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Scent marking intensity of beaver (*Castor fiber*) along rivers of different sizes

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Abstract

The intensity of scent marking by territorial beavers could relate to different numbers of transient beavers. Rivers are, most likely, the main paths of beaver dispersal. It is supposed that the intensity of subadult migration depends upon the size of the river because those basins of larger rivers potentially contain a greater number of beavers. Scent marking intensity (the number of scent mounds) and relative abundance (number of beaver activity signs) of beavers were studied in 18 segments of various rivers in Lithuania during the period of subadult dispersal during April and the first ten days of May. The total length of transect was 157 km. The yield of water (Q) of these river segments varied from 0.4 to 32.2 m^3/s.

The Lithuanian beaver population is considered abundant. Even the smallest peripheral water bodies are densely inhabited by beavers, thus making the dispersal of population surplus rather complicated. The highest scent marking intensity (1.78 scent mounds per 0.25 km of shore line) was found in medium-sized rivers (mean $Q = 4.6$ m^3/s), and the lowest (0.64 scent mounds per 0.25 km of shore line) in the smallest rivers (mean $Q = 0.6$ m^3/s). Scent marking intensity was significantly positively correlated with the relative abundance in most rivers, excluding the smallest ones. The results are discussed in relation to an appropriate response of territory owners to the different intensity of subadult migration in rivers of differing sizes. The scent mound system seems to be an important mechanism of population self-regulation, preventing an overexploitation of ecological resources in rivers where intensive migration of beavers occurs.

Key words: *Castor fiber*, scent marking intensity, rivers, Lithuania

Introduction

Beavers (*Castor fiber* and *C. canadensis*) occupy family territories along the shore line and live at the same sites for a long periods of time. Being sedentary animals, beavers defend their family territories from conspecific intruders by exhibiting aggressive behaviour against strangers (Djakov 1975). An important tool of the territory defence seems to be the scent markings (Rosell and Nolet 1997; Rosell et al. 1998). It was hypothesised that seasonal peaks of scent marking activity could be a response related to the increased stream of transient subadults in spring (Müller-Schwarze and Heckman 1980; Rosell and Nolet 1997), and the scent mound system serves as an important mechanism of population self-regulation (Aleksiuk 1968).

Following natural immigration and reintroduction at the beginning of the 1940s to 1967, the expansion stage of the beaver population in Lithuania came to a conclusion in about 1975. During the last few decades, the density of the Lithuanian beaver population

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has been quite high. The average linear density is very similar in different types of water bodies, varying from 0.8 sites/km of river-bed in natural rivers to 1.1 sites/km in suitable canals. Even the smallest peripheral water bodies, such as small streams and small swamps, are densely inhabited by beavers (Ulevičius 1999). From this it may be predicted that the dispersal of subadults would be rather complicated. It is supposed that the intensity of subadult migration depends on the river size. The larger river basins potentially contain more beaver groups, thus producing more young animals.

The aim of this study was to investigate beaver scent marking intensity along rivers of differing sizes during the period of subadult dispersal (from April to the beginning of May) in an abundant population.

Material and methods

The investigated river segments are situated between 22°15′–25°45′ E and 54°10′–55°40′ N in the Middle and Lower Nemunas Basin (Fig. 1). This basin covers approximately 70% of the whole territory of Lithuania. The density of the hydrographical network including artificial canals varies from 0.7 to 1.4 km/km^2. With respect to total length of the hydrographical network, the smallest streams (of up to 10 km long) account for about 70%. The proportion of artificial canals (from land reclaimation) varies from approximately 40 to 85%.

In April and the first ten days of May 1991–1993, 157 km of shore line transects were investigated in 18 river segments, and these divided into 628 cut-offs (length – 0.25 km). The length of the river segments investigated varied from 5.0 to 15.5 km. Only one river bank was studied. 0.25 km was the shortest distance of shore line which could be geographically restricted without a significant error occurring in its length using timing (within 1 minute) and mapping of each beaver sign found during the field work. Maps of 1 : 50 000 scale were used.

River segments were clustered according to their average water yield. Four clusters of different river sizes were distinguished (Tab. 1). The water yield of the smallest river segments (I cluster) varied from 0.4–0.9 m^3/s, the II cluster from 1.9–2.8 m^3/s, the III cluster from 4.2–5.0 m^3/s, and the IV cluster from 14.8–32.2 m^3/s. The yield of water was estimated using the Lithuanian river cadastre (Jablonskis and Lasinskas 1962).

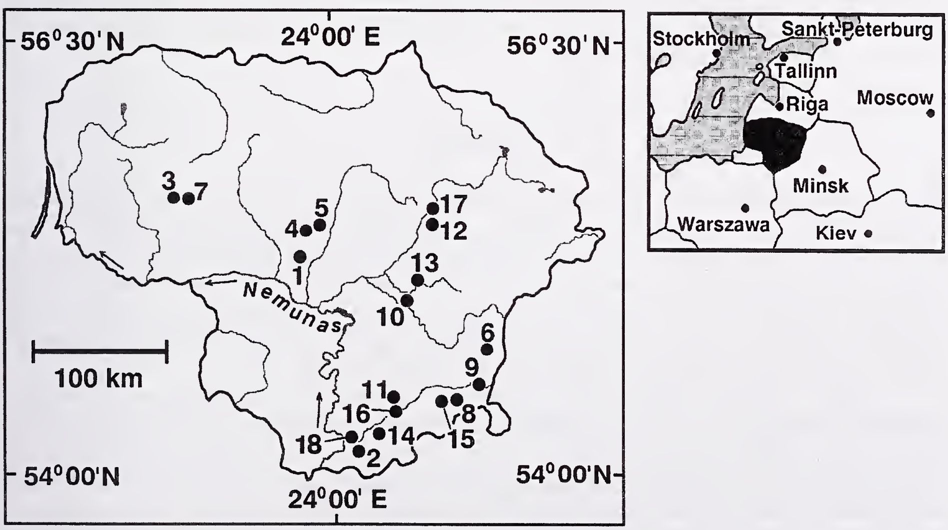

Fig. 1. Study area. The numbers of samples as in table 1.

Table 1. Characteristics and clustering of the river segments investigated

Cluster	No	River	Water yield, m^3/s	Length of segment, km	No of cut-offs
I	1	Aluona	0.4	5.0	20
	2	Skroblus	0.4	6.0	24
	3	Ašvija	0.5	5.0	20
	4	Jaugila	0.7	5.0	20
	5	Dotnuvėlė	0.8	5.5	22
	6	Kena	0.8	11.5	46
	7	Akmena	0.9	4.0	16
Total and average for cluster I			0.6	42.0	168
II	8	Visinčia	1.9	8.5	36
	9	Upper Merkys	2.6	15.5	62
	10	Musė	2.8	6.0	24
	11	Varėnė	2.8	9.0	36
Total and average for cluster II			2.5	39.0	156
III	12	Virinta	4.2	7.5	30
	13	Širvinta	4.3	7.5	30
	14	Ūla	4.8	12.0	48
	15	Šalčia	5.0	8.0	32
Total and average for cluster III			4.6	35.0	140
IV	16	Middle Merkys	18.5	21.0	84
	17	Šventoji	30.0	9.0	36
	18	Lower Merkys	32.2	11.0	44
Total and average for cluster IV			23.9	41.0	164

The number of beaver scent mounds (freshly made, with characteristic odour or without) as well as of other signs of beaver activity (tracks, trails, feeding places) were registered in each 0.25 km cut-off of shore line within an approximately 10 m wide zone from water edge. Two indices – the scent marking intensity (the number of scent mounds per 0.25 km) and relative abundance of beavers (expressed as the number of beaver activity signs except scent mounds per 0.25 km) were analysed. The relation between the scent marking intensity and the relative abundance was investigated using regression analysis. The significance of differences among river clusters was tested using the ANOVA and t-tests with a 5% level of significance.

Results

There was a significant difference in the scent marking intensity between each of the four river clusters (ANOVA test, $\chi^2 = 47.91$, df = 3, $p < 0.000$). It consecutively increased from the smallest rivers (cluster I, 0.6 scent mound/0.25 km) to the medium-sized rivers (cluster III, 1.8 scent mound/0.25 km) (t-test, t = 6.28, df = 307, $p < 0.000$), and then decreased again in the large rivers (cluster IV, 1.0 scent mound/0.25 km) (t-test, t = 3.58, df = 303, $p < 0.000$) (Tabs. 2, 3). The smallest rivers (I cluster) exhibited the most distinct difference in the scent marking intensity compared to the other clusters.

A slightly different pattern was discovered concerning the differences in relative abundance among river clusters (Tabs. 2, 3). Despite statistically significant differences between each of the clusters (ANOVA test, $\chi^2 = 43.41$, df = 3, $p < 0.000$), there was no obvious tendency of increase from cluster I to III. The highest relative abundance was established in the medium-sized rivers (cluster III, 4.8 sign/0.25 km). However, the smallest rivers (cluster I) also exhibited high relative abundance (3.5 sign/0.25 km). The difference between these two clusters was significant (t-test, t = 2.65, df = 307, $p < 0.008$), but lower than in the case of the scent marking intensity. The lowest level of relative abundance was found in the large rivers (cluster IV, 2.4 sign/0.25 km), followed by the small rivers (cluster II, 2.6 sign/0.25 km), and there was no significant difference between these two clusters (t-test, $t = 0.79$, $df = 318$, $p < 0.429$). A significant positive correlation between the scent marking intensity and the relative abundance was established by analysing averages

Table 2. Scent marking intensity (mean number of scent mounds/0.25 km) and relative abundance (mean number of other signs of beaver activity except scent mounds/0.25 km) in clusters of rivers of differing sizes

Cluster of rivers	Mean Q, m^3/s	n	Scent marking intensity, $x \pm SE$	Relative abudance, $x \pm SE$
I	0.6	168	0.6 ± 0.088	3.5 ± 0.320
II	2.5	156	1.3 ± 0.166	2.6 ± 0.226
III	4.6	140	1.8 ± 0.167	4.8 ± 0.364
IV	23.9	164	1.0 ± 0.128	2.4 ± 0.210

Table 3. Matrix of significance of differences in scent marking intensity (top right) and relative abundance (bottom left) between pairwise compared river clusters (t; p); df varies from 295 to 330

River clusters	I	II	III	IV
I		3.53; 0.000	6.28; 0.000	2.53; 0.012
II	2.24; 0.026		2.06; 0.040	1.24; 0.217
III	2.65; 0.008	5.17; 0.000		3.58; 0.000
IV	2.94; 0.003	0.79; 0.429	5.93; 0.000	

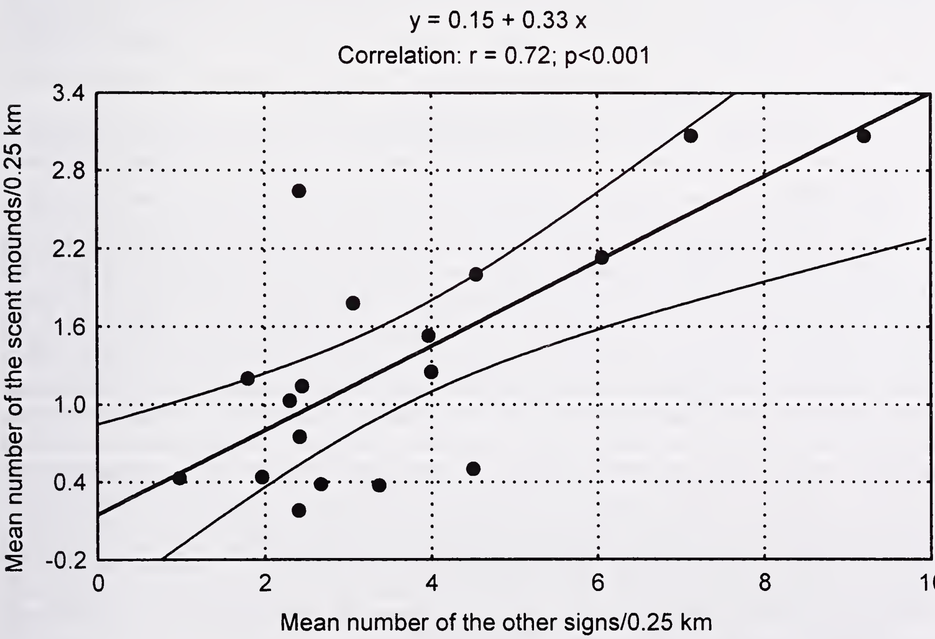

Fig. 2. Relation between the scent marking intensity (y) and the relative abundance (x) of beaver in all the river segments investigated.

Table 4. Correlation between the scent marking intensity and relative abundance per 0.25 km in separate clusters of rivers of different size

Cluster of rivers	Mean Q, m^3/s	n	Coefficient of correlation, r	p<
I	0.6	168	0.02	0.767
II	2.5	156	0.35	0.001
III	4.6	140	0.41	0.001
IV	23.9	164	0.48	0.001

of these indices in the river segments investigated ($r = 0.72$, $p < 0.001$) (Fig. 2). However, some specifities in this relation in separate river clusters were found (Tab. 4). The absolute numbers of the scent mounds and the other signs in 0.25 km cut-offs mostly correlated in the larger rivers (cluster IV, $r = 0.48$; $p < 0.001$). The coefficient of correlation decreased slightly from the large (IV cluster) to small rivers (II cluster), and there was no correlation in the smallest rivers (I cluster, $r = 0.02$; $p < 0.767$).

Discussion

Scent marks are generally considered multifunctional signals (Gosling 1982 for review; Hodgdon and Lancia 1983; Djozhkin et al. 1986; Benhamou 1989). However, one of the most important functions of scent marking is a territory occupancy indication to potential intruders (Gosling 1982; Gosling and Wright 1994; Rosell and Nolet 1997; Rosell et al. 1998). Beavers display very strong and consistent responses to strange scent marks in free-ranging colonies (Müller-Schwarze and Heckman 1980; Müller-Schwarze et al. 1983; Müller-Schwarze and Houlihan 1991; Sun and Müller-Schwarze 1997). In captivity, on the contrary, scent marking activity can be very low, and this can be explained by an absence of motivation (Nitsche 1987). Migrating beavers avoid occupied territories (Aleksiuk 1968). In dense beaver populations, however, the dispersing young very often suffer in encounters with territory owners (Kudriashov 1975).

Scent marking patterns discovered in abundant beaver populations could be explained as a response of territory owners to the differing numbers of transient subadults in rivers of different sizes.

In the smallest rivers, despite high relative abundance, beavers scent marked at relatively low levels. The relatively high isolation of the beaver sites in small streams could be one of the explanations of this phenomenon. The absence of correlation between the scent marking intensity and the relative abundance in small streams also suggests possibly low need for territorial defence. Along the smallest rivers, beaver sites are more isolated from each other and more compactly situated than at the larger streams (Djakov 1975). It has been found in Canadian beaver, that the higher scent marking activity was characteristic for the less isolated beaver families (Butler and Butler 1979; Svendsen 1980). Shallow water and narrow water ways can substantially limit the possibilities of beaver migration. Also, numerous beaver dams in separate sites might be an important impediment for strangers, because dams are intensively controlled by territory owners (Brady and Svendsen 1981). In such conditions, after the first contacts with resident beavers, migrating beavers tend to avoid moving along densely inhabited small streams, and possibly prefer to return to the maternal site or cross watersheds. We have personal reports from Lithuanian foresters and hunters concerning the frequent observations of young beavers in atypical places quite far from water bodies in spring.

There are no beaver dams in the medium-sized rivers, and the water yield conditions are better for migration of transient beavers than those in the smallest rivers. However, the probability of encounters in medium-sized rivers seems to be significantly higher because of the potentially greater number of migrants and the ability to control the whole water area inside the family range by the territory owners. The greater number of migrants possibly initiates more intensive scent marking which is proportional to the beaver activity (relative abundance). In our study this was expressed by the presence of a positive correlation between these two indices.

In the large rivers, a decrease of scent marking might be related to the low probability of contact between the resident and transient beavers. However, in wide open habitats, the scent marking intensity might also be dependent on other factors which can be not so important in small isolated habitats. For example, in large open areas, more so than in compact sites, beavers probably need not only to defend their territories, but also to communicate between the family members by means of scent marking. Beavers can distinguish between the scent mounds marked by relatives from those marked by the unfamiliar non-relatives (Sun and Müller-Schwarze 1997). Other aspects that could be related are the higher investigative activity and movement of beavers inhabiting wide territories along large rivers. The olfactory orientation model suggests that most mammals can use their own scent marks to orient themselves within their home range (Benhamou 1989).

Our study shows that the scent marking intensity could be an informative index for the evaluation of the migrating state of various intrapopulationary beaver groups inhabiting different systems of the hydrographical network, especially the drainage systems of small to medium-sized rivers.

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Zusammenfassung

Intensität von Reviermarkierungen des Bibers (Castor fiber) an unterschiedlich großen Flüssen.

Biber, die ein Revier bewohnen, reagieren in der Intensität ihrer Markierungen auf die unterschiedliche Anzahl durchziehender Biber. Ohne Zweifel sind Flüsse die Hauptwege für die Ausbreitung von Bibern. Da Einzugsgebiete größerer Flüsse potentiell auch eine größere Anzahl von Bibern beheimaten, ist die Intensität der Abwanderung sub-adulter Biber auch abhängig von der Größe des Flusses. Während der Zeit der Abwanderung sub-adulter Biber vom April bis in die erste Mai-Dekade wurden an 18 Abschnitten verschiedener Flüsse in Litauen die Intensität der Markierung (Anzahl der Markierungsstellen pro 0,25 km Uferlinie) und die relative Abundanz (Anzahl der Aktivitätsanzeichen von Bibern pro 0,25 km Uferlinie) untersucht. Die Wasserdurchflußmenge (Q) der Flußabschnitte variierte von 0,4 bis 32,2 m^3/s. Nach unserer Meinung ist die Biberpopulation in Litauen stark. Gerade die kleinsten Randgewässer sind sehr dicht von Bibern besiedelt und das erschwert die Ausbreitung von Nachwuchs besonders.

Die höchste Markierungsintensität (1,8 Markierungsstellen pro 0,25 km Uferlinie) wurde an den mittelgroßen Flüssen (Q im Mittel = 4,6 m^3/s), die geringste (0,6 Markierungsstellen pro 0.25 km Uferlinie) in den kleinsten Flüssen (Q im Mittel = 0,6 m^3/s) gefunden. Die Intensität der Reviermarkierung war positiv signifikant in Bezug auf die relative Abundanz in den meisten Flüssen, nicht aber in den kleinsten. Die Ergebnisse werden unter dem Aspekt diskutiert, daß Biber in besetzten Revieren unterschiedlich auf die Wanderung sub-adulter Biber an Flüssen verschiedener Größenordnungen reagieren. Das System von Reviermarkierungsplätzen zeigt, das es sich hierbei um einen wichtigen Mechanismus zur Selbstregulation einer Biberpopulation handelt.

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