# Compositional analysis and GPS/GIS for study of habitat selection by the European beaver, *Castor fiber* in the middle reaches of the Morava River

František JOHN and Vlastimil KOSTKAN

Department of Ecology and Environmental Sciences, Faculty of Science, Palacký University, tř. Svobody 26, 771 46 Olomouc, Czech Republic; e-mail: frantisek.john@post.cz, kost@prfnw.upol.cz

Received 23 June 2008; Accepted 17 October 2008

A b s t r a c t. The habitat selection of European beaver (*Castor fiber*) was studied in Central Moravia (the Czech Republic). The Global Positioning System and Geographic Information System were used for mapping the habitat types and marks of beaver activity. Used and available habitats were compared by compositional analyses in two levels. Comparison of habitat use from home range compared to habitat availability in the study area gave  $\Lambda = 0.335$  (P = 0.001), a simplified matrix ranked beaver habitat in the order: riverine willow scrub > willow-poplar forests of lowland rivers > hardwood forests > spruce plantations > meadows > reed and tall sedge beds > fields > river gravel banks > ruderal vegetation > oak-hornbeam forests > urbanized areas > ash-alder alluvial forests. Use of the habitat types based on the distribution of cut trees differed significantly from the habitat distribution within the home ranges (for habitat use quantified by number of cut trees  $\Lambda = 0.168$ , P = 0.001; for habitat use quantified by the time a beaver needs to cut trees  $\Lambda = 0.251$ , P = 0.003), the ranking matrix was: riverine willow scrub > willow-poplar forests of lowland rivers > ash-alder alluvial forests > hardwood forests of lowland rivers.

Key words: habitat preference, riparian habitats, home range, alluvial forests, Danube basin

#### Introduction

The European beaver (*Castor fiber*) population was declining until the 19<sup>th</sup> century in most regions in Europe. Thanks to protection, reintroductions and natural spread beavers are returning to areas from which they had been eradicated (H a 11 e y & R o s e 11 2002). In the Morava River basin European beavers were eradicated in the first half of the eighteenth century. Subsequently, 20 individuals were released in 1991 and 1992 to the study area. The releases were situated in Litovelské Pomoraví Protected Landscape Area. European beavers of the subspecies *Castor fiber vistulanus* Matschie, 1907, from the Suwalki area of north-east Poland (K o s t k a n & L e h k ý 1997) were chosen for the beaver release program. In 1996 the population was supplemented by one pair from Lithuania. Beavers also expanded from Austria, after 1980, to the Morava River basin. The Morava River is being continuously settled by beavers and the population is still expanding. The beaver population is also expanding in other parts of the Czech Republic, which were initially colonized by beavers from bordering countries. The regress of beavers is related with management tasks, i.e. knowledge of beaver habitat requirements which are necessary for beaver habitat assessment.

Earlier studies of European beaver habitat have provided only a general habitat description i.e. what is optimal and sub-optimal beaver habitat (Z u r o w s k i & K a s p e r c z y k 1988, H e i d e c k e 1989). However, in the studies carried out on American beaver (*Castor canadensis* Kuhl, 1820) populations the approach has focused more on animal responses related to specific environmental factors. Habitat characteristics

have been investigated in relation to beaver colony density (Slough & Sadleir 1977, Broschart et al. 1989), dam establishment (McComb et al. 1990, Barnes & Mallik 1997, Suzuki & McComb 1998), lodge site selection (Dieter & McCabe 1989), longevity of the beaver colonies (Howard & Larson 1985) and intensity of habitat usage (Beier & Barrett 1987). This focused approach has more recently been adopted by European researches. Hartman (1996) analyzed the disparity in specific features of unoccupied and occupied European beaver habitats in Sweden. Later work by Fustec et al. (2001) along the Loire River (France) analyzed the habitat features associated with beaver sites, then assessed habitat characteristics influencing beaver lodge establishment (Fustec et al. 2003).

An alternative habitat selection study design is to evaluate the habitat types as categorical data (land cover types) and to compare available and used habitat types. The proportional habitat use can be tested by a compositional analysis (A e b i s c h e r et al. 1993), which yields statistical comparisons among habitats and orders habitats in their relative preference. To evaluate habitat as a categorical data is easier than to measure more physical and vegetation habitat variables, which might provide an easier assessment of the habitat suitability for beavers for purposes of beaver management, moreover the existing maps of land cover could be used.

Although habitat selection is regarded as a hierarchical process, ranging from the selection of a geographical range to selection of a particular tree, the importance of the spatial scale of the habitat selection by beaver was not taken into consideration. J o h n s o n (1980) identified hierarchical ordering of selection processes. First-order selection can be defined as the selection of physical or geographical range of a species, within that range second-order selection determines the home range of an individual or social group. Third-order selection pertains to the usage made of various habitat components within the home range and actual procurement of food items from the feeding site can be termed fourth-order selection. The compositional analysis implements requirements for the habitat selection studies animal radio-tracking data are often used to monitor the animal activity patterns and to evaluate habitat use. Similarly signs of animal activity collected using a Global Positioning System (GPS) hand-handle receiver represent a sample of animal behavior patterns which could be used for habitat selection assessment.

This study describes habitat selection by beavers in floodplain forests, agricultural and urban landscapes along the Morava River. A method for evaluating habitat characteristics as categorical data (land cover types) using GIS and also a method for recording beaver activity signs using GPS were tested. Compositional analysis, which enables the comparison of used and available habitats at two scales, was carried out for evaluating habitat selection. At one scale the home range selection by beavers within the study area, at another scale habitat selection by beavers based on the locations of cut trees within the home range. By assessing the relative importance of a particular habitat type for beavers, it should be possible to propose a suitable landscape management system in relation to the conservation of a healthy beaver population.

#### **Study Area**

The study area was in Central Moravia (the Czech Republic) in a section of the Morava River (Danube basin) and along a semi-natural channel, Mlýnský Stream (Fig. 1). The Morava River section studied comprises a stretch (82 km) which falls from 290 m a.s.l. at 304<sup>th</sup> r. km.



Fig. 1. Map of the study area (A-upstream end of the study area, B-downstream end of the study area).

to 200 m a.s.l at 221<sup>st</sup> r. km. The full length of the Mlýnský Stream was studied (30 km); it branches out of the Morava River at 268<sup>th</sup> r. km and falls from 237 m a.s.l. to 205 m a.s.l. at the confluence with Morava River at 233<sup>rd</sup> r. km. Near Olomouc, the Morava River has an average flow of 20 m<sup>3</sup>s<sup>-1</sup>. The Morava River varies in width from 7 to 50 m; the Mlýnský Stream varies in width from 5 to 15 m. Annual precipitation ranges from 550 to 650 mm and mean temperature is 8.5 °C.

Of the studied water bodies, 31% of length has a natural character and flows through relatively well-preserved alluvial forests (Litovelské Pomoraví Protected Landscape Area), 55% is mostly regulated and stabilized and flows in an agricultural landscape (in this part the banks are often surrounded by remains of ash-alder alluvial forests) and 14% flows through the urban landscape and the banks are often stabilized by boulders.

The main part of the study area is upstream from the city of Olomouc and lies in the Litovelské Pomoraví Protected Landscape Area, a Ramsar Wetland of International Importance. The study area is also largely situated in two sites of Community Importance (SCIs) CZ0714073 – Litovelské Pomoraví (upstream from the city of Olomouc) and CZ0714085 – Morava – Chropyňský luh (downstream from the city of Olomouc). These are protected sites designated under the European Commission Directive on the conservation of natural habitats and of wild fauna and flora (92/43/EEC), also known as the Habitats Directive.

Thanks to the expansion of the beaver population the Morava River seems to be continuously settled by beavers. There are no beaver dams in the study area, because the studied stretches provide stable water levels, moreover the river is too large for beavers to dam.

#### **Material and Methods**

The study area (from the viewpoint of compositional analysis) was arbitrarily defined as the 50 m wide zone parallel to the water's edges on both banks and included any islands in the channels. The choice to limit the study area to that distance from the river-edge was based on earlier observation of the limits of beaver activity marks (feeding sites) (K ostkan et al. 2002). In Geographic Information System (GIS) (ArcView v. 3.1, Environmental Systems Research Institute) the study area was delineated on the basis of aerial photography (pixel 0.5 m, optimizing for the scale 1: 5000, Geodis Brno 2003). At first, the shorelines were delineated, which were buffered with a fixed width of 50 m. In the study area, habitats were mapped and classed into twelve groups: ash-alder alluvial forests, hardwood forests of lowland rivers, willow-poplar forests of lowland rivers, riverine willow scrub, river gravel banks, reed and tall sedge beds, oak-hornbeam forests, meadows, fields, spruce plantations, ruderal vegetation outside human settlements and urbanized areas. The characteristics of habitat types (plant communities) were derived from the habitat catalogue of the Czech Republic (Chytrý et al. 2000). The habitat types were mapped from May 2004 to September 2005 using hand-handle GPS receiver (Meridian Color) and aerial photography, delineated in GIS by georeferenced aerial photographs. The field study was conducted by foot and by canoe.

From December 2005 to March 2006 all current signs of beaver presence (cut trees, bark stripping, tracks, scent mounds, lodges etc.) were collected using a hand-handle GPS receiver. Cut trees and shrubs were recorded by genus and grouped into classes based on their diameter (cm) at the cut: 0 - 2.5, 2.5 - 6, 12 - 20, 20 - 30, 30 - 40 and 40 - 50. Interval widths were smaller for the first three classes to capture more detail of smaller diameters which dominated (K o s t k a n et al. 2002).

For each colony the home range was estimated in the GIS environment using the GPS locations of the signs of beaver presence. The colony is a fundamental unit of a beaver population; it typically consists of four to eight related individuals occupying a pond or section of a stream (J e n k i n s & B u s h e r 1979). Traditionally, a defended area is termed a territory, while the entire area which is used by an animal or a group is termed the home range. The feeding areas more distant from the water can be consider as being part of the beavers home range, while the beavers territory encompasses the impoundments with lodges, dams, canals, trails and food caches (M ü l l e r - S c h w a r z e & S u n 2003). Locations of colony sites were readily determined from the presence of recent lodges, feeding sites and scent mounds. The primary indicator of a beaver colony's location was

therefore considered to be an active winter lodge. If no lodge was identified during the field work, the winter food store or a site with heavy cutting was considered as a secondary indicator of a beaver colony location.. The individual beaver family home ranges were separated by a section of stream without beaver signs, but there was difficulty in delineating colony borders where such a section did not exist. In these cases we used the method proposed by F u s t e c et al. (2001). Because the beaver territory in a river system is linear, two territories A and B could be differentiated by measuring the spacing between four successive signs (s1, s2, s3, s4). Each home range size was assessed by the distance separating each newly found sign (s2) from the previously found sign (s1). When the distance between s2 and s3 (s2, s3) was greater than both distances (s1, s2) and (s3, s4), s1 and s2 were attributable to territory A, s3 and s4 to territory B. Home range was measured as a linear distance along the channel in the width of study area (50 m on both banks). In such defined home range polygons the habitats used by the beaver family were highlighted using GIS.

According to J o h n s o n (1980), available and used habitats were compared at two scale levels; examining home range selection within the total study area first (Johnson's second-order selection), the proportional habitat use based on the locations of cut trees within the home range (Johnson's third-order selection). In the second-order selection used and available habitats were compared with the proportion of areas of habitat types. In the third-order selection available habitats were quantified as shapes of habitats available in home ranges and habitat utilization was quantified in a separate analyses as i) the proportion of GPS locations of cut trees within each habitat type. The values of the time required by a beaver to cut a tree matched to the diameter class midpoints were computed using the model by B e l o v s k y (1984), in which cutting time (T) was estimated as T = 0.63 exp(0.24d), r2 = 0.94, p ≤ 0.05, where d = stem diameter (cm).

For comparison of used and available habitats compositional analysis was used (A e b i s c h e r et al. 1993) implemented in package Adehabitat v. 1.7.1. (C a l e n g e 2006) of the statistical software R (R Development Core Team 2007). The randomization test was used with the number of repetitions 1000; the zero values occurring in the matrix of used habitats were replaced with the small number 0.01. Seven colonies in which only one used habitat occurred were dropped from the third-order habitat selection. The habitat types with the lowest ranking in the second order selection were dropped in the third order selection, apart from the ash-alder alluvial forests. Although this habitat type is generally avoided, 516 cut trees (13% of all cut trees) were found in ash-alder alluvial forests. It was considered that such a significant percentage should be included in the third order selection. In the unfavoured habitats dropped from the third order selection analysis there were only 54 cut trees, which is only 1.3% of all cut trees.

## Results

Hardwood forests of lowland rivers represented 26% of the habitats and together with other floodplain forests (ash-alder alluvial forests and willow-poplar forests) they covered 43% of the study area. Habitat types in which bushy and tall Salicaceae are dominant species (riverine willow scrub and willow-poplar forests of lowland rivers) covered only 10.1%. Agricultural habitats (fields, meadows) covered 35% of the study area (Fig. 2).



**Fig. 2.** Proportions of particular habitat types in the study area (HF-hardwood forests of lowland rivers, F-fields, UA-urbanized areas, M-meadows, AA-ash-alder alluvial forests, WP-willow-poplar forests of lowland rivers, RW-riverine willow scrub, RG-river gravel banks, OH-oak-hornbeam forests, RU-ruderal vegetation outside human settlements, RT-reed and tall sedge beds, SP-spruce plantations).

In total, 4992 signs of beaver activity were recorded in the study area, 80% were cut trees (n = 4017), seventy seven percent of them were willows (*Salix* spp.). Other foraging tree species were poplars (*Populus* spp.) 7.2%, bird-cherry (*Padus avium* Mill.) 5.2%, alders (*Alnus* spp.) 3.5%, ash tree (*Fraxinus excelsior* L.) 3.4%, common hazel (*Corylus avellana* L.) 2.6%. Other used woody species, representing 1.1% of all cut trees, included: lime (*Tilia* spp.), silver birch (*Betula pendula* Roth.), oak (*Quercus* spp.), spruce (*Picea* spp.), elder (*Sambucus nigra* L.), apple (*Malus domestica* Borkh.), spindle (*Euonymus* spp.), European hornbeam (*Carpinus betulus* L.) and dogwood (*Cornus sanguinea* L.).

Fifty eight beaver colonies were distinguished from the data collected on beaver activity signs. Mean length of a colony home range was  $1246 \pm 70$  SE m, min 416 m, max 2456 m. The average beaver colony density was 0.5 colonies.km<sup>-1</sup>. Per colony there were recorded  $69 \pm 14$  SE cut trees.

Comparison of habitat use from home range with habitat availability in the study area (second-order selection) gave  $\Lambda = 0.335$  (P = 0.001), i.e. beavers do not establish a home range at random. A simplified matrix (Table 1) ranked beaver habitat in the order: riverine willow scrub > willow-poplar forests of lowland rivers > hardwood forests of lowland rivers > spruce plantations > meadows > reed and tall sedge beds > fields > river gravel banks > ruderal vegetation outside human settlements > oak-hornbeam forests > urbanized areas > ash-alder alluvial forests.

Use of the habitat types based on GPS locations of cut woody plant distribution differed significantly from the habitat proportions within the home ranges ( $\Lambda = 0.168$ , P = 0.001). A ranking matrix (Table 2) ordered the habitat types in the sequence: riverine willow scrub > willow-poplar forests of lowland rivers > ash-alder alluvial forests > hardwood forests of lowland rivers.

Table 1. Simplified ranking matrices based on comparing proportional habitat use within home range with proportions of habitats available in the study area (+ preference, - avoidance, a triple sign represents significant deviation from random at P < 0.05, abbreviations of habitat types are the same as in Fig. 2).

Habitats	RW	WP	HF	SP	М	RU	F	RG	RT	OH	AA	UA
Riverine willow scrub	0	+	+	+++	+++	+++	+++	+++	+++	+++	+++	+++
Willow-poplar forests	-	0	+	+	+	+++	+	+++	+++	+++	+++	+++
Hardwood forests	-	-	0	+	+	+	+	+	+++	+++	+++	+++
Spruce plantations		-	-	0	+	+	+	+	+++	+++	+++	+++
Meadows		-	-	-	0	+	+	+	+++	+++	+++	+++
Ruderal vegetation			-	-	-	0	+	+	+++	+++	+++	+++
Fields		-	-	-	-	-	0	+	+++	+++	+++	+++
River gravel banks			-	-	-	-	-	0	+++	+++	+++	+++
Reed and tall sedge beds									0	+	+	+++
Oak-hornbeam forests									-	0	+	+++
Ash-alder alluvial forests									-	-	0	+
Urbanized areas											-	0

**Table 2.** Simplified ranking matrices based on comparing the proportions of GPS points of cut tree locations for each home range in each habitat type with the proportion of each habitat type within the home range (+ preference, - avoidance, a triple sign represents significant deviation from random at P < 0.05, abbreviations of habitat types are the same as in Fig. 2).

Habitats	RW	WP	AA	HF
Riverine willow scrub	0	+++	+++	+++
Willow-poplar forests		0	+	+++
Ash-alder alluvial forests		-	0	+
Hardwood forests			-	0

**Table 3.** Simplified ranking matrices based on comparing the proportion of time a beaver took to cut a woody plant within each habitat type with the proportion of each habitat type within the home range (+ preference, - avoidance, a triple sign represents significant deviation from random at P < 0.05, abbreviations of habitat types are the same as in Fig. 2).

Habitats	RW	WP	AA	HF
Riverine willow scrub	0	+	+++	+++
Willow-poplar forests	-	0	+	+++
Ash-alder alluvial forests		-	0	+
Hardwood forests			-	0

The compositional analyses carried out on the proportions a beaver took to cut trees in each habitat type gave  $\Lambda = 0.251$ , P = 0.003, a ranking matrix (Table 3) ordered the habitat types in the sequence: riverine willow scrub > willow-poplar forests of lowland rivers > ash-alder alluvial forests > hardwood forests of lowland rivers. When the habitat use was quantified based on comparing the proportions of cut tree locations for each home range in each habitat type, willow-poplar forests against riverine willow scrub (and visa versa) was significant.

### Discussion

Although there are more home range estimators that could infer about the intensity of habitat use based on utility distribution, i.e. harmonic mean (D i x o n & C h a p m a n 1980) or kernel

methods (Worton 1989), in our study a method was used that ignored all information that could provide interior data points (locations of feeding sites, lodges etc.). We suggested that the used method for home range estimation and quantification corresponds to the tested hypothesis of habitat use measured by compositional analyses in two levels. The hypothesis about different intensity of use in parts of home ranges was tested in the third order habitat selection. From this point of view, the used home range estimator provides a more sensitive index than an arbitrarily defined study area. The used home range estimator could sufficiently quantify habitats used by a beaver family within the study area and quantify habitats available for individuals of the beaver family within the home range. The most commonly used animal home range estimator is the minimum convex polygon (MCP) (Hayne 1949). We suggested that the home range estimator used in our study is more precise for animals living in a linear riverine habitat because the MCP could incorporate large areas that are not used by beavers, i.e. agricultural fields at a distance of hundreds of meters from the banks in meanders. The MCP estimator was used by C a m p b e 11 et al. (2005) in the Biesbosch (Netherland) for beaver home range determination, where MCP is more suitable with regard to estuary habitat. A similar method to that used in our study based on measurement of linear distance of beaver home range was used by F u s t e c et al. (2001) in Loire River (France).

In this study beaver home range was determined to be  $1246 \pm 70$  SE long; such a size was considered to be relatively close to home range estimates for American beaver in South Carolina, where extreme activity points within one colony, in one year, were from 84 to 1863 m apart (D a v i s et al. 1984). However, it is suspected that European beaver may prefer a larger home range. In the Loire River a beaver colony home range was determined to be 5.54 km, in this particular beaver population the home range size had a negative relationship with vegetation cover (F u s t e c et al. 2001). This is in a contrast to a study on beaver populations in the Biesbosch and Telemark (Norway), that report a positive trend between territory size and proportions of deciduous habitat (C a m p b e 11 et al. 2005). Territory size in the Biesbosch was 12.8 km and in Telemark 4 km. In this study, settlement pattern and reproductive history had a lasting impact in the territorial system of beavers due to a combination of low adult mortality, high dispersal costs, and avoidance of resource depletion. The smaller beaver home ranges in Morava River in comparison with other European beaver studies could be caused by relatively rich habitats and the late phase of colonization. The beaver population in the study area appears to be at carrying capacity. C a m p b e 11 et al. (2005) described a settlement pattern where the territories of the beavers released first were roughly twice the size of the territories of beavers released in later years.

In our study signs of beaver activity were used to indicate beaver location data and habitat use. Another methodological approach, which could be used throughout the year, is radio tracking. This method could provide more detailed information about space use by beavers and may describe more aspects of beaver behavior, not only the cutting of the trees. The presented results provide an analysis of beaver habitat use at a large (landscape) scale. Telemetry has often been used for studying beaver dispersal (D a v i s et al. 1984, S u n et al. 2000, C a m p b e 11 et al. 2005, M c N e w & W o o 1 f 2005), nevertheless, until now beaver locations were not used sufficiently in beaver habitat selections studies.

The results of third order selection do not depend much on the method of quantification of the cut trees. The difference in significant selection of willow scrub against the willowpoplar forests was based on the fact that in the willow scrub the trees of smaller diameter classes occurred more frequently than in other habitat types. If the cut trees were quantified frequently based on the time the beaver needs to cut a tree, the trees with a larger stem diameter are of greater importance in the habitat used matrix against trees with a smaller stem diameter. It means the rate of cut trees among habitat types is greater in willow scrub when the habitat use was quantified frequently based on number of cut trees. To estimate the cutting time the model by B e l o v s k y (1984) was chosen because an alternative model published by F r y x e 11 & D o u c e t (1993) is usable only for smaller stem diameters under 5 cm. Another quantifying method is to evaluate cut trees based on the biomass of the cut trees. Comparing the models for predicting biomass of cut trees and for evaluation of cutting time (B e l o v s k y 1984, F r y x e 11 & D o u c e t 1993, B r u c e & B r i a n 1995) it may be stated that the estimator based on the biomass of the cut trees. It means that compositional analysis using cut trees based on biomass could have similar results as the estimators used in this study.

The preference of habitat types corresponds with the importance of trees as food, for lodge building and canopy cover. Many beaver food studies indicated that beavers prefer willows (Salix spp.) and poplars (Populus spp.), in the study area the importance of willows and poplars in beaver food were described by K o s t k a n et al. (2002). Preferred willows (S. triandra L., S. viminalis L., S. fragilis L., S. purpurea L.) are the dominant species of the most preferred habitat type in both selection orders riverine willow scrub, moreover the trunk diameter of these willow species is small and beavers are know to prefer small diameter trees in the study area (K o s t k a n et al. 2002). Willows (S. alba L., S. fragilis L.) and poplars (P. alba L., P. nigra L.) are the dominant species of the second most preferred habitat type in both selection orders willow-poplar forests of lowland rivers. The less preferred cut trees occurred in the less preferred habitat types. Food selection by beavers also depends on factors other than tree species and trunk diameter. In their foraging behaviour, beavers move out from the water to select and cut trees, and then transport the cut wood to aquatic feeding stations before consumption (J e n k i n s 1980). In keeping with the central-place foraging theory, the beaver foraging intensity declined with increasing distance from the safety of the lodge (Fryxell & Doucet 1991, Fryxell 1992, Haarberg & Rosell 2006). In addition, the selection of riparian woody habitats depends also on their spatial distribution. The most preferred habitat type, riverine willow scrub, is generally located near the water or in the water during floods. The second most used habitat, willow-poplar forests, are generally behind the riverine willow scrub, closer to water's edge than the hardwood forests or ash-alluvial forests. Some avoided habitat types are characterized with absent tree canopy cover. The importance of tree canopy cover and physical variables in habitat suitability for beaver has been noted in several studies (Slough & Sadleir 1977, Howard & Larson 1985, Dieter & McCabe 1989, M c C o m b et al. 1990, F u s t e c et al. 2001), whereas in other studies it was reported that the vegetative characteristics added little to the beaver habitat models and geomorphic variables were more important (Beier & Barrett 1987, Hartman 1996, Suzuki & McComb 1998). Beavers can also establish colonies in the urban landscape (P a c h i n g e r & H u l i k 1999); this habitat type may only get used when the population density is high. F u s t e c et al. (2003) noted that favorable beaver lodge sites decreases as the human impact increases.

Intact riparian willow woods with a natural water regime are of crucial importance to the conservation of healthy beaver populations (N o l e t & R o s e 11 1998). In the study area

habitats in which bushy and tall Salicaceae are the dominant species covered only 10.1%, however, these habitats are characterized by fast natural reproduction. Riverine willow scrub and willow-poplar forests of lowland rivers are important not only due to trophic needs, but also because beavers often establish their lodges in these habitat types. During floods other habitat types, which provide more appropriate sites for lodge establishment, in which dry places are available, are more important. Such habitat types often occur on the top of the riverbank; these are ash-alder alluvial forests and hardwood forests of lowland rivers. Litovelské Pomoraví Protected Landscape has such a mosaic of relatively well-preserved riparian woods and is an area where river dynamics are allowed to shape the flood plain in a natural way. It is considered that in such a natural river system beavers attain a higher fecundity than elsewhere.

Although the beaver can use more habitat types, our research indicates that the most preferred habitats are riverine willow scrub and willow-poplar forests. Although depending on river conditions, ash-alder alluvial forests and hardwood forests of lowland rivers are often used with a higher intensity. This result could be used in management decisions. The presence of preferred habitat types is crucial for the long term survival of beaver populations.

Acknowledgements

This study was supported by the Universities Development Foundation (FRVS G4 53/2004).

## LITERATURE

- Aebischer N.J., Robertson P.A. & Kenward R.E. 1993: Compositional analysis of habitat use from animal radiotracking data. *Ecology* 74: 1313–1325.
- Barnes D.M. & Mallik A.U. 1997: Habitat factors influencing beaver dam establishment in a northern Ontario watershed. J. Wildl. Manage. 61: 1371–1377.
- Beier P. & Barrett R.H. 1987: Beaver habitat use and impact in the Truckee Basin, California. J. Wildl. Manage. 51: 794–799.
- Belovsky G.E. 1984: Summer diet optimization by beaver. Am. Mid. Nat. 111: 209-222.
- Broschart M.R., Johnston C.A. & Naiman R.J. 1989: Predicting beaver colony density in boreal landscapes. J. Wildl. Manage. 53: 929–934.
- Bruce W.B. & Brian S.C. 1995: Predicting biomass of beaver food from willow stem diameters. J. Range Management 48: 322-326.
- Calenge C. 2006: The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* 197: 516–519.
- Campbell R.D., Rosell F., Nolet B.A. & Dijkstra V.A.A. 2005: Territory and group sizes in Eurasian beavers (Castor fiber): echoes of settlement and reproduction? Behav. Ecol. Sociobiol. 58: 597–607.
- Chytrý M., Kučera T. & Kočí M. 2000: Katalog biotopů České republiky: Interpretační příručka k evropským programům Natura 2000 a Smaragd (Habitat Catalogue of the Czech Republic: Interpretation Manual for the European programmes Natura 2000 and Emerald). AOPAK ČR, Praha, 262 pp. (in Czech with English summary)
- Davis J.R., Recum A.F., Smith D.D. & Guynn D.C. 1984: Implantable telemetry in beaver. *Wildl. Soc. Bull.12:* 322–324.
- Dieter C.D. & McCabe T.P. 1989: Factors influencing beaver lodge-site selection on a prairie River. Am. Mid. Nat. 122: 408-411.

Dixon K.R. & Chapman J.A. 1980: Harmonic mean measure of animal activity areas. Ecology 61: 1040–1044.

Fryxell J.M. 1992: Space use by beavers in relation to resource abundance. Oikos 64: 474-478.

- Fryxell J.M. & Doucet C.M. 1991: Provisioning time and central place foraging in beavers. Can. J. Zool. 69: 1308–1313.
- Fryxell J.M. & Doucet C.M. 1993: Diet choice and the functional response of beavers. Ecology 74: 1297-1306.
- Fustec J., Cormier J.P. & Lodé T. 2003: Beaver lodge location on the upstream Loire River. CR Biol. 326: 192-199.
- Fustec J., Lode T., Le Jacques D. & Cormier J.P. 2001: Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. *Freshwat. Biol.* 46: 1361–1371.
- Haarberg O. & Rosell F. 2006: Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. J. Zool. 270: 201–208.
- Halley D.J. & Rosell F. 2002: The beaver's reconquest of Eurasia: status, population development and management of a conservation success. *Mammal Rev. 32: 153–178*.
- Hartman G. 1996: Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. J. Zool. 240: 317–325.
- Hayne D.W. 1949: Calculation of size of home range. J. Mammal. 30: 1-18.
- Heidecke D. 1989: Ökologische Bewertung von Biberhabitaten. Säugetierkundliche Informationen 3: 13–28 (in German).
- Howard R.J. & Larson J.S. 1985: A stream habitat classification system for beaver. J. Wildl. Manage. 49: 19-25.
- Jenkins S.H. 1980: A size-distance relation in food selection by beavers. Ecology 61: 740-746.
- Jenkins S.H. & Busher P.E. 1979: Castor canadensis. Mammalian species 120: 1-8.
- Johnson D.H. 1980: The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- Kostkan V. & Lehký J. 1997: The Litovelské Pomoraví floodplain forest as a habitat for the reintroduction of the European beaver (*Castor fiber*) into Czech Republic. *Global Ecol. Biogeogr. 6: 307–310.*
- Kostkan V., John F. & Vávrová P. 2002: Kácení dřevin bobrem evropským (Castor fiber L.) na střední Moravě (Wood foraging in central Moravia by the European beaver (Castor fiber L.)). Přírodovědné studie Muzea Prostějovska 5: 87–97 (in Czech with English summary).
- McComb W.C., Sedell J.R. & Buchholz T.D. 1990: Dam-site selection by beavers in an eastern Oregon basin. Great Basin Naturalist 50: 273–281.
- McNew L. & Woolf A. 2005: Dispersal and survival of juvenile beavers (*Castor canadensis*) in southern Illinois. *Am. Mid. Nat.* 154: 217–228.
- Müller-Schwarze D. & Sun L. 2003: The beaver: Natural history of a wetlands engineer. Cornell University Press, Ithaca, 208 pp.
- Nolet B.A. & Rosell F. 1998: Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. *Biol. Conserv.* 83: 165–173.
- Pachinger K. & Hulik T. 1999: Beavers in an urban landscape: The recent activity of beavers (*Castor fiber*) in the greater Bratislava area. In: Busher P. & Dzieciolowski R.M. (eds), Beaver protection management and utilization in Europe and North America. *Kluwer Academic/Plenum Publishers, New York: 53–60.*
- R Development Core Team 2007: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at: http://www.R-project.org.
- Slough B.G. & Sadleir R.M.F.S. 1977: A land capability classification system for beaver (*Castor canadensis*). *Can. J. Zool. 55: 1324–1335.*
- Sun L., Müller-Schwarze D. & Schulte B.A. 2000: Dispersal pattern and effective population size of the beaver. Can. J. Zool. 78: 393–398.
- Suzuki N. & McComb W.C. 1998: Habitat classification models for beaver (*Castor canadensis*) in the streams of the central Oregon coast range. *Northwest Sci.* 72: 102–110.
- Worton B.J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.
- Zurowski W. & Kasperczyk B. 1988: Effects of reintroduction of European beaver in the lowlands of the Vistula basin. Acta Theriol. 33: 325–338.