). We then transferred the recordings to a computer and timed individual behaviours with a behavioural analysis software package (The Observer[®], Noldus Information Technology, Wageningen, the Netherlands; Visser 1993).

For each response to an ESM, we recorded (*i*) the time spent sniffing the ESM on land within a distance of approximately 5 cm ("sniffing response"), (*ii*) the time spent physically interacting with the ESM ("physical response"), and (*iii*) the total time spent responding to the ESM ("total response") (Sun and Müller-Schwarze 1997). If a beaver did not respond to one of the ESMs ("null response"), the corresponding behaviours were recorded as lasting 0 s. There can be temporal overlap between the sniffing and physical responses. Usually a beaver starts sniffing the ESM and then starts touching the ESM with its front feet while it is still sniffing. Both behaviours were timed in their entirety, which is why total response can be shorter than sniffing and physical responses added together. The physical response can be subdivided into the following behaviours: (*i*) "pawing" the ESM with front feet, (*ii*) "straddling" the ESM with hind feet, and (*iii*) "overmarking" the ESM (presence of fresh castoreum odour, as determined by the observer) (Sun and Müller-Schwarze 1997). Because these behaviours do not always occur in a complete sequence, we used "response completeness" (number of behaviours shown, including sniffing and the components of the physical response) to measure response intensity (Sun and Müller-Schwarze 1997).

We did not record subsequent territorial behaviours such as scent mounding and patrolling because it would have been impossible to know which one of the two scents beavers were responding to after having returned to the water.

Data analysis

We tested the scent playback data for equal variances and normality using the Levene's and Anderson–Darling tests,

Table 1. Mean (\pm SE) beaver (*Castor canadensis*) response duration (s) to adult and subadult scent stimuli (castoreum) for both sexes combined and separate.

Response	Sex	Stimulus scent		Effect size	95% CI	n
		Adult	Subadult			
Sniffing	Combined	8.5 \pm 2.4	13.8 \pm 2.8	5.3 \pm 4.7	(-4.9, 15.5)	13
	Male	8.0 \pm 2.0	9.2 \pm 3.5	1.2 \pm 3.7	(-8.4, 10.7)	6
	Female	10.4 \pm 4.8	17.2 \pm 4.7	6.8 \pm 9.4	(-17.4, 31.1)	6
Physical	Combined	8.7 \pm 2.8	8.9 \pm 2.3	0.1 \pm 3.8	(-8.1, 8.3)	13
	Male	9.7 \pm 2.6	11.9 \pm 3.6	2.2 \pm 3.5	(-6.9, 11.2)	6
	Female	9.2 \pm 5.7	7.4 \pm 3.0	-1.9 \pm 7.7	(-21.7, 19.0)	6
Total	Combined	15.2 \pm 4.1	18.9 \pm 3.5	3.7 \pm 6.7	(-10.8, 18.2)	13
	Male	16.9 \pm 4.2	15.5 \pm 4.2	-1.4 \pm 5.5	(-15.6, 12.8)	6
	Female	16.1 \pm 7.7	22.1 \pm 6.5	6.1 \pm 13.6	(-28.9, 41.0)	6

Note: 95% confidence intervals (CI) are shown for the observed mean (\pm SE) effect sizes.

respectively. Based on the outcomes of these tests, we used paired *t* tests to compare response times (sniffing, physical, and total responses) and the sign test to compare response completeness towards adult and subadult ESMs (Sokal and Rohlf 1995). To aid the interpretation of nonsignificant results, we present 95% confidence intervals for the observed effect sizes (Colegrave and Ruxton 2003). All analyses were carried out for each sex separately and for both sexes combined. The results are presented as means \pm SE and all tests were two-tailed with a significance level of 0.05. We used Pearson's product moment correlation to determine whether the response time to an individual ESM correlated with the mass of the scent donor used to treat that ESM. For this analysis we excluded all ESMs that beavers did not respond to. We carried out all statistical analyses in MINITAB® version 14 (Minitab Inc. 2004).

Results

Adult versus subadult scent

We lumped responses of males and females together because a previous study (Rosell and Bjørkøyli 2002), as well as preliminary analysis of these results (Herr 2005), revealed no differences in response intensities between the two sexes. Beavers responded to both ESMs on six occasions, to adult scent only on two occasions, and to subadult scent only on five occasions. There was no significant difference between the time beavers spent sniffing adult scent and the time they spent sniffing subadult scent (paired *t* test: $t = -1.12$, $df = 12$, $P = 0.28$). Similarly, we found no significant difference in the duration of the physical response ($t = -0.04$, $df = 12$, $P = 0.97$) or the total response ($t = -0.56$, $df = 12$, $P = 0.58$) between the two types of castoreum. The 95% confidence intervals for the observed effect sizes were wide for all three response types (Table 1). There was also no evidence that beavers differed in their response completeness (sniffing, pawing, straddling) to castoreum from adult (1.8 ± 0.4) and subadult (2.0 ± 0.3) beavers (sign test: $n = 13$, $P = 1.00$). Incorporating overmarking (as perceived by the observer) into the response completeness did not change this outcome ($n = 12$, $P = 0.75$).

The average difference in body mass between scent donors within pairs was 8.7 ± 0.8 kg. We found no evidence that the mass of the scent donor influenced the way a beaver re-

sponded to that scent. Neither sniffing (Pearson's correlation: $r_p = -0.34$, $n = 19$, $P = 0.15$) nor physical ($r_p = 0.35$, $n = 19$, $P = 0.14$) or total response times ($r_p = 0.08$, $n = 19$, $P = 0.75$) correlated with the mass of the scent donor (Fig. 1).

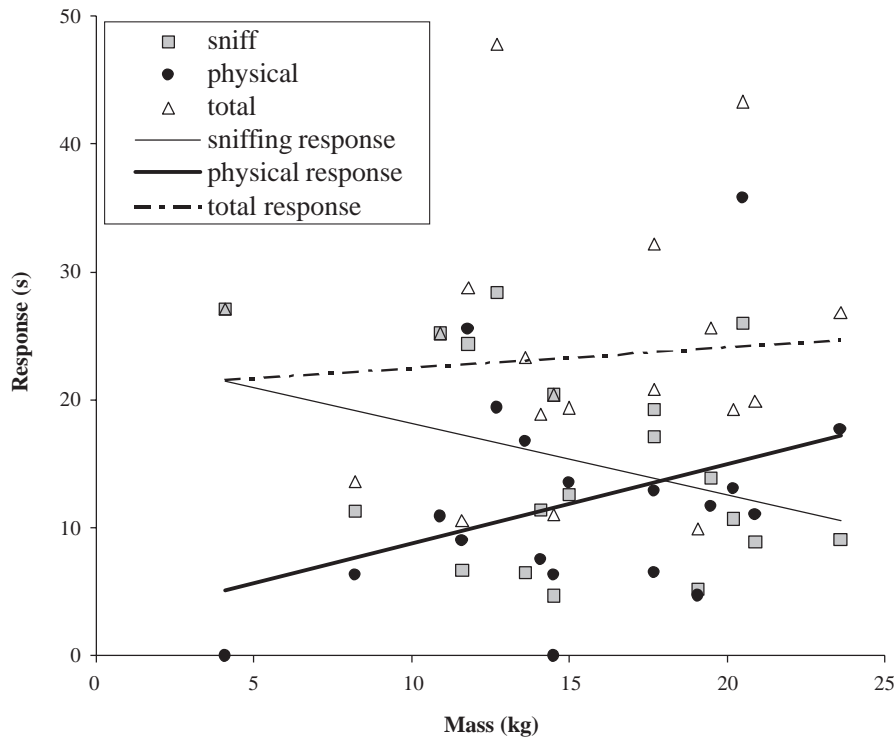
Sex-specific responses

Six males, six females, and one animal of unknown sex responded to the ESMs. Males did not differ in their sniffing (paired *t* test: $t = 0.32$, $df = 5$, $P = 0.76$), physical ($t = 0.61$, $df = 5$, $P = 0.57$), or total responses ($t = -0.25$, $df = 5$, $P = 0.81$) to adult and subadult scents (Table 1). Similarly, female beavers were not found to differ in their sniffing (paired *t* test: $t = 0.72$, $df = 5$, $P = 0.50$), physical ($t = -0.24$, $df = 5$, $P = 0.82$), or total responses ($t = 0.45$, $df = 5$, $P = 0.68$) to both types of scent (Table 1). The 95% confidence intervals were wider for females than for males (Table 1).

Discussion

Our results do not support our prediction that beavers would discriminate between scent from adult and subadult intruders by reacting more strongly to subadult scent. The small sample size, however, likely resulted in the large 95% confidence intervals for the observed effect sizes. However, Rosell and Bjørkøyli (2002) demonstrated discriminatory ability in beavers using the same behavioural categories with relatively low sample sizes ($n = 16$). Similarly, Sun and Müller-Schwarze (1997) found discrimination based on AGS ($n = 22$) but not castoreum ($n = 12$). Because mean values for the two main treatment groups are so close, it is unlikely that adding more tests would have changed the outcome. This leads us to believe that the lack of observable discrimination has a true biological basis and is not simply due to small sample size. Indeed, our results are comparable to Schulte's (1998) even though both studies used different experimental setups (i.e., simultaneous versus sequential stimuli) and recorded different behavioural variables. Thus, either all strange intruders are considered to be an equal threat and hence are treated similarly or castoreum does not contain reliable information on age, size, or dominance status of the signaler, so that an additional assessment strategy is needed. It is also conceivable that information extraction may be important for both scents but for different reasons. We found no consistent sex differences in the observed responses. This is in line with the majority of other beaver

Fig. 1. Correlations between beaver (*Castor canadensis*) response (sniffing, physical, and total) duration (s) to individual experimental scent mounds treated with castoreum and the mass (kg) of the castoreum donor.



studies (Hodgdon 1978; Svendsen and Huntsman 1988; Schulte 1998; Rosell and Bjørkøyli 2002; Thomsen 2002; Herr and Rosell 2004).

Strangers and neighbours

Temeles (1994) pointed out that strangers generally pose a higher threat to a resident than neighbours do because, unlike neighbours, strangers do not yet own a territory or a mate and hence would be more likely to attempt to take over the resident's territory. As a consequence, residents should respond more vigorously towards a stranger. Rosell and Bjørkøyli (2002) demonstrated this "dear enemy phenomenon" in the Eurasian beaver using adult scent stimuli only. Schulte (1993) hypothesized that in beavers, juvenile neighbours should be treated like strangers because they will also need to disperse and acquire a territory and a mate, which would make them a higher threat. In our study, all scent donors were caught outside the study area and hence were complete strangers to the responding beavers. Since it is not uncommon for adult beavers to go through a phase of secondary dispersal as adults (Sun et al. 2000), any intruding strange beaver, regardless of age or size, could be considered a potential threat and would likely be dealt with in the same way, especially if it left a scent mark in the resident's territory.

Direct assessment?

Another explanation for the lack of discrimination is that castoreum does not contain any information that would allow beavers to discriminate between individuals of different age, dominance status, or size. L. Sun (personal communication 2004) did not find any consistent age-related differences in the chemical profiles of castoreum, although he did not

test specifically for steroids. Age-related urine changes have, however, been shown in mice (*Mus musculus* L., 1758) (Osada et al. 2003) and deer mice (*Peromyscus maniculatus* (Wagner, 1845)) (Ma et al. 1999), while dominance-related changes are known from moose (*Alces alces* (L., 1758)) (Whittle et al. 2000), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) (Miller et al. 1998), and mice (Harvey et al. 1989; Novotny et al. 1990).

Although in our experiments we used castoreum rather than castor fluid, we do not think that this altered the outcome. In fact, Svendsen and Huntsman (1988) reported that beavers never responded to pure bladder urine, which suggests that beaver urine itself does not contain information responsible for triggering an overt territorial response. Thus, the territorial response would be stimulated by the castoreum contained in castor fluid rather than the urinary component itself. This is supported by Schulte (1998), who found no differences between the responses to dried castoreum and castor fluid. Johnston (2003) also pointed out that most rodents have discrete odour sources and that the signals can differ between these sources. Hence, rodents can obtain more subtle information by comparing scents from different odour sources. Consequently it is quite possible that castoreum alone does not provide beavers with a means to fully assess a competitor's competitive ability. Because AGS has been shown to code for individuality and kinship (Sun and Müller-Schwarze 1999), its potential function in age discrimination in conjunction with castoreum should also be investigated.

Scent matching

According to Gosling's (1982) scent matching hypothesis, it is sufficient for most scent-marking mammals to be able

to memorize the scent of a mark and then match that scent to the corresponding opponent when they meet. Assessment thus occurs during the actual encounter between two opponents rather than when the scent mark is first encountered (Gosling 1982), so intrinsic information on competitive ability in the scent mark is not necessary. Rosell and Bjørkøyli (2002) demonstrated that Eurasian beavers can indeed memorize previously encountered castoreum scent marks, and Sun and Müller-Schwarze (1998) found further evidence supporting the scent matching hypothesis in the North American beaver. Beavers often patrol their territory after having detected strange scent marks (Rosell et al. 2000; J. Herr, personal observation), which indicates that they are looking for the intruder and are making themselves available for scent matching (see Rosell 2002 for further discussion).

Conclusion

We conclude that there is no evidence that resident North American beavers discriminate between castoreum scent marks from adult and subadult strangers. We propose that the mechanism of scent matching is a more likely scenario than direct assessment based on the scent mark alone. To resolve this issue, the experiment described above should be performed using castor fluid and AGS from adult and subadult neighbours. This would allow us to determine whether age discrimination occurs when opponents are familiar individuals as opposed to strangers. Because experimental context can influence the outcome of experiments (Taylor and Dewsbury 1990), future studies should also control for the distance between the scent playback sites and the lodge or the border of the territory. Additionally, chemical analysis of the castoreum volatiles using a headspace technique, as described by Novotny et al. (1974), should be performed to reveal whether there are consistent differences in the volatile components of adult and subadult castoreum.

Acknowledgements

We thank the staff members and undergraduate and graduate students at the Adirondack Ecological Center for their help with live-trapping, and the trappers for providing us with castor sacs from dead beavers. J.H. was supported by an Alexander Wetland Research Award from the State University of New York College of Environmental Science and Forestry (SUNY ESF) and a Bourse de formation-recherche from the Ministère de la Culture, de l'Enseignement supérieur et de la Recherche (Luxembourg). Trapping licenses were issued by the New York State Department of Environmental Conservation and all procedures were reviewed by the Institutional Animal Care and Use Committee at SUNY ESF. L.C. Drickamer, R. Swaisgood, and an anonymous reviewer provided useful comments on an earlier draft of the manuscript.

References

Aleksiuk, M. 1968. Scent-mound communication, territoriality, and population regulation in beaver (*Castor canadensis* Kuhl). *J. Mammal.* **49**: 759–762.

Archer, J. 1988. *The behavioural biology of aggression*. Cambridge University Press, Cambridge.

Bollinger, K.S., Hodgdon, H.E., and Kennelly, J.J. 1983. Factors

affecting weight and volume of castor and anal glands of beaver (*Castor canadensis*). *Acta Zool. Fenn.* **174**: 115–116.

Bradbury, J.W., and Vehrencamp, S.L. 1998. *Principles of animal communication*. Sinauer, Sunderland, Mass.

Colegrave, N., and Ruxton, G.D. 2003. Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. *Behav. Ecol.* **14**: 446–447. doi:10.1093/beheco/14.3.446.

Fisher, J. 1954. Evolution and bird sociality. *In* *Evolution as a process*. Edited by J. Huxley, A.C. Hardy, and E.B. Ford. Allen & Unwin, London. pp. 71–83.

Godard, R., and Wiley, H. 1994. “Dear enemy” notes. *Nat. Hist.* **103**: 36–41.

Gorman, M.L. 1990. Scent marking strategies in mammals. *Rev. Suisse Zool.* **97**: 3–29.

Gosling, L.M. 1982. A reassessment of the function of scent marking in territories. *Z. Tierpsychol.* **2**: 89–118.

Harvey, S., Jemiolo, B., and Novotny, M. 1989. Pattern of volatile compounds in dominant and subordinate male mouse urine. *J. Chem. Ecol.* **15**: 2061–2072. doi:10.1007/BF01207438.

Herr, J. 2005. Chemical communication in a stable beaver (*Castor canadensis*) population. M.Sc. thesis, State University of New York College of Environmental Science and Forestry, Syracuse, N.Y.

Herr, J., and Rosell, F. 2004. Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*). *J. Zool.* **262**: 257–264.

Hodgdon, H.E. 1978. Social dynamics and behavior within an unexploited beaver (*Castor canadensis*) population. Ph.D. thesis, University of Massachusetts, Amherst, Mass.

Hurd, P.L., and Enquist, M. 2001. Threat displays in birds. *Can. J. Zool.* **79**: 931–942. doi:10.1139/cjz-79-6-931.

Hurst, J.L., Beynon, R.J., Humphries, R.E., Malone, N., Nevison, C.M., Payne, C.E., Robertson, D.H.L., and Veggerby, C. 2001. Information in scent signals of competitive social status: the interface between behaviour and chemistry. *In* *Chemical signals in vertebrates IX*. Edited by A. Marchlewska-Koj, J.J. Lepri, and D. Müller-Schwarze. Kluwer Academic / Plenum Publishers, New York. pp. 43–52.

Johnson, C.E. 1927. The beaver in the Adirondacks: its economics and natural history. *Roosevelt Wild Life Bull.* **4**: 501–641.

Johnston, R.E. 2003. Chemical communication in rodents: from pheromones to individual recognition. *J. Mammal.* **84**: 1141–1162. doi:10.1644/BLLe-010.

Kroodsmas, D.E., Byers, B.E., Goodale, E., Johnson, S., and Liu, W. 2001. Pseudoreplication in playback experiments, revisited a decade later. *Anim. Behav.* **61**: 1029–1033. doi:10.1006/anbe.2000.1676.

Ma, W., Wiesler, D., and Novotny, M. 1999. Urinary volatile profiles of the deer mouse (*Peromyscus maniculatus*) pertaining to gender and age. *J. Chem. Ecol.* **25**: 417–431. doi:10.1023/A:1020937400480.

Miller, K.V., Jemiolo, B., Gasset, J.W., Jelinek, I., Wiesler, D., and Novotny, M. 1998. Putative chemical signals from white-tailed deer (*Odocoileus virginianus*): social and seasonal effects on urinary volatile excretion in males. *J. Chem. Ecol.* **24**: 673–683. doi:10.1023/A:1022342219469.

Minitab Inc. 2004. MINITAB[®], release 14 for Windows [computer program]. Minitab Inc., State College, Pa.

Müller-Schwarze, D. 1992. Castoreum of beaver (*Castor canadensis*): function, chemistry and biological activity of its components. *In* *Chemical signals in vertebrates. VI*. Edited by R.L. Doty and D. Müller-Schwarze. Plenum Press, New York. pp. 457–464.

Müller-Schwarze, D., and Heckman, S. 1980. The social role of scent marking in beaver (*Castor canadensis*). *J. Chem. Ecol.* **6**: 81–95.

- Müller-Schwarze, D., and Houlihan, P.W. 1991. Pheromonal activity of single castoreum constituents in beaver, *Castor canadensis*. *J. Chem. Ecol.* **17**: 715–734.
- Müller-Schwarze, D., and Schulte, B.A. 1999. Behavioral and ecological characteristics of a “climax” population of beaver (*Castor canadensis*). In *Beaver protection, management, and utilization in Europe and North America*. Edited by P.E. Busher and R.M. Dzieciolowski. Kluwer Academic / Plenum Publishers, New York. pp. 161–177.
- Müller-Schwarze, D., and Sun, L. 2003. The beaver: natural history of a wetlands engineer. Cornell University Press, Ithaca, N.Y.
- Müller-Schwarze, D., Heckman, S., and Stagge, B. 1983. Behavior of free-ranging beaver (*Castor canadensis*) at scent marks. *Acta Zool. Fenn.* **174**: 111–113.
- Novak, M. 1987. Beaver. In *Wild furbearer management and conservation in North America*. Edited by M. Novak, J.A. Baker, M.E. Obbard, and B. Malloch. Ontario Trappers Association and Ontario Ministry of Natural Resources, Toronto, Ont. pp. 283–312.
- Novotny, M., Lee, M.L., and Bartle, K.D. 1974. Some analytical aspects of the chromatographic headspace concentration method using a porous polymer. *Chromatographia*, **7**: 333–338. doi:10.1007/BF02269346.
- Novotny, M., Harvey, S., and Jemiolo, B. 1990. Chemistry of male dominance in the house mouse, *Mus domesticus*. *Experientia (Basel)*, **46**: 109–113.
- Osada, K., Yamazaki, K., Curran, M., Bard, J., Smith, B.P.C., and Beauchamp, G.K. 2003. The scent of age. *Proc. R. Soc. Lond. B Biol. Sci.* **270**: 929–933.
- Osborn, D.J. 1955. Techniques for sexing beaver, *Castor canadensis*. *J. Mammal.* **36**: 141–142.
- Parker, G.A. 1974. Assessment strategy and evolution of fighting behaviour. *J. Theor. Biol.* **47**: 223–243. doi:10.1016/0022-5193(74)90111-8. PMID: 4477626.
- Peterson, A.M., Sun, L., and Rosell, F. 2005. Species and sub-species recognition in the North American beaver. In *Chemical signals in vertebrates. X*. Edited by R.T. Mason, L. McMaster, and D. Müller-Schwarze. Plenum Press, New York. pp. 56–63.
- Piechocki, R. 1977. Ökologische Todesursachenforschung am Elbebiber (*Castor fiber albicus*). *Beitr. Jagd-Wildforsch.* **10**: 332–341.
- Rosell, F. 2002. The function of scent marking in beaver (*Castor fiber*) territorial defence. Ph.D. thesis, Norwegian University of Science and Technology, Trondheim, Norway.
- Rosell, F., and Bjørkøyli, T. 2002. A test of the dear enemy phenomenon in the Eurasian beaver. *Anim. Behav.* **63**: 1073–1078. doi:10.1006/anbe.2002.3010.
- Rosell, F., and Nolet, B.A. 1997. Factors affecting scent-marking behavior in Eurasian beaver (*Castor fiber*). *J. Chem. Ecol.* **23**: 673–689. doi:10.1023/B:JOEC.0000006403.74674.8a.
- Rosell, F., and Schulte, B.A. 2004. Sexual dimorphism in the development of scent structures for the obligate monogamous Eurasian beaver (*Castor fiber*). *J. Mammal.* **85**: 1138–1144. doi:10.1644/BPR-106.1.
- Rosell, F., and Steifetten, Ø. 2004. Subspecies discrimination in the Scandinavian beaver (*Castor fiber*): combining behavioral and chemical evidence. *Can. J. Zool.* **82**: 902–909. doi:10.1139/z04-047.
- Rosell, F., and Sundsdal, L.J. 2001. Odorant source used in Eurasian beaver territory marking. *J. Chem. Ecol.* **27**: 2471–2491. doi:10.1023/A:1013627515232. PMID: 11789953.
- Rosell, F., Johansen, G., and Parker, H. 2000. Eurasian beavers (*Castor fiber*) behavioral response to simulated territorial intruders. *Can. J. Zool.* **78**: 931–935. doi:10.1139/cjz-78-6-931.
- Schulte, B.A. 1993. Chemical communication and ecology of the North American beaver (*Castor canadensis*). Ph.D. thesis, State University of New York College of Environmental Science and Forestry, Syracuse, N.Y.
- Schulte, B.A. 1998. Scent marking responses to male castor fluid by beavers. *J. Mammal.* **79**: 191–203.
- Schulte, B.A., and Rasmussen, L.E.L. 1999. Signal-receiver interplay in the communication of male condition by Asian elephants. *Anim. Behav.* **57**: 1265–1274. doi:10.1006/anbe.1999.1092. PMID: 10373260.
- Schulte, B.A., Müller-Schwarze, D., and Sun, L. 1995a. Using anal gland secretion to determine sex in beaver. *J. Wildl. Manage.* **59**: 614–618.
- Schulte, B.A., Müller-Schwarze, D., Tang, R., and Webster, F.X. 1995b. Bioactivity of beaver castoreum constituents using principal components analysis. *J. Chem. Ecol.* **21**: 941–957. doi:10.1007/BF02033800.
- Sokal, R.R., and Rohlf, F.J. 1995. *Biometry*. 3rd ed. W.H. Freeman and Co., New York.
- Sun, L., and Müller-Schwarze, D. 1997. Sibling recognition in the beaver: a field test for phenotype matching. *Anim. Behav.* **54**: 493–502. doi:10.1006/anbe.1996.0440. PMID: 9299035.
- Sun, L., and Müller-Schwarze, D. 1998. Beaver response to recurrent alien scents: scent fence or scent match? *Anim. Behav.* **55**: 1529–1536. doi:10.1006/anbe.1997.0709. PMID: 9641998.
- Sun, L., and Müller-Schwarze, D. 1999. Chemical signals in beaver — one species, two secretions, many functions? In *Advances in chemical signals in vertebrates. VIII*. Edited by R.E. Johnston, D. Müller-Schwarze, and P.W. Sorensen. pp. 281–288. Kluwer Academic / Plenum Publishers, New York.
- Sun, L., Müller-Schwarze, D., and Schulte, B.A. 2000. Dispersal pattern and effective population size of the beaver. *Can. J. Zool.* **78**: 393–398. doi:10.1139/cjz-78-3-393.
- Svendsen, G.E. 1980. Patterns of scent-mounding in a population of beaver (*Castor canadensis*). *J. Chem. Ecol.* **6**: 133–147. doi:10.1007/BF00987533.
- Svendsen, G.E., and Huntsman, W.D. 1988. A field bioassay of beaver castoreum and some of its components. *Am. Midl. Nat.* **120**: 144–149.
- Taylor, S.A., and Dewsbury, D.A. 1990. Male preferences for females of different reproductive conditions: a critical review. In *Chemical signals in vertebrates. V*. Edited by D.W. MacDonald, D. Müller-Schwarze, and S.E. Natynczuk. pp. 184–198. Oxford University Press, Oxford.
- Temeles, E.J. 1994. The role of neighbours in territorial systems: when are they ‘dear enemies’? *Anim. Behav.* **47**: 339–350. doi:10.1006/anbe.1994.1047.
- Thomsen, L. 2002. Sex difference in scent marking in a monogamous mammal, the Eurasian beaver (*Castor fiber*). M.Sc. thesis, University of Aarhus, Aarhus, Denmark.
- Visser, M.E. 1993. The Observer, a software package for behavioural observations. *Anim. Behav.* **45**: 1045. doi:10.1006/anbe.1993.1127.
- Walro, J.M., and Svendsen, G.E. 1982. Castor sacs and anal glands of the North American beaver (*Castor canadensis*): their histology, development, and relationship to scent communication. *J. Chem. Ecol.* **8**: 809–819. doi:10.1007/BF00994781.
- White, A.M., Swaisgood, R.R., and Zhang, H. 2003. Chemical communication in the giant panda (*Ailuropoda melanoleuca*): the role of age in the signaller and assessor. *J. Zool.* **259**: 171–178.
- Whittle, C.L., Bowyer, R.T., Clausen, T.P., and Duffy, L.K. 2000. Putative pheromones in urine of rutting male moose (*Alces alces*): evolution of honest advertisement? *J. Chem. Ecol.* **26**: 2747–2762. doi:10.1023/A:1026485725805.
- Williams, C.L., Breck, S.W., and Baker, B.W. 2004. Genetic meth-

- ods improve accuracy of gender determination in beavers. *J. Mammal.* **85**: 1145–1148. doi:10.1644/BPR-104.1.
- Ydenberg, R.C., Giraldeau, L.A., and Falls, J.B. 1988. Neighbours, strangers, and the asymmetric war of attrition. *Anim. Behav.* **36**: 343–347.
- Zahavi, A. 1993. The fallacy of conventional signalling. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **340**: 227–230. PMID: 8101657.