CrossMark

ORIGINAL PAPER

Seasonal variation in the home range size of the Eurasian beaver: do patterns vary across habitats?

Jana Korbelová[1] · Lenka Hamšíková[1] · Jaroslav Maloň[2] · Lenka Válková[2] · Aleš Vorel[1]

Abstract Spatial use by animals is one of the most important topics in animal ecology, because the proper description of spatial patterns is essential for the better understanding of animal's behaviour. Seasonal variation might reflect varying behavioural or energy balance requirements of the animals. Our aim was to test whether the space use of Eurasian beavers (*Castor fiber*) seasonally varies and whether the pattern comprises diverse habitats. We studied beaver's spatial use from autumn to spring at three different habitats diverging in several environmental conditions. We captured, tagged and released 42 Eurasian beavers in three sites within the Czech Republic; 33 individuals were tracked during at least one season. From 2006 to 2010, a total of 5074 night locations were recorded during three consecutive seasons. We used 95 % of fixes in the appropriate season to determine seasonal space requirements; then, we estimated the effective sizes of utilised space, i.e. home ranges (HR_{95}). The beaver's HR_{95} sizes varied substantially among seasons, whereas the seasonal pattern was similar among different habitats. Our results revealed that spring HR_{95} were significantly larger than in other seasons; the smallest HR_{95} were observed in winter. The largest HR_{95} were observed in lowland floodplain forests; the smallest HR_{95} were found on sub-mountain hilly streams. In general, the mean HR_{95} was similar for different sexes and age classes. An overlap of spatial use between neighbouring home ranges was recorded in only one case.

Keywords Eurasian beaver (*Castor fiber* L.) · Home range size · Radio-tracking · Seasonality · Habitat type

Introduction

During the 20th century, both beaver species (*Castor fiber* and *C. canadensis*) re-established large parts of their former range, and their populations have grown continuously (Baker and Hill 2003; Halley et al. 2012). The increasing importance of beavers as key mammalian species makes it necessary to understand their basic population parameters. The ecological role of beavers (especially within human-modified landscapes) is a subject of significant interest to wildlife managers and conservationists. Our study should reveal whether seasonal patterns in spatial usage by beavers vary among different habitats.

In animal ecology, spatial use is primarily defined by the home range (Powell 2000), a term that includes the area covered during the daily activities of the individual (or groups of individuals) as well as seasonal variation in spatial use. Börger et al. (2008) state that, generally, the difference between the analysis of home range and territory lies in what proportion of locations are used, i.e. the home range estimation includes all of the data obtained, whereas the definition of a territory uses only the appropriate parts (exclusive use of spaces within home ranges). Generally, the size of mammalian territories is determined by the distribution of critical resources that can be protected from conspecifics (Börger et al. 2008), although constraints on the territory size are influenced by many other factors (individual fitness, heterogeneity of resources, etc.) However, patterns of spatial use also vary across seasons or due to habitat restrictions (Mitchell and Powell 2004).

✉ Aleš Vorel
vorel@fzp.czu.cz

[1] Department of Ecology, Faculty of Environmental Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21, Praha 6, Suchdol, Czech Republic

[2] Department of Ecology, Faculty of Science, Palacký University Olomouc, tř. Svobody 26, 771 46 Olomouc, Czech Republic

Springer

Differences among seasonal patterns might also be influenced by the methodology used (i.e. how the home range was estimated).

Beavers are large, territorial rodents living in social units (families) (Wilsson 1971). In general, all members of a family use the same space, with low levels of spatial dissimilarity among individuals of the same family (Herr and Rosell 2004). According to Bradt (1938) and Aleksiuk (1968), who originally described spatial use by beavers, beavers form territories in close proximity to their lodges. Although both the home range and territory are used to describe spatial use by beavers, (e.g. Müller-Schwarze 2012), the majority of the beaver literature (reviewed by Novak 1987) does not precisely define these terms. Indeed, major studies that consider the spatial behaviour of beavers analyse and discuss the home range concept rather than the territorial concept (reviewed by Novak 1987; Baker and Hill 2003), probably because the terminology associated with the home range concept is clearer. In beaver research, the use of spatial data sets and the definition of major spatial patterns are misleading. For example, Campbell et al. (2005) defined territory size by including almost all of the obtained records of beaver activity (except these classified as "on tour"), whereas Havens et al. (2013) used the same concept to describe a home range. However, even for other species, the ultimate definition of these spatial concepts is not clear (Börger et al. 2008).

In general, there are two approaches to quantify beaver spatial requirements. First, the size of home ranges in river systems is expressed as the sum of the lengths of river banks, i.e. they are expressed in one-dimensional space (e.g. Nolet and Rosell 1994; Fustec et al. 2001; Herr and Rosell 2004; Campbell et al. 2005). The second approach, which is necessary for the description of nonlinear flooded areas, expresses the size of home ranges as a conglomerate of terrestrial and aquatic patches used by family members in two-dimensional space (e.g. Wheatley 1997a; Bloomquist et al. 2012).

Seasonal patterns in beaver home range sizes have been studied by many researchers, and the documented sizes varied considerably among regions and seasons. Davis et al. (1994) recorded the greatest total daily movement during autumn and winter, whereas the maximal distance between locations was measured in spring. In contrast, Wheatley (1997a) described the largest home ranges in summer and the smallest ones in winter. Nolet and Rosell (1994) determined seasonal patterns of spatial use, and they also showed a larger range of activities during spring and summer compared with winter. Unlike previous authors, Bloomquist et al. (2012) found the largest ranges in winter as well as in summer; they also described substantial changes in the home range size among years.

The aim of this study was a better comprehension of seasonal variations of beaver spatial use (home range size); as a second question we asked whether a captured seasonal pattern is habitat sensitive. Here, we take in the term habitats as to be areas of diverse climate and environmental quality. We predicted that (a) beavers will exhibit diverse seasonal patterns of home range sizes (due to conditional spatial requirements across seasons), and (b) based on the previous prediction, we assumed that if seasonal effects will be evident than there would be low differences between diverse habitats. Furthermore, we had to adopt the prediction that whilst year-to-year variation of spatial use within one habitat is non-significant than it would be possible to compare space use acquired in diverse years and sites. For all modelling, we attributed sex and age of each individual as covariates of home range size variation. To evaluate the role of intraspecific relationships in determining the home range size, we estimated the degree of overlap of home ranges among neighbouring families.

Materials and methods

Study sites

We studied spatial use of beavers in three study sites around the Czech Republic where different habitats and climate conditions existed (see Fig. 1). The first site (hereafter *lowl* habitat) was at an intense agricultural landscape in the lowlands of South Moravia where both dense human population and exploitation exists. Beaver population here occupies temperate production deciduous floodplain forests surrounding the rivers Morava and Dyje (accompanied by a widespread system of natural or artificial channels); the rapidity of water flow is very low or minor in the river systems. The climate is warm (Pannonian environmental zone *sensu* Metzger et al. 2005) with altitudes of approximately 150 m.a.s.l., the mean temperature in July is 21.3 °C and in January 2.4 °C, and the total annual precipitation is 500–550 mm. The second site (hereafter *subm* habitat) was at a hilly sub-mountain landscape in West Bohemia with extensive human land use. Here, beavers inhabit a system of small flowing streams with an intense system of beaver dams; the occurrence of beavers is mostly in production forests or mosaic pastures. Here is cold climate (Alpine South environmental zone sensu Metzger et al. 2005) with an altitude of 500–650 m.a.s.l. with a mean temperature in July of 16.1 °C and in January of −5.5 °C, and the total annual precipitation is 800–1200 mm. The last site (hereafter *wriv* habitat) was in North Bohemia in an industrial landscape surrounding a wide river. Near surrounding of both river banks is intensively exploited by people. Beavers here inhabit the broad and free-flowing unregulated river Labe, but human interest is partly distant from the wide alluvium of the river, due to the frequent water level fluctuation. A mild continental climate is common here (Continental environmental zone

Fig. 1 Location of study sites
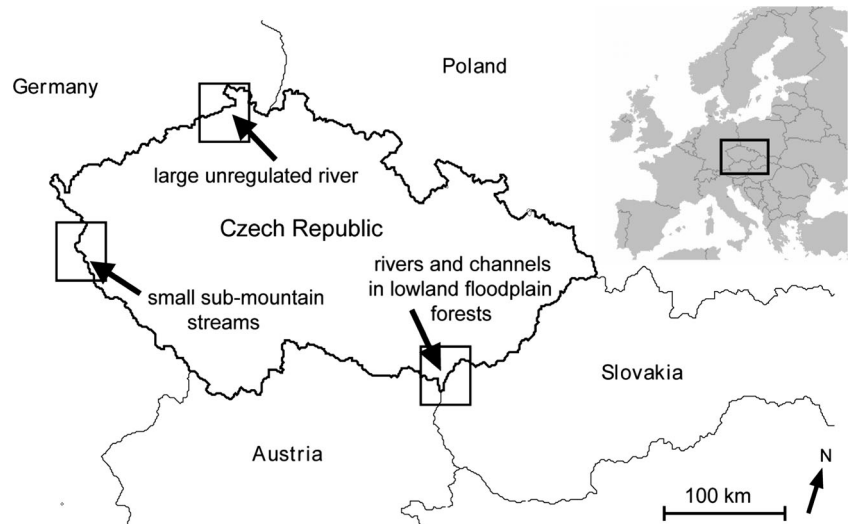
sensu Metzger et al. 2005) with an altitude of 110–140 m.a.s.l., a mean temperature in July of 19.4 °C and in January of 0.9 °C, and the total annual precipitation is 700–900 mm.

Our two beaver populations originated from reintroduction programmes conducted in Austria (South Moravia, see Kollar and Seiter 1990) and Bavaria (West Bohemia, see Zahner 1997), third one the population in North Bohemia, was established by dispersion from the refugium near Magdeburg (Šafář 2002; Vorel et al. 2012). All studied populations are far from the initial phase of the population growth (Vorel et al. 2012; Barták et al. 2013), with a minimum population age of at least 20 years, i.e. population densities of study sites were not substantially different (mean pop. density = 0.27 terr./km, with ranges = 0.21–0.29 terr./km [see Table 1], Vorel et al. unpublished data). In study sites, we did not record any successful predation of beavers by foxes or lynxes, and the presence of wolves and bears was not confirmed (Mitchel-Jones et al. 1999; Anděra et al. 2012). Despite the legal ban on the hunting of beavers in the Czech Republic, we recorded infrequent instances of illegal hunting in South Moravia (Vorel et al. unpublished data).

Data collection

Out of each study site, we randomly selected home ranges where we traced the individuals. We considered only those home ranges that were established on linear stream systems (brooks, rivers, artificial channels, river branches and small streams with beaver dam systems). We captured animals from the middle of July up to the first decade of October. For trapping, we used Hancock live traps (with bark and phloem of Salicaceae combined with beaver anal gland secretion as a lure) set close to beaver lodges, burrows or dams. We categorised all captured beavers according to their weight into

the age classes as follows: kits (<8.0 kg), subadults (8.0–15.9 kg) and adults (≥16.0 kg) (Vorel & Hamšíková, unpublished data); beavers we sexed on the basis of anal gland secretion colour (Rosell and Sun 1999). To trace beavers, we used modified ear tags, M3530 (made by ATS Inc.), operating at 150 MHz (weight 28 g, $42 \times 52 \times 17$ mm and with a 200-mm antenna). The placement of the antenna on the animal's tail was performed in accordance with Rothmeyer et al. (2002). The area of the tail where the radio transmitter was mounted was locally anaesthetized with a 1 % solution of trimecain hydrochloridum (MESOCAIN®), using a dose of 1 ml per 10 kg of body weight. Fifteen minutes after the injection, we pierced the tail with piercing pliers then the tag was fitted using a split cotter pin and shim. We only applied radio transmitters to subadults and adults. Immediately after the application, the animals were released at the same place from where they were captured; during our captures no deaths or post-operative complications occurred as a result of the transmitter application.

Between 2006 and 2010 in the summers and autumns in total, we trapped 75 beavers in study areas and attached transmitters to 42 of them. Subsequently we followed 33 of the tagged animals ($n_{subm} = 13$, $n_{wriv} = 7$, $n_{lowl} = 13$). After three seasons of operation in the wild, 19 radio transmitters remained fully functional. During the tracking period, we located 14 radio transmitters that had fallen off. One transmitter abruptly malfunctioned during the first day after mounting, and another two transmitters suddenly stopped transmitting during the tracking period. One male probably dispersed, as he was repeatedly located more than 10 km distant from the site of capture, before we lost his signal without any further relocation. Five individuals died during tracking: two females died within the first two weeks after release, one male was poached three weeks after release, one female died in October and one male in May. Despite the fact that four transmitters

Table 1 Detailed information regarding the study sites

Study sites	North Bohemia	South Moravia	West Bohemia
SCI (Natura 2000 site)	CZ0424111	CZ0624119, CZ0624099	CZ0323151
WGS coordinates of the site centre	N 50.72040°, E 14.19308°	N 48.64370°, E 16.94528°	N 49.67171°, E 12.59807°
Habitat description	Large river with fragmental flood plain forests	Well-developed flood plain forests	Deciduous riparian forests within spacious spruce monoculture
Water regime	High amplitude of water level	Steady water level	Steady water level
Water character	Wide river with adjacent pools	System of alluvial rivers, natural river branches and artificial channels	Small upland streams
Mean water width (m)	100	5–50	<5
Mean elevation (metres above sea level)	125	150	575
Mean temperature (°C)			
In winter	0.9	2.4	−5.5
In summer	19.4	21.3	16.1
Annual precipitation (mm)	700–900	500–550	800–1200
Dominant riparian woody vegetation	*Salix, Populus, Corylus, Alnus, Acer*	*Salix, Acer, Fraxinus, Quercus, Populus, Prunus, Swida*	*Salix, Alnus, Betula, Populus, Acer, Picea*
Beaver dam systems[a] (%)	0.00	6.25	100.00
Population density[b] (families/kilometre)	0.29	0.28	0.21
No. of observed individuals / in families	7/5	13/8	13/8

[a] Beaver dam systems means percentage of home ranges with beaver dams occurrence

[b] Vorel et al. unpublished data

remained functional for more than 1 year, in analyses we entered only data from the first year of tracing.

We traced the animals regularly during the period when transmitters were functional; each individual was tracked at least every 3–4 weeks. Animals were followed from evening (one h before sunset) until morning (one h after sunrise). Positions of each individual were recorded at least hourly during the tracking campaign, to avoid obtain spatially autocorrelated data was the shortest interval among two consecutive fixes always half an hour.

Beavers were located using a Yagi antenna from at least 20 m away from the river bank (to avoid disturbing the individuals). We saved fixes, i.e. the position where the transmitter signal was strongest with the antenna held perpendicular to the linear water system. To determine the actual position of the beavers within the stream system, we used an orthogonal projection (in GIS software, ESRI 2000) to transfer the fixes to the central line of the water course. Neither the distance of the beaver from the researcher, nor the distances of the beaver from the shoreline were determined.

Data analysis

All analyses were conducted using the R software (R Core Team 2014). At first, we tested spatial autocorrelation of time series data; analysis (partial autocorrelation function in the R software, www.R-project.com) showed a 2-h lag as a minimal interval between two fixes, to avoid autocorrelated data. Therefore, we removed all fixes which did not respond to obtained lag; for

further analyses of space patterns we used only the purged dataset (*sensu* Harris et al. 1990). To define the beaver's home range, we omitted 5 % of the outlying fixes (in accordance with Powell 2000); thus, we included 95 % of the more central fixes to constitute the home range length. The length of the stream system within extreme fixes is often considered as valid home range size—one-dimensional approach (e.g. Fustec et al. 2001, Campbell et al. 2005). Appropriateness of this approach lacks for stream systems where beaver dam systems occur, because flooded areas by beavers usually comprise of important foraging areas (as well as banks). Thus, exclusion of dam systems out of the measurement of home range size (which in fact considers one-dimensional approach) might underestimate the real size of the home range. Whilst our beaver sites contained intense beaver dam activity, we therefore forsook measuring home ranges linearly and used a two-dimensional approach. The size of home ranges (HR_{95}) we expressed as the sum of 20-m wide strips of stream system (on both banks) within the 95 % fix extremes. Strips 20-m wide comprised most of beaver foraging activity (Vorel et al. unpublished data; Jenkins 1980; Nolet et al. 1994). When dams and beaver ponds occurred within HR_{95}, we included also entire flooded areas of beaver dam systems and its 20 m strips into its size. Seasonal HR_{95} were defined using fixes obtained only during the appropriate season; the seasons we set as follows: autumn (23.9.–21.12.), winter (22.12.–20.3.) and spring (21.3.–20.6.).

Prior to testing the main hypothesis, we tested the question whether variation of the autumn's and winter's home ranges (HR_{95}) follows changes of autumn and winter

severity. We compared autumn's and winter's home ranges (HR_{95}) from one site (of one climate region) during 3 years. We related acquired home range sizes to the sum of daily temperatures of dates when the tracking campaign took place (separately per autumn and winter). Whilst autumns and winters during three years were diversely severe (i.e. mean autumnal temperatures were 8.6 °C in 2006, 10.3 °C in 2007 and 9.3 °C in 2009 and winter's were 2.4 °C in 2006/2007, −2.7 °C in 2007/2008 and −3.6 °C in 2009/2010), ANOVA showed that patterns of home range sizes in neither season did not follow the effect of seasonal year-to-year temperature shifts (autumn: $F\text{test}_2 = 1.343$, $p = 0.291$; winter: $F\text{test}_2 = 0.038$, $p = 0.963$). Thus, the variation of home range sizes is not attributable to seasonal severity at one site; therefore, it might be used for measures of differences in home range sizes based on variation among diverse sites. Home range sizes of beavers tracked during autumn 2009 and winter 2009/2010 were not used in further modelling analyses because of insufficient numbers of winters and spring's fixes.

Mixed modelling approach was taken to analyse variation of the home range size, because the structure of tested factors was loaded by complex of random effects. Built models asked HR_{95} as the explained variable, where the normal structure of errors was fitted (by square root transformation). Due to tracking limitations, we had to establish two models in the *wriv* site. All transmitters were lost at the end of winter or during spring. The first model (GLMMa) answered the variation during three consecutive seasons, whilst the sufficiently tracked individuals were only from two studied sites (West Bohemia [habitat *subm*] and South Moravia [habitat *lowl*]). Second, we established another model (GLMMb) where we used data from three different study sites recorded only during autumn and winter. In both established models, we defined random parts of model formula such hierarchical structure of effects: −1|*year/family/individual/season*. However, according to Crawley (2008, p. 640), we checked whether the complexity of random effects is necessary, or it is possible to simply the hierarchical structure as well as reduce overall complexity of the models, lower AIC was here used as indication of winning model among the tested. Whilst the simplification was justified for both GLMMs, then all random effects remained in models but in simplified structure of the random framework (for details see Crawley 2008).

In fixed effect part of model formula, we asked factors as *area*, *season*, and as covariate factors we controlled for *age* and *sex*. We used deleting test to establish best fitting model, based on lowest parsimony—evaluated with use of AIC (Burnham and Anderson 2004). Here, we used library *nlme* of the R 3.1.3 (R Core Team 2014) www.R-project.com).

We also estimated the extent to which HR_{95} overlapped between resident beavers and their neighbours; we quantified the size of the common area and the proportion of overlap relative to each adjacent HR_{95}.

Results

During the study period, we radio-tracked 33 beavers from 21 families, including 13 subadults, 20 adults, 21 males and 12 females (for details, see Table 2). The HR_{95} size did not differ (ANOVA: $F_1 = 1.06$, $p = 0.3060$) between males (5.03 ± 2.91 ha) and females (4.68 ± 2.67 ha). Although the mean HR_{95} of adults (5.14 ± 3.06 ha) was slightly larger than that of subadults (4.34 ± 2.06 ha), the difference was not significant (ANOVA: $F_1 = 0.50$, $p = 0.4820$). During 82 nights of tracking in three seasons, we obtained 5074 fixes (mean = 6.34 fixes per animal per night, with a range from 3 to 20 fixes per night). The greatest number of fixes were collected during autumn (3356), fewer during winter (999) and spring (719).

The GLMMa allowed testing home range sizes (HR_{95}) of 19 individuals living in two habitats during three consecutive seasons. The modelling showed that sizes of home ranges were influenced by the effects of habitat, season and age (for details see Table 3). HR_{95} were smaller in *subm* habitat than in *lowl* ($\beta = 74.357$, $p < 0.0001$), furthermore in both habitats home range sizes in spring were larger than autumn's ($\beta = 42.540$, $p = 0.025$), whilst home range size in winter were the smallest (although the difference was not significant, $\beta = -24.397$, $p = 0.193$). Mean autumnal size of HR_{95} was 4.44 ± 1.72 ha, winter size was 3.69 ± 2.40 ha and spring size was 6.76 ± 3.14 ha (for detailed information see Table 4 and Fig. 2). Although the factor age was significant ($\beta = 46.0124$, $p = 0.042$), it could not be considered because of insufficient occurrence of all factor levels across other factor groups. The difference of home range sizes among sexes was not substantial ($\beta = -15.611$, $p = 0.441$). No significant first order interactions were revealed between explanatory of the model.

GLMMb allowed analyse patterns of 27 sizes of beaver home ranges, whilst the individuals lived in three habitats where seasonal effect comprised only autumn and winter home ranges. Results showed substantial differences in HR_{95} only between habitats and seasons (without their mutual interaction); no other factors were revealed as contributing to understand the variation of HR_{95}, for more details see Table 3. Home ranges in *lowl* were larger than in *subm* ($\beta = 45.431$, $p = 0.002$), also HR_{95} in *wriv* were substantially larger in comparison with *subm* ($\beta = 46.011$, $p = 0.020$). When comparing *wriv* and *lowl* to each other, it seems that in both sites home ranges were quite similar; no effect was revealed ($\beta = 0.580$, $p = 0.975$). Mean HR_{95} size of *wriv* was 5.48 ± 2.48 ha, of *subm* it was 3.96 ± 2.74 ha and of *lowl* it was 5.74 ± 3.32 ha. Home ranges within this model were again larger in autumn in comparison to winter ($\beta = -25.358$, $p = 0.047$), here the difference was significant. Mean autumnal size of the HR_{95} was 4.50 ± 1.71 ha and mean winter size was 3.65 ± 2.15 ha.

Out of the twelve potential cases of contact between adjacent HR_{95}, we found only one instance of overlap between the home ranges of two neighbouring families; this occurred in

Table 2 Detailed information on the long-term radio-tracked beavers

ID	Habitat type	Sex	Age	Year of capture	Total no. of fixes	Autumn			Winter			Spring		
						d	f	HR_{95}	d	f	HR_{95}	d	f	HR_{95}
1	*lowl*	M	S	2006	194	18	113	8.27	5	38	3.97	8	39	12.03
2	*lowl*	M	S	2006	82	16	63	2.74	3	17	2.74			
3	*lowl*	M	A	2006	173	18	110	4.44	5	37	1.73	6	20	11.35
4	*lowl*	M	A	2006	156	17	106	6.40	5	25	7.23	5	23	6.65
5	*lowl*	M	A	2006	195	18	121	2.27	5	46	9.49	7	25	6.21
6	*lowl*	F	A	2007	140	15	41	6.24	11	27	1.80	12	55	7.55
7	*lowl*	M	S	2007	155	17	65	6.48	12	35	6.85	13	40	6.44
8	*lowl*	M	S	2007	104	14	67	4.12	16	28	2.66			
9	*lowl*	M	A	2007	151	18	65	4.27	13	36	2.27	15	49	4.01
10	*lowl*	M	A	2007	132	12	58	1.77	12	43	7.47	12	31	8.49
11	*lowl*	M	A	2007	156	19	77	6.03	11	29	4.18	14	46	6.87
12	*lowl*	M	A	2007	142	15	68	7.82	16	26	5.30	16	40	5.42
13	*lowl*	M	A	2007	66	12	39	3.28	11	27	5.04			
14	*subm*	F	S	2008	260	11	125	5.38	5	44	2.19	9	59	11.24
15	*subm*	F	S	2008	257	11	126	5.81	5	43	3.90	9	57	6.11
16	*subm*	F	S	2008	240	11	132	4.63	5	49	3.90	6	46	10.73
17	*subm*	F	S	2008	224	13	158	2.48	4	34	2.39	3	21	5.30
18	*subm*	F	S	2008	140	12	118	7.64						
19	*subm*	F	S	2008	139	12	117	5.52						
20	*subm*	F	A	2008	241	11	127	4.36	5	43	3.70	9	55	13.51
21	*subm*	F	A	2008	212	12	143	2.92	5	46	1.18	2	22	0.06
22	*subm*	F	A	2008	213	12	157	4.42	4	47	1.44			
23	*subm*	M	S	2008	201	11	126	4.65	5	43	2.26	2	16	3.86
24	*subm*	M	A	2008	254	13	157	2.18	4	34	1.12	8	54	2.18
25	*subm*	M	A	2008	197	12	136	3.55	5	39	0.56	2	21	7.41
26	*subm*	M	A	2008	128	14	116	0.36						
27	*wriv*	F	S	2010	165	12	97	3.35	7	44	3.51			
28	*wriv*	F	A	2010	152	12	96	8.31	5	39	5.01			
29	*wriv*	M	S	2010	162	12	97	3.55	8	46	3.10			
30	*wriv*	M	A	2010	119	13	100	8.02						
31	*wriv*	M	A	2010	120	13	75	7.39	4	34	5.80			
32	*wriv*	M	A	2010	87	8	69	3.36						
33	*wriv*	M	A	2010	117	12	91	14.32						

lowl lowland floodplain forest of South Moravia, *subm* small sub-mountain streams of West Bohemia, *wriv* wide unregulated river of North Bohemia, *F* female, *M* male, *A* adult, *S* subadult, *d* number of days with fixes per season, *f* number of fixes in appropriate season, HR_{95} seasonal home range size in hectares *Total no. of fixes* sum of all fixes per focal individual (during all seasons)

the *subm* habitat during the spring. The area of overlap was 1.52 ha, i.e. 4.25 % of the adjacent home ranges.

Discussion

Our results showed that home range sizes seasonally vary, the shortest are during winter, then longer during autumn and the longest are in spring. Furthermore, we demonstrated that this seasonal pattern show beavers living in different habitats; mean sizes of seasonal home ranges across the habitats followed similar patterns. On the other side, we proved substantial differences when comparing home ranges of three diverse habitats; beavers inhabiting small sub-mountain streams (*subm*) had significantly smaller home ranges in comparison to beavers living in fluvial habitats (*wriv* and *lowl*). Although we hypothesised a potential climate shift in spatial activity based on diverse climate conditions of three sites, we

Table 3 Results of GLMM analyses. In GLMMa, we tested variation of HR_{95} in two different habitat types and three consecutive seasons; second model GLMMb analysed variation of HR_{95} in three different habitat types and two consecutive seasons. Results of models are introduced in detail in the "Results" section

GLMMa—Two sites, three seasons					
	Beta	SE	DF	t value	p value
Intercept	155.027	19.597	52	7.911	0.000
Area					
subm × lowl	74.357	19.452	52	3.823	0.000
Season					
autumn × winter	−24.397	18.477	52	−1.320	0.193
autumn × spring	42.540	18.477	52	2.302	0.025
spring × winter	−66.937	18.477	52	−3.623	0.001
Age					
Adult × subadult	46.012	22.056	52	2.086	0.042
GLMMb—Three sites, two seasons					
	Beta	SE	DF	t value	p value
Intercept	224.732	10.941	50	20.540	0.000
Area					
subm × wriv	46.011	19.174	50	2.400	0.020
subm × lowl	45.431	13.632	50	3.333	0.002
wriv × lowl	0.580	18.531	50	0.031	0.975
Season					
autumn × winter	−25.358	12.475	50	−2.033	0.047

lowl lowland floodplain forest of South Moravia, *subm* small sub-mountain streams of West Bohemia, *wriv* wide unregulated river of North Bohemia

Fig. 2 Seasonal pattern of the HR_{95} size **a** within two different habitat types in three consecutive seasons, in accordance with GLMMa and **b** within three different habitat types in two consecutive seasons, in accordance with GLMMb. *Horizontal lines inside the boxes* are medians, *points* represent mean home range sizes and the *line connecting these points* shows the trend in the home range size between consecutive seasons (each habitat type is distinguished by a different line style: lowland floodplain forests (*L*)—*short dashed*, small sub-mountain streams (*S*)—*long dashed*, and wide unregulated river (*W*)—*full*). Habitat types are differentiated by colours: lowland floodplain forests (*L*)—*white*, small sub-mountain streams (*S*)—*light grey*, and wide unregulated river (*W*)—*dark grey*

cannot confirm such reasoning of the variation—*wriv* and *lowl* habitats were not close in severity of winters and warmth of summers, but the observed home ranges (either seasonal or totally) were not different enough. Whereas we traced beavers of one habitat during three consecutive years (when diverse severity of seasons were evident) the autumnal and winter home range variation did not follow variation of seasons among the years.

It is evident that a seasonal variation in home range size (confirmed in a similar pattern across habitats) falls under ethological and population biorhythms of beavers, whilst
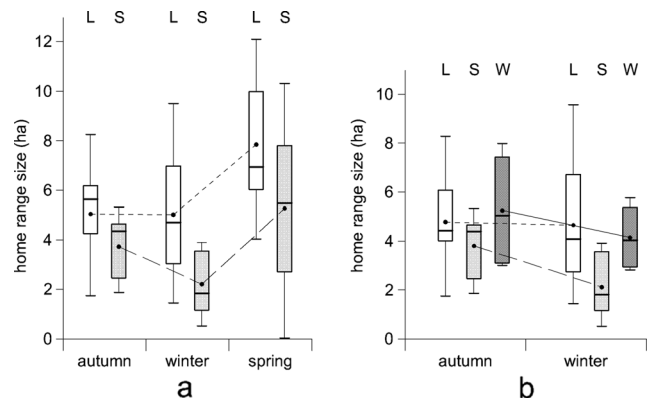
captured differences among habitats reflect rather habitat characteristics. As showed by Wheatley (1997b), habitat type influences the spatial activity of beavers. Our study, similarly as Wheatley (1997b), showed that beavers living in rivers exhibit larger home ranges than those creating beaver dam systems. Although we did not compare habitat quality allocated within home ranges of the focal individuals, the habitat richness (sufficient quality and quantity of resources) is probably the main cause of significant differences of home ranges among habitat types. As stated by Mitchell and Powell (2012), spatial activity of animals (which determines sizes and positioning of home rages) in basic concentrates where rich food supply is located, and these behaviours imply formation of home ranges. Indeed, that is what we observed in our study sites; beavers tend to reduce spatial activity where is it possible. In general, when beavers flood parts of their home ranges by the dam system, they enlarge their efficient area because they improve the potential for more food supply. Furthermore,

Table 4 Mean seasonal home range sizes and SD (in hectares) for different habitat types, sexes and age classes

	Habitat type			Sex		Age	
	subm	wriv	lowl	F	M	S	A
Autumn	3.96 ± 1.75	6.65 ± 3.77	4.79 ± 1.71	4.85 ± 1.73	4.86 ± 2.88	4.50 ± 1.36	5.01 ± 2.88
Winter	2.14 ± 1.14	4.15 ± 1.23	4.66 ± 2.30	2.88 ± 1.15	4.10 ± 2.46	2.76 ± 0.70	4.03 ± 6.84
Spring	6.00 ± 3.60	–	7.45 ± 2.47	6.96 ± 3.55	6.65 ± 2.87	6.54 ± 2.46	6.84 ± 3.35
All	3.96 ± 2.74	5.48 ± 2.48	5.74 ± 3.32	4.68 ± 2.67	5.03 ± 2.91	4.34 ± 2.06	5.14 ± 3.06

subm small sub-mountain streams of West Bohemia, *wriv* wide unregulated river of North Bohemia, *lowl* lowland floodplain forests of South Moravia, *F* females, *M* males, *S* subadults, *A* adults

the foraging might be realised more secured, because dam systems are anti-predation provision against predators (Fryxell and Doucet 1991). There are two approaches to improve resources quantity and quality within home ranges. Firstly, it is the dam system building which enlarges internal parts of home ranges; secondly, it is the stretching of home range length along a water systems. However, the dam systems are probably more efficient because they provides more food supply opportunities within existing home ranges (Krojerová-Prokešová et al. 2010) without increasing of ranges of spatial requirements. Whilst the behavioural modification (i.e. dam building behaviour) is impossible in broad river habitats (i.e. on floating rivers with a width of more than 20 m), foraging in these habitats might be carried out only from the river banks, thus to meet the needs it is only one way of how to enlarge the home range size—stretching of spatial activity. Indeed, beavers on *subm*, where intense dam behaviour occurred, had substantially shorter and wider home ranges in comparison with sites in *lowl* and *wriv* habitat.

Home range sizes of *wriv* and *lowl* exhibited similar results, although the habitats were qualitatively different. Breck et al. (2001) demonstrated that a river system with a regulated water level (artificial dam systems) provides better conditions to improve beaver fitness; however, in comparison to a free-flowing river, they evidenced no detectable differences in home ranges of beavers. Although our *wriv* and *lowl* habitats represent similar habitats in case of water type, the water regime as well as food opportunities at these sites were both considerably distinct. Firstly, the habitat *wriv* is a free-flowing unregulated large river whilst in the *lowl* area the water regime is based on a system of slowly flowing rivers and channels (for detailed description see the Study sites section in Materials and methods); secondly, at *wriv* there are rarely fragmented riparian forms with willows and poplars as main trees (for detailed woody vegetation description see Vorel et al. 2015). In contrast (to *wriv*) in the *lowl* habitat, there are rich and widespread deciduous floodplain forests (dominated by maples, ashes, willows, oaks, etc., Vorel et al. 2015) accompanied by a well-developed system of river branches or channels. Thus, there are substantial differences when comparing both habitats (*wriv* vs. *lowl*); however, we showed that home range sizes of both habitats were almost identical and both significantly larger than in comparison to the *subm* habitat. Nolet and Rosell (1994) described seasonal differences in territory size as dependent on the time allocation. Thus, additional explanation for smaller sizes of home ranges with beaver dams (in *subm* habitat) might be that the dam maintenance needs more time to the detriment of territorial patrolling and consequently smaller home ranges might be more preferable.

Seasonal variation of animal space use is common across the taxonomic spectrum and is especially well-known for large mammalian species. There are two contradictory processes which cause seasonal variation. The first principle is that the poorest quality of resources during the winter season enlarges home ranges to ensure the sufficient amount of resources when are of lesser quality, as for instance showed Säid et al. (2009) for roe deer. The second process says that there is restricted space activity due to energy balance ensuring thermoregulatory processes because during the colder months are higher energy expenditures (van Beest et al. 2011). Whilst beavers are able to collect and store food resources (as fat reserves or in built winter caches, e.g. Novakowski 1967), the first described general principle is probably not playing important role for beaver seasonal space use. But Nolet and Rosell (1994) and Wheatley (1997a) both showed restrictions of space use of beavers under colder conditions. Nolet and Rosell (1994) examined that travelling during territorial activity positively correlates with daily temperatures; they argue that restrictions are caused by the thermoregulation constraints caused by cold weather. Aleksiuk and Cowan (1969) however mentioned winter depression in activity is not common for beavers across its whole range of distribution; animals in southern latitudes behave not so restrictive during winters in comparison to arctic beavers. Although we studied beavers under diverse climate conditions, we did not confirm the described shift in behaviour affected by climate; on the other side, beavers in this study did not fulfil such distinct climate regimes. However, seasonal variations in beavers' space use also reflect changing feeding needs and biorhythm throughout the year: energetic costs associated with territory defence (Rosell et al. 1998) and energy balance (the costs and benefits of energy yield) (Novakowski 1967; Lancia et al. 1982). Although we did not explicitly record the foraging activity of the tracked beavers, one might predict that spatial use will reflect seasonal changes in foraging due to seasonal variations in the accessibility and availability of the diet. Heterogeneously distributed food resources and intense preparation of food and fat reserves probably increase the home range size during autumn (Svendsen 1980; Nolet and Rosell 1994). Another aspect that causes larger spring spatial activity expansion of the home ranges after winter is most likely caused by more intense patrolling due to the defence of home ranges against intruders, primarily dispersing subadult beavers (Rosell and Nolet 1997; Rosell et al. 1998).

Showed seasonal pattern is not valid across a whole range of beaver distribution (both beaver species), because substantially diverse climatic conditions might influence the expression of seasonal behaviours of that showed in this study. In Manitoba (Canada), beavers must limit their territorial behaviour and seasonal foraging to the short period without ice cover (indeed, this period compresses late spring, summer and early autumn) because during the rest of the year, ice cover restricts all above-ice activities (i.e. foraging, territorial defences). In our study, long-lasting ice cover is uncommon (typical snow cover is observed for approximately 2–3 months of the year only in the *subm* habitat; ice cover is usual only in *subm* with duration app. 1 month, in *lowl* habitat occurring at most for 1 week).

Although beavers in our study maintained unfrozen accesses during ice cover days (the foraging was possible above ice cover) spatial use in the winter was still markedly reduced. Wheatley (1997a) has found that the autumn foraging sites were usually located within established summer home ranges (near the lodges); however, the food there was not used during the summer. In contrast to all previous authors, Bloomquist et al. (2012) documented a different seasonal pattern in Illinois (USA), a more temperate region (when compared to ours) without any ice cover days documented. There beavers established the largest home ranges during winter and the smallest ones during summer. The authors argued that the winter home ranges depend on the winter high water level fluctuations, and therefore, beavers forage within newly flooded areas. Although we also tracked several beavers on a highly fluctuating river (*wriv* habitat), we did not prove the described changes in the seasonal pattern. During our tracking period on the Labe River, three high amplitude fluctuations occurred (with a cumulative increase of more than 3, 5 and 7 m above the typical water level); however, we found no expansion of spatial use. On the other side, there still exist differences among climate for our and their study sites.

During late winter and spring, subadult beavers exhibit dispersal behaviour, and thus, they conduct several exploratory trips to nearby areas (Hodgdon and Lancia 1983; McNew and Woolf 2005; Bloomquist and Nielsen 2010). In principle, dispersal behaviour might expand the late winter and spring home range sizes of subadults in comparison with adults. For example, Havens et al. (2013) did not record this exploratory behaviour until the end of winter. In our study, we traced 7 subadults and 12 adult beavers (from autumn up to spring); when the adult's HR_{95} were slightly smaller in autumn, larger in winter and smaller spring (not significantly). In our study, only one subadult female acted as an intruder when she visited the adjacent home range of another family several times (with three other tracked beavers). We believe that the spring overlaps of home ranges are related to the fact that subadults conduct exploratory trips into surrounding areas before dispersing. The number of cases of overlap in home ranges was lower in our study than those documented by Bloomquist et al. (2012), who also studied beavers in a dense population that was close to carrying capacity; However, they used fixed kernel procedure for home range capturing. In our opinion, the procedure artificially extends the proposed ranges of activity of the animals (here figures artefact of probabilistic approach), which at final might represent larger spatial requirements than in reality.

Our results showed no sex effects on the home range variation, notwithstanding Herr and Rosell (2004) showed minor disparities in space use when analysing home range sizes of adult males and females. However, they studied sexual dimorphism of space use from spring up to the end of summer, when the differences in home range sizes are more expectable than during the rest of the year—pregnant females are more restricted in spatial activity whilst males more patrol the home

ranges, and supply the paired females (Wilsson 1971). Whereas in our models, the summer data were not included then we did not obtained the proposed sexual effect.

The way how we estimated home ranges is uncommon in beaver literature (compare e.g. Wheatley 1997a; Fustec et al. 2001; Campbell et al. 2005; Bloomquist et al. 2012). Our aim was to equalise given differences of home range sizes come out of occupation of diverse habitat types (linear water systems vs. squared systems where beavers induced wetlands–dam systems); to fulfil to make compatible comparisons we used two-dimensional measuring of home ranges. It allowed us to include effective parts of linear home ranges to obtain home range areas where beavers carry forage regardless of complexity of utilised space. This approach came out of the premise that the food supply is the most important reason of existence of the home range concept (Mitchell and Powell 2012), than in fact we measured only efficient area of the home ranges. Seemingly is the two-dimensional approach for linear river systems redundant—due to the apparent multiplication of the length of occupied river system only by the size of 20-m wide belts (per each bank). However, if the flooded areas occurred within the established home ranges, is the one-dimensional interpretation inaccurate because of underestimating the real spatial use? The two-dimensional approach allows us comparing the home range sizes of beavers in river systems without dams to those containing the areas flooded by dam system.

Knowledge of home range sizes (and seasonal and habitat variation) should contribute in ecological studies as well as to proper management planning. At first, we propose the studies estimating population sizes require basic parametrization for beaver populations. We showed that space acquisition is spatiotemporally dependent what has to be considered in estimation of dynamics of different populations—the main tool for planning or optimisation of management tasks. Showed effects might help the understanding of the variation of beaver populations; also results showed that beaver dam systems are less demanding in space point of view and in fact more efficient in resources allocation. Our contribution also defined mean home range sizes for basic ecosystems in Central Europe, what essential data still lacks in recent beaver research.

References

Aleksiuk M, Cowan IMT (1969) Aspects of seasonal energy expenditure in the beaver (*Castor canadensis* Kuhl) at the northern limit of its distribution. Can J Zool 47:471–481

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

Anděra M, Gaisler J, Savci CR (2012) Mammals of the Czech Republic. Czech Republic, Academia Praha

Baker BW, Hill EP (2003) Beaver (*Castor canadensis*). In: Feldhamer GA, Thompson BC, Chapman JA (eds) Wild mammals of North America: biology, management, and conservation. Second edition. The Johns Hopkins University Press, Baltimore, MD, USA, pp 288–310

Barták V, Vorel A, Šímová P, Puš V (2013) Spatial spread of Eurasian beavers in river networks: a comparison of range expansion rates. J Anim Ecol 82:587–597

Bloomquist CK, Nielsen CK (2010) Demographic characteristics of unexploited beavers in southern Illinois. J Wildl Manag 74:228–235

Bloomquist CK, Nielsen CK, Justin JS (2012) Spatial organization of unexploited beavers (*Castor canadensis*) in southern Illinois. Am Midl Nat 167:188–197

Börger L, Dalziel BD, Fryxell JM (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol Lett 11:637–650

Bradt GW (1938) A study of beaver colonies in Michigan. J Mammal 19: 139–162

Breck SW, Wilson KR, Andersen DC (2001) The demographic response of bank-dwelling beavers to flow regulation: a comparison on the Green and Yampa rivers. Can J Zool 79:1957–1964

Burnham KP, Anderson DR (2004) Multimodel inference understanding AIC and BIC in model selection. Sociol Method Res 33:261–304

Campbell RD, Rosell F, Nolet BA, Dijkstra VAA (2005) Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? Behav Ecol Sociobiol 58:597–607

Crawley MJ (2008) The R book. Wiley, New Delhi

Davis JR, Guynn DC, Gatlin GW (1994) Territorial behavior of beaver in the Piedmont of South Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 48:152–161

ESRI (2000) ArcView GIS. Version 3.2. Environmental Systems Research Institute, Redlands, CA, USA

Fryxell JM, Doucet CM (1991) Provisioning time and central-place foraging in beavers. Can J Zool 69:1308–1314

Fustec J, Lode T, Le Jacques D, Cormier JP (2001) Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. Freshw Biol 46:1361–1371

Halley D, Rosell F, Saveljev A (2012) Population and distribution of Eurasian beaver (*Castor fiber*). Balt For 18:168–175

Harris S, Cresswell WJ, Forde PG, Trewhella WJ, Woollard T, Wray S (1990) Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. Mammal Rev 20:97–123

Havens RP, Crawford JC, Nelson TA (2013) Survival, home range, and colony reproduction of beavers in east-central Illinois, an agricultural landscape. Am Midl Nat 169:17–29

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

Hodgdon HE, Lancia RA (1983) Behavior of the North American beaver, *Castor canadensis*. Acta Zool Fenn 174:99–103

Jenkins SH (1980) A size-distance relation in food selection by beavers. Ecology 61:740–746

Kollar HP, Seiter M (1990) Biber in den Donau-Auen östlich von Wien. Eine erfolgreiche Wiederansiedlung. [Beaver in the Danube wetlands east of Vienna. A successful reintroduction]. Verein für Ökologie und Umweltforschung, Wien. Austria

Krojerová-Prokešová J, Barančeková M, Hamšíková L, Vorel A (2010) Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources. J Zool 281:183–193

Lancia RA, Dodge WE, Larson JS (1982) Winter activity patterns of two radio-marked beaver colonies. J Mammal 63:598–606

McNew LB, Woolf A (2005) Dispersal and survival of juvenile beavers (*Castor canadensis*) in southern Illinois. Am Midl Nat 154:217–228

Metzger MJ, Bunce RGH, Jongman RHG, Mücher C, Watkins JW (2005) A climatic stratification of the environment of Europe. Global Ecol Biogeogr 14:549–563

Mitchel-Jones AJ, Amori G, Bogdanowicz W, Krystufek B, Reijnders PJH, Spitzenberge F, Stubbe M, Thiessen JBM, Vohralik V, Zima J (1999) The atlas of the European mammals. T & AD Poyser Ltd., London, UK

Mitchell MS, Powell RA (2004) A mechanistic home range model for optimal use of spatially distributed resources. Ecol Model 177:209–232

Mitchell MS, Powell RA (2012) Foraging optimally for home ranges. J Mammal 91:1313–1321

Müller-Schwarze D (2012) The beaver: its life and impact, 2nd edn. Cornell University Press, New York

Nolet B, Rosell F (1994) Territoriality and time budgets in beavers during sequential settlement. Can J Zool 72:1227–1237

Nolet BA, Hoekstra A, Ottenheim MM (1994) Selective foraging on woody species by the beaver *Castor fiber*, and its impact on a riparian willow forest. Biol Conserv 70:117–128

Novak M (1987) Beaver. In: Novak M, Baker JA, Obbard ME, Malloch B (eds) Wild furbearer management and conservation in Northern America. Ashton-Potter Limited, Concord, Ontario, Canada, pp 283–312

Novakowski N (1967) The winter bioenergetics of a beaver population in northern latitudes. Can J Zool 45:1107–1118

Powell RA (2000) Animal home ranges and territories and home range estimators. In: Boitani L, Fuller TK (eds) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, NY, USA, pp 65–110

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rosell F, Bergan F, Parker H (1998) Scent-marking in the Eurasian beaver (*Castor fiber*) as a means of territory defense. J Chem Ecol 24:207–219

Rosell F, Nolet BA (1997) Factors affecting scent-marking behavior in Eurasian beaver (*Castor fiber*). J Chem Ecol 23:673–689

Rosell F, Sun L (1999) Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *C. fiber*. Wildl Biol 5:119–123

Rothmeyer SW, McKinstry MC, Anderson SH (2002) Tail attachment of modified ear-tag radio transmitters on beavers. Wildl Soc Bull 30: 425–429

Saïd S, Gaillard JM, Widmer O, Débias F, Bourgoin G, Delorme D, Roux C (2009) What shapes intra-specific variation in home range size? A case study of female roe deer. Oikos 118:1299–1306

Svendsen GE (1980) Seasonal change in feeding patterns of beaver in southeastern Ohio. J Wildl Manag 44:285–290

Šafář J (2002) Novodobé rozšíření bobra evropského v České republice [Modern distribution of the Eurasian beaver (*Castor fiber* L., 1758) in the Czech Republic]. Příroda 13:161–196

van Beest FM, Rivrud IM, Loe LE, Milner JM, Mysterud A (2011) What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? J Anim Ecol 80:771–785

Vorel A, Šafář J, Šimůnková K (2012) Recentní rozšíření bobra evropského (*Castor fiber*) v České republice v letech 2002–2012 (Rodentia: Castoridae) [Recent expansion of *Castor fiber* in the

Czech Republic during 2002–2012 (Rodentia: Castoridae)]. Lynx 43:149–179

Vorel A, Válková L, Hamšíková L, Maloň J, Korbelová J (2015) Beaver foraging behaviour: seasonal foraging specialization by a choosy generalist herbivore. Behav Ecol Sociobiol 69: 1221–1235

Wheatley M (1997a) Home range size and patterns of use in the taiga of southeastern Manitoba: I. Seasonal variation. Can Field Nat 111: 204–210

Wheatley M (1997b) Home range size and patterns of use in the taiga of southeastern Manitoba: III. Habitat variation. Can Field Nat 111: 217–222

Wilsson L (1971) Observations and experiments on the ethology of the European beaver (Castor fiber L.): a study in the development of phylogenetically adapted behaviour in a highly specialized mammal. Viltrevy 8:115–266

Zahner V (1997) Der Biber in Bayern. Eine Studie aus forstlicher Sicht [Beaver in Bayern. A study from forest view]. Bayerische Landesanstalt für Wald und Forstwirtschaft, Freising. Germany