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SHORT COMMUNICATION

Tool-use in a display behaviour by Eurasian beavers (*Castor fiber*)

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Abstract Tool use is rare amongst rodents and has never been recorded in connection with agonistic displays. We witnessed a behaviour, stick display (StD), involving tool use in free-living Eurasian beavers (*Castor fiber*) that we conclude is a display behaviour. Two beavers were the main performers of the signal that was observed in at least six beavers from three families. Beavers reacted to displays by increased evasive and agonistic behaviours compared with their usual behavioural patterns when at territory borders. The behaviour was almost exclusively seen between rivals at territory borders. We suggest that the display is used in agonistic encounters, mainly in a territorial context.

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Introduction

Tool use is defined by Beck (1980) as ''the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool''.

Tools are used by non-human animals mainly as a means to obtain food (Beck 1980), but also seen in agonistic displays in for instance apes (Tuttle 1986) and elephants (Chevalier-Skolnikoff and Liska 1993). Though tool use by rodents has been recorded in four species (Beck 1980; Shuster and Sherman 1998), there have been no reports of rodents using tools in displays. Here, we describe a previously unrecorded behaviour in Eurasian beavers (*Castor fiber*) involving tool use in a display that we propose is linked to the intimidation of potential rivals.

The display which we named 'stick display' (StD) is a display where a beaver picks up an object (a stick if available), rises up on its hind legs, and moves its upper body rapidly up and down while holding the object with mouth and forepaws (Fig. 1, and see video clip S1). Beavers were only witnessed picking up tools (usually sticks) from the same location they were used and no modification of tools was seen. When doing StD the beaver will often be situated in shallow water and thus the movement of the stick will create some splashing of the surrounding water. Displays on land or with short objects (e.g. weeds) have been witnessed with no significant sound produced. Thus, we assume StD is primarily a visual signal based on

Fig. 1 Beaver performing stick display at a territory border (Photo by O. Bozsér)

movements and possibly an auditory signal whenever the display causes splashing of water. However, the sound of StD would not carry very far compared to tail slapping (another signalling behaviour, see below).

Eurasian beavers live in family groups with a dominant breeding pair and offspring of various ages (Wilsson 1971; Nolet and Rosell 1994). Each beaver family occupies and defends a territory by scent marking, primarily at territorial borders (Rosell 2002). Communication by Eurasian beavers is based on olfactory signals (scent marking), sounds (tail-slapping and vocalisation) and touch (nose-to-nose contact, mutual grooming, wrestling and fights) whereas visual signals seemed to play a minor role (Wilsson 1971). Of the above only scent marking, tail-slapping and fights are seen during interactions between extra-familial rivals. When scent marking a beaver makes distinct movements with its body (Wilsson 1971). This may be perceived by a nearby rival, however, scent marks are deposited regardless as to whether a rival is around since its main funtion is the olfactory defence of the territory. Slapping of the tail hard against the water's surface is used as a warning signal to alert family members and could be used to convey that the signaller has noticed a would-be predator or a rivalling beaver (Wilsson 1971). Tail slaps can be heard from a distance of several hundred metres (personal observation). Fights between rivalling beavers do occur, but are relatively infrequent when compared with non-physical aggression (personal observation).

Methods

During field studies in two consecutive years (2000 and 2001) observational studies of 28 Eurasian beavers from 11 family groups was conducted in southeast Telemark, Norway (see Sharpe and Rosell 2003 for methodologies). Focal animal sampling (Martin and Bateson 1999) was used on animals fitted with radio-transmitters and a single beaver visually followed each observation night. When visual contact was lost radio-transmitters could be used to locate the animal again. Spotlights were used during dark periods. We first observed StD during these field studies and not knowing what it was, decided to record each occurrence whether performed by our study subject or another animal in sight. Signallers and receivers were identified where possible from coloured ear tags and/or radio signals. Position and time were also recorded. Behaviour preceeding and following StD was noted if possible.

We defined instances of StD as one StD bout if the behaviour would continue within one minute and/or would not be interrupted by another behaviour. Most bouts would last no longer than 10–15 s. But some would last for several minutes. Exact timings were not possible to ascertain under field conditions.

To analyse whether StD would have any effect on the receiver, we categorised the general behaviour of receivers when near territory borders into three groups; *agonistic*—scent marking, wrestling, tail slapping, fighting and other agonistic interaction; *neutral*—grooming, foraging, walking, sniffing, social behaviours such as allogrooming, brief visit to bank and standing still; *evasive*—diving, running, and alert. Receiver behaviour was recorded as the behaviour immediately following the exposure to StD. We excluded all swimming behaviours from our analysis since it is usually difficult to classify and may cover several categories. StD was also omitted as including it in one of the categories would presuppose its function. We only used observations from radio-tagged (tracked) animals for statistical analysis of receiver behaviour since behaviours by other animals outside these chance observations of StD events were unknown.

To investigate any seasonal difference that may have been due to reproductive behaviour, we divided our data into two periods: spring (March–May) and summer (June–August). Parturition usually takes place around June 1st, and was therefore chosen as the division date (Wilsson 1971; Rosell unpublished data).

Results

During 175 nights of observation of 28 beavers, StD was recorded 131 times by four adult males, two adult females plus five unidentified animals (Table 1). The beavers came from two adjacent territories in the Lunde River except for one male from Gvarv River. The two rivers are 8 km apart (straight line distance) and both empty into the same lake (lake Nordsjø). Recording of StD were ad libitum and thus observations may be skewed in favour of the animals that

Table 1 Senders and recievers of stick display

Sender[a] status territory	No. of stick displays total[b]	No. nights tracked[c]	No. of stick displays during tracking[d]	Stick display per tracking night[e]	Receivers[f]
Birgit f/ad/dom L2a	68	12.5 (8.5/4)	41 (35/6)	3.3 (4.1/1.5)	4 × **Ørjan** (1)
					2 × **Adrian** (m/subad/subdom, L2a)
					7 × Frode (2)
					2 × Asle (1)
					2 × Margit/Asle
					9 × Unidentified
					42 × None
Ørjan m/ad/dom L2a	6	11 (7/4)	5 (5/0)	0.5 (0.71/0)	1 × **Birgit** (1)
					2 × Frode
					2 × Unidentified (1)
					1 × None
Frode m/ad/dom L2b	47	11 (8/3)	38 (33/5)	3.5 (4.2/1.7)	10 × Birgit (2)
					6 × Ørjan (1)
					2 × Birgit/Ørjan
					2 × Grønn (m/ad/dom, L3)
					8 × Unidentified
					19 × None
Margit f/ad/subdom L2b	1	NT	NT	NT	1 × None
Asle m/ad/subdom L2b	3	NT	NT	NT	2 × Birgit
					1 × Birgit/Ørjan
Unidentified L2b	5	NT	NT	NT	5 × Ørjan (1)
Marcus m/ad/dom Evju	1	3 (2/1)	1 (0/1)	1.0 (0/1.0)	1 × Observers[g]

Status and territory of senders, number of displays, status and territory of receivers and number of times received

[a] Tracked animals marked with bold text. *m* male, *f* female; *ad* adult (>3 years), *subad* subadult (2–3 years), *dom* dominant, *sub* subdominant. Territory L2a, L2b and L3 are in the Lunde river and Evju is in the Gvarv river

[b] Total number of stick displays recorded by each beaver (including observations while tracking other animals)

[c] Number of nights tracked. Numbers in brackets show tracking nights in spring (March–May) and summer (June–August). *NT* the beaver was not tracked

[d] Number of stick displays recorded whilst the beaver was being tracked. Numbers in brackets show number of stick displays in spring (March–May) and summer (June–August). *NT* the beaver was not tracked

[e] Figures based on number of stick displays recorded while the focal animal was tracked divided by number of nights tracked. Numbers in brackets show average display rate in spring (March–May) and summer (June–August). *NT* the beaver was not tracked

[f] Number of times a particular beaver was receiver of the display made by the particular sender. Family members of sender denoted with bold text. Abbreviations see[a]. Numbers in brackets are number of times the receiver's reaction to stick display would be to display in return

[g] Animal displayed at two human observers

were tracked. It was clear from our observations that one female (Birgit) and one male (Frode) were the main performers with a contribution of 51.9 and 35.9%, respectively to the total number of StD's observed (Table 1). Only six displays were seen by the mate of Birgit (Ørjan) and none seen by the mate of Frode (not figured in the table) even though they were also tracked. Average displays per night were 3.3 and 3.5 for the main performers, in contrast to 1.0 and 0.5 by the other two beavers tracked. When examining seasonal difference we found a higher display rate during spring than summer (Table 1). However, it must be stressed that there were not many tracking nights after 1st of June.

StD was not sex-specific, both sexes displayed intra- and inter-sexually (Table 1). StD was almost exclusively seen at borders (97.7%) and only outside the border zone (defined as 100 m bank length on both riversides at shared borders) when directed at family members. Behaviour preceding StD was dominated by scent marking (34.7%) and StD (33.7%). Other behaviours were swim (16.3%), alert (5.1%), forage (4.1%), social interaction (3.1%) and other (3.1%). Behaviour following StD was also dominated by scent marking (37.9%) and StD (26.7%). Other behaviours were swim (17.2%), forage (9.5%), alert (3.4%), social interaction (2.6%) and other (2.6%). In total 48.4% of all stick displays were in

direct connection with scent marking. Outside the lodge, beaver behaviour in our study site normally tend to be dominated by foraging and swimming (Sharpe and Rosell 2003).

Identified receivers were most often from adjacent territories except for seven incidents (14.0%) where a beaver from the L2a-territory would display at a family member (Table 1). Often no receiver could be seen (48.9%). A receiver might have been present, but not in view of the human observers. Alternatively, StD may have functioned as an auditory signal even though tail slaps would be heard a lot further. Beaver eye-sight is quite poor, thus if a receiver was indeed not present within visible or audible reach, the beaver may have reacted to the smell of rivalling beavers from, for instance, scent marks at the border and this could have elicited the display.

Out of all StD incidences that involved a receiver, the receiver was seen responding to StD with StD ten times (14.4%)—of these three were double replies; i.e. one animal displayed StD, the other replied with StD and the first animal displayed again. Receivers responded to StD with a variety of non-StD behaviours, which we categorised into agonistic, evasive, and neutral (see Methods). We compared allocation to each category under three exclusive scenarios (1) no other beaver or only family present ($N = 159$), (2) a beaver from another territory present ($N = 878$), and (3) reaction to StD ($N = 23$). Receiver identity was entered as a categorical predictor in the analyses (see below). We combined scenarios involving the presence of family members at the border and no animals at the border since they can both be seen as non-territorial situations and were not different from each other in terms of the proportion of behaviours allocated to each category (SAS CATMOD log linear model, $X_2^2 = 5.01$, $df = 2$, $P = 0.08$). Allocation to evasive and agonistic behaviours were significantly higher under scenario three, than under other scenarios ($X_2^2 = 13.93$, $df = 4$, $P = 0.007$) There was no evidence that the pattern differed among animals ($X_2^2 = 5.51$, $df = 12$, $P = 0.939$). Scenarios one and two did not differ significantly ($X_2^2 = 0.10$, $df = 2$, $P = 0.952$). It thus seems that StD influences the behaviour of a receiver whereas the simple presence of a competitor does not.

Personal communications with other beaver researchers in Europe ($N = 12$) and North America ($N = 7$) revealed only one behaviour resembling StD. This behaviour had been witnessed three times at two different sites with North American beavers (*C. canadensis*) in the Kouchibouguac National Park, New Brunswick, Canada (L. Léger personal communication). The beavers bobbed their front body at human observers, but without holding anything in their mouths, except for one male who was lodge-building and held a branch in his mouth.

Discussion

It is clear that StD is a case of tool use as defined by Beck (1980). Our results suggest that StD has an effect on the behaviour of receivers, and so may function as a signal. This hypothesis is supported by the structure of the behaviour in that it consists of vigorous stereotyped movements which are often associated with displays (Guilford and Dawkins 1991). However, the nature of the signal and the reasons this behaviour may have arisen in our study population require further discussion.

To interpret the nature of a display one can look at the situation under which it occurs to obtain information on the motivational state of the performer (MacFarland 1993). StD almost exclusively occurred at borders and was mainly directed at potential rivals. This strongly suggests that it is a signal used in agonistic conflict. Another factor to examine is the behaviour preceding or following a signal (MacFarland 1993). In our case this was often scent marking, which has a strong territorial function (Rosell et al. 1998). This too supports the notion that StD is a signal playing a role in agonistic encounters and delimiting territories.

StD has not been recorded in the extensive literature on beavers, including many visual observations, and thus it seems that StD is either a behaviour that beavers rarely exhibit or a behaviour specific to certain populations. Indeed, if StD had not been observed in two separate locations in our study site, we might have concluded that the behaviour was an idiosyncratic individual discovery that spread to neighbours through some form of social learning. A behaviour resembling StD was witnessed a few times in a population of North American beavers. However, currently there is not enough information to ascertian whether this behaviour could be classified as StD.

In our study population there appeared to be an ongoing territorial dispute between the families with the most active StD performers (L2a and L2b). Occupied lodges were within 100 m of the shared border, which resulted in more interaction at this border than at other borders in the study area. By far the highest scent marking rates were seen by animals from these two territories and there was a minor movement of the border between 2000 and 2001 (Rosell and Thomsen 2006). No other territory border in our study area exhibited measurable changes over this period. It seems likely that members of the two territories were under unusual pressure to defend their territory. The beaver from Evju, on the Gvarv River (Table 1) had recently lost his mate and could be expected to be under pressure as the sole defender of his territory. He himself died a few weeks later and thus no more data was available. StD might only be triggered under high-pressure situations, but without detailed information about territorial interactions (e.g. border

disputes) from other beaver populations, we cannot conclude that beavers in our study population were under greater territorial pressure than other populations. A higher rate of StD in spring might indicate that breeding influences this behaviour, perhaps due to allocation of time from territorial defense to care of offspring, but more data is needed to make any conclusions.

Apart from incidences involving StD, scent marking in the presence of a rival was rarely seen (total study area $N = 6$). Since StD was often interspersed with scent marking one might speculate that receivers responded to scent marking instead of StD. The response to scent marking would be to swim away or to stay alert until the scent marking beaver or the receiver swims off. This indicates that scent marks alone may elicit evasive responses in contrast to the prevalence of agonistic responses associated with StD (Fig. 2).

The apparent absence of receivers in almost half the cases of StD could be considered as evidence against StD being a genuine signal. However, even though beavers have poor eyesight, the signal might attract the attention of conspecifics further away because of the rapid movements. Additionally, the sound of splashing water often associated with the signal could carry sound beyond the visual range. Whether beavers react to the sound of splashing water associated with StD remains to be tested.

Because of the recent discovery of the StD behaviour, it is as yet too early to assess what adaptive benefits, if any, it may have. Threat signals are designed to transmit information about the sender's physical condition, e.g. size or strength (Bradbury and Vehrencamp 1998). Displaying costs the sender energy and can thus be a reliable indication of an animal's strength (e.g. Perry et al. 2003). This in turn means a threat signal can be an honest signal in the sense of Zahavi's handicap principle (Zahavi 1977; Zahavi and Zahavi 1997) preventing conflicts from escalating into fights. The beaver StD may be a better indicator of strength than the information contained in the scent marks and could thus reduce physical conflict with rivals (sensu Krebs and Dawkins 1984).

In summary, StD is an example of a display using object manipulation that can be considered as tool-use. The Eurasian beaver is the first rodent recorded to use a tool in a display. Further observation of this unique behaviour could shed light on its ontogeny and adaptive benefits in the social organisation of beavers.

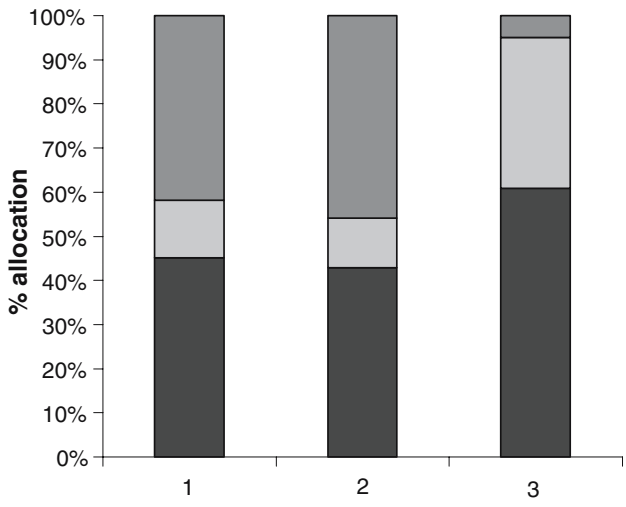

Fig. 2 *Histogram* showing allocation of receiver behaviours to categories—agonistic (*black*), evasive (*light grey*), and neutral (*dark grey*) under 3 scenarios: (1) no other beaver or only family present, $N = 159$, (2) a beaver from another territory present, $N = 878$, and (3) reaction to stick display, $N = 23$

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