ECOGRAPHY

Research

The importance of spatial scale in habitat selection by European beaver

Adrian Zwolicki, Rafał Pudełko, Katarzyna Moskal, Joanna Świderska, Szymon Saath and Agata Weydmann

A. Zwolicki (http://orcid.org/0000-0003-2710-681X) (adrian.zwolicki@ug.edu.pl), K. Moskal, J. Świderska and S. Saath, Univ. of Gdańsk, Dept of Vertebrate Ecology and Zoology, Gdańsk, Poland. – A. Weydmann, Univ. of Gdańsk, Inst. of Oceanography, Gdynia, Poland. AZ and AW also at: AZB analysis and software, Gdynia, Poland. – R. Pudełko, Inst. of Soil Science and Plant Cultivation State Research Inst., Dept of Bioeconomy and Systems Analysis, Puławy, Poland.

We evaluated habitat selection by European beaver *Castor fiber* L. across a spatial gradient from local (within the family territory) to a broad, ecoregional scale. Based on aerial photography, we assessed the habitat composition of 150 beaver territories along the main water bodies of the Vistula River delta (northern Poland) and compared these data with 183 randomly selected sites not occupied by the species. The beavers preferred habitats with high availability of woody plants, including shrubs, and avoided anthropogenically modified habitats, such as arable lands. Within a single family territory, we observed decreasing woody plant cover with increasing distance from a colony centre, which suggests that beaver habitat preferences depend on the assessment of both the abundance and spatial distribution of preferred habitat elements. We tested the importance of spatial scale in beaver habitat selection with principal coordinates of neighbour matrices analysis, which showed that the geographical scale explained 46.7% of the variation in habitat composition, while the local beaver density explained only 10.3% of this variability. We found two main spatial gradients that were related to the broad spatial scale: first, the most important gradient was related to the largest distances between beaver sites and was independent of woody plant cover and the local beaver site density. The second most important gradient appeared more locally and was associated with these variables. Our results indicate that European beaver habitat selection was affected by different scale-related phenomena related 1) to central place foraging behaviour, which resulted in the clumped distribution of woody plants within the territory, and 2) local population density and woody plant cover. Finally, 3) habitat selection occurs independently across the largest spatial scale studied (e.g. between watersheds), which was probably due to the limited natal dispersal range of the animals.

Keywords: *Castor fiber*, spatial habitat structure, space dependent habitat selection, Vistula River delta

Introduction

The importance of spatial scale in ecology has been increasingly appreciated, and has been quantitatively expressed since the 1980s and '90s (Wiens 1989, Steele 1991, Levin 1992). Rooted in the concept that variation in ecological metrics often changes with different geographical scales, it is increasingly clear that numerous ecological phenomena are scale-dependent, including animal behaviour and the related theme of habitat selection (Schneider 2001, Mayor et al. 2009a, Cassini 2013).

All animals consume resources. Therefore, habitat selection must rely on a qualitative assessment of different types of resources mostly related to the foraging ecology of a species, including food quality and availability, but also the availability of resting and hiding places, or breeding areas (Morris 2003). Additionally, preferences towards certain environmental conditions are scale-dependent because the distribution of resources often changes spatially (Morris and Davidson 2000, Cassini 2013). The process of habitat selection is also modified by biotic interactions such as predator avoidance, as well as intra- and inter-specific competition (Fretwell and Lucas 1969, Rosenzweig 1981, Morris 2003). Moreover, the area over which any individual is able to assess environmental features or quality is limited both by their own sensory capabilities and by the dispersal distances of individuals, which are often smaller than a population distribution (Morris 1992). The valuation of local resources in herbivorous animals is mainly related to food availability and vegetation phenology (Mayor et al. 2009b, Mancinelli et al. 2015, Dupke et al. 2017). The spatial scale over which selection occurs varies among species and is influenced by their mobility and the senses employed, such as sight. Hence, caribou *Rangifer tarandus* habitat selection in Newfoundland was most evident at distances up to 15 km (Mayor et al. 2009b), while red deer *Cervus elaphus* in the Pyrenees Mountains responded to their environment at the scale of approximately 1 km (Schaefer et al. 2008).

Habitat selection at broad scales constrains that at lower levels, and the costs of habitat selection also vary with spatial scale (Johnson 1980, Cassini 2013). During selection within the scale of habitat patches, animal costs are linked to a foraging strategy and to time spent moving through suboptimal microhabitat patches, when this time could be used for exploiting the habitat or potentially better ones (Cassini 2013). At the macrohabitat or landscape scale, the costs are linked to emigration and, hence, can be modelled as the time lost to reproduction during this process (Morris 1987). Habitat selection plays an important role, especially in long-lived and territorial herbivores, such as beavers *Castor*, for which a settlement decision is crucial, and has long-lasting consequences for the survival and reproduction of a colony (Fryxell 2001, Campbell et al. 2005).

The European beaver *Castor fiber* L. is the largest native rodent in Europe and was common until the Middle Ages, after which it was driven to the verge of extinction by over-hunting for fur and castoreum. In Poland, beaver populations were fully extirpated by 1945, but they have since been successfully reintroduced (Żurowski and Kasperczyk 1986, Dzięciołowski and Gozdziewski 1999). The recolonization by beavers in Europe is relatively well documented, as the species disperses and occupies habitat along watercourses, leaving visible marks of their occupancy, such as lodges, dams, or freshly cut trees (Nolet and Rosell 1998, John and Kostkan 2009). In the dispersal phase, beavers follow a logistic population growth pattern with a characteristic dampening as the population approaches carrying capacity (Bartak et al. 2013). In recent decades, after nearly a half-century of absence, beavers have rapidly colonized their historical distribution (Rosell et al. 2012), making them a useful model species for characterizing the process of habitat selection in different stages of a population development (Hartman 1995, Pinto et al. 2009, John et al. 2010, Swinnen et al. 2017).

During the initial phases of recolonization, beaver populations are relatively sparse and optimal habitats are the first to be selected. As preferred habitats are occupied, population density gradually increases, forcing beavers to occupy less-attractive territories (Nolet and Rosell 1994, Hartman 1995, Fustec et al. 2001, John et al. 2010). The sequence of arrival of parental pairs into unoccupied areas is likely to play an important role in determining the size of the family territory, as early arrivals occupy larger and higher-quality territories, even after a few years of colonization (Campbell et al. 2005).

Habitat selection is the result of the preference for particular food sources, which, for beavers, comprise deciduous woody plants, and in European riparian habitats, this is mostly represented by willow-scrub communities (Nolet et al. 1994, Fustec et al. 2001, John and Kostkan 2009, Pinto et al. 2009). Outside the period of vegetative growth, woody plants are often the only food source, and consequently, they are crucial for winter survival (Jenkins and Busher 1979, Tyurnin 1983). Therefore, beaver habitat quality could be related to the proportion of woody plant cover within family territories.

Beavers actively mark and defend their territories to protect resources. They normally live as a family unit (colony), which consists of a monogamous adult pair, yearlings born the previous year, and any kits born in the current year (Rosell et al. 2006). Older young (2–3 yr) generally emigrate to new areas, although they may delay dispersal up to the age of 7 yr (Mayer et al. 2017), or if these young beavers fail to establish territories, they may return to the parental colony (Collen and Gibson 2001). The local density of a beaver population is influenced largely by habitat quality, and family home ranges depend on vegetation cover, which implies that extensive growth of preferred plants on riverbanks is needed to maintain a beaver population (Fustec et al. 2001). Moreover, territoriality and habitat selectivity are interrelated because a settlement decision must consider existing territories. Consequently, European beavers meet the predictions of an ideal despotic model (IDD; Fretwell and Lucas (1969).

Habitat selection is a hierarchical process based on behavioural decisions governed by the assessment or usage of resources at different scales. Johnson (1980) described four orders of this hierarchy, which range from the geographical distribution of a species (1st order) to the home range or territory (2nd order), the utilization of habitat patches within these home ranges/territories (3rd order), and the preferences for particular food items within these habitat patches (4th order). The importance of both biotic and abiotic factors has been recognized for habitat selection mostly across 2nd and 3rd order of Johnson's scale (Beier and Barrett 1987, Hartman 1996, Fustec et al. 2001, Campbell et al. 2005, Pinto et al. 2009, John et al. 2010) for both the European and Canadian beaver *C. canadensis* Kuhl. John and Kostkan (2009), in the Morava River, described 2nd and 3rd-order selection, in which habitat preferences were non-random. However, they did not describe the spatial variability between habitats in 2nd-order selection, and did not test beaver preferences relative to the spatial distribution of certain resources within a territory.

The goal of our study was to assess the importance of spatial scale in habitat selection by European beaver across a gradient of scales, from a local scale related mostly to the distribution of woody plants within a family territory, which might be determined by the central place foraging strategy (3rd order selection of Johnson's scale), to a broad geographical ecoregion scale, which could depend on the local population density and differences in habitat quality between distant water bodies or animal dispersion limitations (2nd order selection). As a suitable place to study this phenomenon, we selected the Vistula River delta, which is an anthropogenically modified environment that was quite recently recolonized by European beavers.

Material and methods

Study area

The Vistula River flows in a northerly direction across Poland for over 1000 km. It is the largest unregulated river in Europe, and at its outlet to the Baltic Sea the river forms a wide delta called the Vistula Delta or Żuławy Fens (Fig. 1), which covers an area of ca 2320 km² and has an average human population density of 145 inhabitants per km² (Pruszak et al. 2005). Geologically, the Vistula Delta is relatively young (ca 6000 yr old); the flat area is covered by relatively homogenous alluvial soils, and it is located between hills of glacial origin to the east and west and sandbars to the north. Because a large part of the area (30%) is located below sea level, systems of rivers, channels, ditches, and pumping stations have been constructed in the area over the past several centuries. The rivers and channels in the delta area spread and flow in different directions, forming a network of multiple watercourses which are generally shallow and slow-flowing. The delta has very homogenous geomorphology, geology, and soil structure that, along with the genesis related to fluvial processes and climate similarities, results in homogeneous vegetation (Kondracki 2000, Cassini 2013). Our study area covers all main watercourses in the Vistula River delta and includes a mosaic of habitat qualities, from semi-natural areas such as the Vistula River, to highly modified areas, including the Piaskowy, Śledziowy, Linawa, and Panieński channels.

Within the Żuławy Fens system, we also studied the Drużno Reserve, located on the east side of the Vistula River delta (Fig. 1a) and surrounded by extensive mires and swamp-forest. While the landforms and the canal-system of
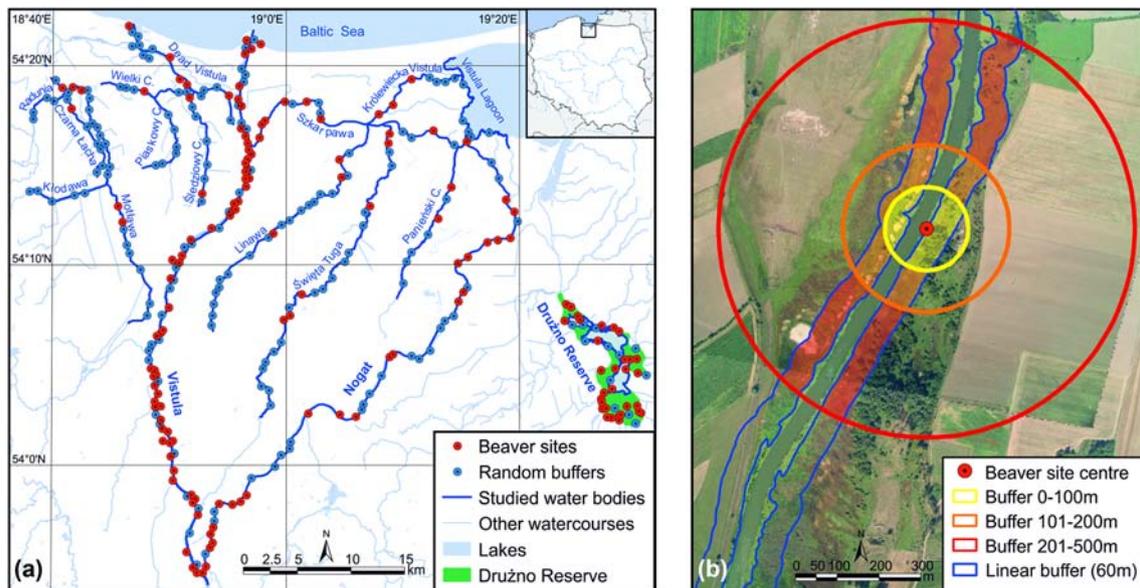
Figure 1. Beaver territories and randomly distributed sites in the Vistula River delta, including the Drużno Reserve (a), and an example of buffer designation as applied to orthophotomaps around a beaver centre point located in the Nogat River (b).

Drużno Reserve (the lake and the surrounding canals) make it similar to the watercourses of the Vistula Delta, it is a protected nature reserve that is located within the European Union network of protected areas Natura 2000 and listed under both the Habitats Directive and the Birds Directive (PLH280028 and PLB280013, respectively), which makes it a suitable location to study beaver behaviour in an optimal, natural habitat.

The recolonization of beavers in the Vistula Delta likely began in the mid-90s (Gromadzka 1996). In 2001, four beaver families were reported in the western part of the Vistula Delta (Aszyk and Kistowski 2002). The first signs of beaver in the Drużno Reserve were noted in 2001, and the first lodge was found in 2002 (Ciechanowski et al. 2013). One potential source of this population was natural dispersal from other rivers of the Vistula River basin, where beavers had been reintroduced. The nearest introduction occurred in 1979 in the Wda River basin, which flows into the Vistula approximately 70 km south of the study area (Aszyk 1994).

Fieldwork

Fieldwork was carried out during two consecutive seasons: Nov 2011 – Apr 2012 and Oct 2012 – Apr 2013. The dates were chosen according to the seasons of high beaver activity in late autumn, winter, and early spring, when traces of their presence, such as tree cuts, girdles, food piles, and scent mounds, are clearly visible. The study area, which covered all main water bodies of the Vistula River delta (rivers, channels, and ponds), as well as the Drużno Reserve (total shoreline length of 794.51 km, see the Supplementary material in Appendix 1 for details), were checked for evidence of beaver activity, mainly from the banks and along watercourses from a canoe. We explored the waterbodies and their surroundings up to 60 m perpendicular to the shoreline; previous studies have documented a sharp decline in the activities of these semiaquatic animals over this distance from water (Jenkins 1980, Fryxell 1992, Donkor and Fryxell 1999).

The geographic positions of all signs of beaver activity up to 60 m from the water were registered by Garmin GPS receivers (accuracy ~5m); this included tracks, faeces, scent mounds, canals, feeding stations, cut trees and branches, bark stripping, dams, burrows, building of lodges, and winter food caches. The latter two signs, along with additional information based on observations and scent mounds, were regarded as evidence of recently occupied territories (colonies, beaver sites) and treated as the central points of family home ranges (Simunkova and Vorel 2015).

Beaver colony status

The presence of beavers in a given area can be detected based on the key signs of their activity, which are (in this order of importance): 1) winter food supply, 2) beaver lodge, 3) main den, and 4) geographical centres of feeding remains (e.g.

heaps of tree or shrub branches located on the shoreline). Based on the presence of old and fresh signs of beaver activity, colonies were assigned to three types: 1) abandoned, with the presence of old signs only; 2) uncertain, clearly separated from other signs and family territories with a few new signs of beaver activity but without any key signs; and 3) of a certain functional status. All analyses presented in this study were performed on data from selected beaver sites, characterized as those in which at least one of the fresh key signs was present (most frequently a winter food supply and/or a family lodge with fresh signs of activity) and usually contained numerous other fresh signs (mostly slides and indications of feeding).

An important step in distinguishing the beaver sites was to determine a centre and the borders of a family territory. In the field, potential boundaries were defined preliminarily during tracking. This was followed by verification based on a visual analysis of the distribution of the key signs, scent marking mounds, and all types of feeding signs with the use of digital maps. The colony centre was defined by the presence of key signs, according to above order of importance, such that, for example, in the absence of any winter food supply (key sign no. 1), a family lodge (key sign no. 2) was defined as a centre point, etc.

GIS analyses

Aerial photography

To document the current state of land use, assess beaver habitat preferences, and evaluate food resources over the study area, we took a series of aerial photographs using a gyro-stabilized photographic platform attached to a Cessna 172 aircraft (flights taken on 10 and 11 Sept 2012). Aerial photography was taken with a Fujifilm IS-1 digital camera in the visible band. Due to the available flight altitude, the ground resolution of the resulting photos was between 0.2 and 0.7 m. Maintenance of the vertical optical axis during image triggering enabled semi-automatic calibration and mosaicking of the photos to the orthophotomap, which covered the selected watercourses and the shores of Lake Drużno, as well as a buffer zone of 60 m.

Data processing

Digital image interpretation and spatial analysis of the beaver habitat were performed in Quantum GIS (Lisboa 1.8.0 release). Selected aerial photos were calibrated using the Raster/Georeferencer module. We applied a polynomial transformation method with nearest-neighbour resampling. Mapping used the PUWG 1992 coordinate system, and the pixel resolution of the orthophotomap was set at 0.5 m. Due to the altitude (1500–2000 m a.g.l.) of the aerial photography and the almost completely flat terrain, the calibration of the photographs did not require a digital elevation model. Image calibration reference points were determined on the ground by measuring, with a GPS receiver, the position of locations in the field that were readily identified in aerial photographs. An analysis of the accuracy of the orthophotomap

was carried out on an independent sample of ground control points and showed a root mean square error (RMSE) of less than 5 m.

Because beavers exploit habitats only in the immediate vicinity of water, all further analyses were restricted to a linear 60 m buffer along the studied watercourses (Jenkins 1980, Donkor and Fryxell 1999, John and Kostkan 2009; Fig. 1b), similar to that employed during fieldwork. Based on the aerial photography within this buffer, a comprehensive land cover map was prepared by manual digitalisation. This process was conducted as precisely as possible with a special focus on separating vegetation land use classes. The quality control performed on 60 selected fragments showed that the differences between the surfaces of the digitized polygons and their actual surfaces were ≤ 1%. We distinguished eight land use classes: 1) 'arable land' – all cultivated arable fields (cadastral parcels; during the survey (Sept), the fields were most often ploughed, which further facilitated the recognition of this land use class); 2) 'grassland' – all cadastral agricultural parcels used as meadows and pastures; 3) 'shrubs' – large shrub clusters; 4) 'forest' – detached complexes where trees dominated; 5) 'trees and shrubs' – single trees and small clusters of shrubs that were located far from the larger complexes classified as class 3 or 4 in polygon format (this latter class was registered as a point layer; thus, it was possible to record all objects important to beaver food resources in detail in all defined classes (polygons)); 6) 'fallow land' – non-shrub area covered mostly by natural vegetation (this class also covers areas that are difficult to define as other land use patterns, including flood embankments, ground roads, paths, undeveloped tracts, and unused parts of agricultural and urban parcels); 7) 'urban area' – all artificial areas covered by any type of anthropogenic infrastructure: buildings, paved roads, landfills, and fenced areas; 8) 'small water bodies' – old riverbeds, small canals, and tributaries of other watercourses. The land use types that were distinguished could be described as habitat components or patches differing from their surroundings (Cassini 2013). Therefore, in our study, habitat composition is defined as the proportion of different land use patches in the 60 m linear buffer along a shoreline.

To compare areas occupied by beavers with those not inhabited, a series of random points were selected along the studied watercourses and > 500 m from the nearest beaver territory. This resulted in the selection of 183 areas (Fig. 1a) that were used for comparison with occupied territories. To assess coverage by designated land use classes within the beaver territories and in randomly selected areas, we designated a buffer of 0–500 m around the centres of both the beaver territories and the 183 randomly selected points; to reiterate, these include only the area within the 60 m buffer adjacent to the shoreline (Fig. 1b). The size of this buffer was based on previous findings that the average beaver territory included approximately 1 km of river (hence, 2 km of shoreline) (Hartman 1994, Rosell et al. 1998, Rosell and Hovde 2001, Fustec et al. 2003). As such, in many cases this buffer did not cover the entire territory. However, according to a

study in a similar riparian habitat, the buffer included the most exploited part of the beaver home range, where the usage of *Salix* species decreased rapidly up to 500 m from the den (Nolet et al. 1994).

In addition, to investigate the spatial land use structure within the 0–500 m buffers, we distinguished multiple ring buffers (nested polygons of successive concentric zones that do not overlap) of 0–100, 101–200 and 201–500 m in both beaver and random areas. In all cases we only measured and compared land use data within the 60 m linear buffer along the shoreline. The buffer ranges extracted by this method are presented in Fig. 1b.

Statistical analyses

To test general beaver habitat preferences (2nd-order selection), we compared the composition of all land use types in territories occupied by beavers and randomly selected unoccupied territories using a permutational multivariate analysis of variance (PERMANOVA with 999 permutations) with a repeated measures design, where 0–100, 101–200, and 201–500 m rings were tested jointly between beaver sites and random sites (Anderson et al. 2008). SIMPER (similarity percentages) analysis was run to decompose the average Bray-Curtis dissimilarities between each land use type at beaver and random sites (Clarke 1993). The analysis operates at the level of each dependent variable, resulting, in our case, in a percentage value of mean dissimilarity between the groups of each land use type separately. This allows us to quantify the percent contribution of a certain land use type to differences between the beaver and random sites, and thus, to identify the likely major contributors to these differences. Land use class data were square-root transformed and standardized per sample (Clarke and Gorley 2006).

To test 3rd-order selection, which describes the local scale pattern within the 2nd-order selection of land use composition between beaver sites and randomly selected sites, we applied a repeated measures analysis of variance (rmANOVA) for all multiple ring buffers (0–100, 101–200 and 201–500 m). To reduce the number of zeros in the land use class data, which could bias the results due to the different area sizes of the repeated buffers, we combined the following land cover classes into higher categories: shrubs, forest, as well as trees and shrubs (categories 3 to 5 above) were combined with the woody plants category, while arable land, grassland, fallow land and urban area (categories 1, 2, 6 and 7, respectively) were combined with the anthropogenic category. The grouping was based on beaver preferences, understood as major contributors to differences between the beaver and random sites, as indicated by the SIMPER analysis performed beforehand (Supplementary material Appendix 1 Table A2).

A detrended correspondence analysis (DCA) was used to explore the theoretical environmental gradients in the data (Supplementary material Appendix 1 Table A3) and: 1) to illustrate variability between the beaver and random sites, 2) to calculate the variability in the land use composition in

the beaver sites only, which was then used to calculate the efficiency of constrained models (Supplementary material Appendix 1 Table A4). Both DCA models were based on all land use classes within the 0–500 m buffer (ter Braak and Šmilauer 2012).

Due to the importance of spatial scale in ecological research, a number of studies have assessed and quantified the influence of scale on species or communities. A recently developed method that has been applied successfully to both terrestrial (Legendre et al. 2009, Peres-Neto and Legendre 2010) and marine systems (Weydmann et al. 2014) is principal coordinates of neighbour matrices (PCNM), also known as Moran's Eigenvector Maps (MEM). This method can be applied to a set of sites with good sampling area coverage to quantify the spatial structure of ecological data that originates either from the physical forcing of environmental variables or from community processes (Borcard and Legendre 2002). Based on the order of the principal coordinates (PCO, eigenfunctions), it also provides an opportunity to assess the significance of different spatial scales (broad, intermediate, or fine) on the model species or community under consideration (Legendre et al. 2009). In the PCNM method, spatial variables are used to determine distances between studied sites, especially the neighbouring ones. These distances, which are presented as the Euclidean distance matrix and calculated from spatial data (e.g. latitude and longitude values), are then decomposed into a new set of independent spatial variables (orthogonal eigenfunctions), which may be used as independent variables in constrained ordination analyses.

Therefore, we used the PCNM method with variation partitioning analysis (VP) to test how variation in habitat composition among beaver sites depends on their spatial distribution and on the density of beaver sites (Supplementary material Appendix 1 Table A5). Variation partitioning attempts to resolve the explanatory power (described by the percent of explained variation) of different independent variables in relation to the set of multivariate response variables. This way, it is possible to assess the unique and shared (partitioned) fraction of variation in data, explained by different independent variables. VP could be calculated based on constrained ordination, which in this study followed unimodal canonical correspondence analyses (CCA), resulting in the partitioning of data variation between the spatial variable, calculated previously by PCNM, and the density of beaver sites (Økland and Eilertsen 1994, Borcard and Legendre 2002).

We calculated the efficiency with which environmental variables from the constrained ordination models (CCA, VP) explained non-random variability in the data (%) by dividing the percentage of the variability explained by a given environmental factor by that explained by the first four axes of the DCA (ter Braak and Šmilauer 2012). The number of axes in the ordination models was defined based on their eigenvalues. Also, we used four axes in all presented models to compare both CCA and VP with the same unconstrained model, this way the efficiency values of each variable were

coherent between the models. In all ordination techniques, a log-transformation $[x' = \log(x + 1)]$ was used to normalize the data. The verification of statistical hypotheses was performed with the Monte Carlo test (999 permutations). For multiple comparisons, we used Holm's (1979) correction to control the familywise type I errors.

To determine the relationship between local density of beaver sites (for the 0–500 m buffer between the overlapping areas of neighbouring beaver colonies) and cover of woody plants and anthropogenic land use, we performed Spearman's rank correlation. The local density was calculated as the proportion of the overlapping area of the 500 m buffers between neighbouring colonies, while the latitude and longitude of a colony centre were used as the geographical location. To present these relationships, we employed generalized additive models (GAMs) with the Akaike information criterion (AIC) to find the best fit of the model.

PERMANOVA and SIMPER analyses were run in PRIMER ver. 6.0 (Plymouth Marine Laboratory, Plymouth, UK), while Spearman's rank correlation and rmANOVA in STATISTICA ver. 13.1 (<www.statsoft.com/Products/STATISTICA-Features>). The ordination techniques like VP with PCNM, DCA, CCA and GAMs were performed in Canoco ver. 5.10 (ter Braak and Šmilauer 2012).

Results

Density and distribution of beaver sites

Based on 10 540 signs of beaver activity, we distinguished 150 recently occupied territories in the Vistula River Delta (Supplementary material Appendix 1 Table A1). The greatest number of territories were noted in the Vistula River (n = 49), Drużno Reserve (30), and the Nogat River (25), while the lowest number was found in channels (Linawa (3), Panieński and Śledziowy (2 each), and Czarna Łacha (1); Fig. 1a). The highest beaver densities were also recorded for the Vistula River and the ponds within its floodplains (0.41 and 0.87 colonies km^{-1}, respectively), Drużno Reserve (0.39, 0.86 on the canals), followed by the rivers: Szkarpawa (0.18), Nogat (0.17) and Wisła Królewiecka (0.16). The lowest density was found in the channels (0.05–0.07 colonies km^{-1}).

Habitat selection

Significant differences in land use composition between beaver sites (n = 150) and randomly distributed sites not inhabited by beavers (n = 183) were revealed based on the PERMANOVA repeated measures analysis (ID of sites nested in beavers vs random factor, p = 0.001; Table 1a). The post hoc comparisons showed significant differences between the beaver vs random sites in all ranges (pairs in the 0–100 m, 101–200 m, and 201–500 m rings; p = 0.001). Additionally, beaver sites and random sites differed significantly in the composition of land cover (habitat types) with increasing

Table 1. PERMANOVA comparisons of all distinguished land use types (a) and repeated measures ANOVA of woody plant cover (combination of trees and shrubs, forest, and shrubs) and anthropogenic areas (combination of fallow land, arable land, grassland, and urban area) (b) between the sites occupied by beavers and randomly selected unoccupied sites. The post hoc results from the ANOVA are presented in Fig. 2. *: 0–100, 101–200 and 201–500 m rings.

(a)

Variables	PERMANOVA, Factor/design	df	SS	MS	Pseudo-F	p
All land use types	Beaver vs random	1	67027.0	67027.0	17.7	0.001
	Beaver vs random × distance*	2	4251.5	2125.8	3.5	0.004
	ID of sites nested in (beaver vs random)	331	1264400.0	3819.8	6.4	0.001
	Residuals (unexplained)	658	395790.0	601.5	–	–
	Total	994	1745300.0	–	–	–

(b)

Variables	ANOVA, Factor/design	df	SS	MS	F	p
Woody plants	Beaver vs random	1	56560.9	56560.9	46.6	< 0.001
	Beaver vs random × distance*	2	7141.6	3570.8	10.4	< 0.001
Anthropogenic	Beaver vs random	1	78926	78926	62.7	< 0.001
	Beaver vs random × distance*	2	9782	4891	13.3	< 0.001

distance from the territory centre (beaver vs random x distance from the nested colony centre point; Table 1a).

Detailed comparisons of all distinguished land cover types between beaver sites and randomly distributed sites were clearly described by the SIMPER analysis (Supplementary material Appendix 1 Table A2). The average dissimilarity between the sites reached the highest value of 60% between the 0–100 m rings and decreased gradually with increasing distance from the colony centre (101–200 m, 55.7% and 201–500 m, 51.6%). For all distances, the most differentiating land cover type was Arable land, which dominated the randomly distributed areas and reached up to 23.6% of the observed dissimilarity in the 0–100 m ring. Fallow lands had the highest average cover in all ranges, reaching up to 28.1% in the 0–100 m ring, and had the second highest dissimilarity between respective rings (21.2%) with higher proportions in the outer two rings in beaver sites, apart from the ring closest to the centres of the beaver territories (beaver 26.2% vs random 28.1% in 0–100 m). Generally, beaver sites showed higher mean values for all types of woody plant land cover (trees and shrubs 16.2% vs 3.0%, forest 0.4% vs 0.1% and shrubs 0.9% vs 0.3%; all in the 0–100 m range), with trees and shrubs representing the greatest proportion and having the highest contribution to the dissimilarity, reaching 20.7% in the 0–100 m ring. The lowest contribution to the dissimilarity between beaver sites and randomly distributed sites was revealed for small water bodies (up to 3.1% in the 0–100 m ring), although the beaver sites were characterized by at least five times greater average cover of this land use type in all three nested rings. Urban area were lower in beaver sites than in random site in all compared rings (Supplementary material Appendix 1 Table A2).

Spatial distribution of resources within beaver family territories

Based on the SIMPER results, we grouped land use types as either preferred woody plants (shrubs, forest, trees and shrubs) or avoided anthropogenic lands (arable land, grassland, fallow land, urban area) to analyse the distribution of these broader classes within beaver buffers. The rmANOVA revealed a significantly higher average cover of woody plants, and lower cover of anthropogenic lands, in all rings within beaver sites relative to random sites (Table 1b, Fig. 2), with the proportion of woody plants reaching the highest values in the 0–100 m ring and decreasing in 101–200 and 201–500 m rings (Fig. 2a), while the average proportion of anthropogenic land use increased with increasing distance from the centre of the beaver territory (Fig. 2b). There was no such gradient in the case of the random sites, where the distribution of the tested land cover types remained similar in the 0–100, 101–200 and 201–500 m rings, which indicates that the differences between beaver sites and random areas were additionally increased by different spatial distributions of the avoided and preferred land use types (see ANOVA interaction: beaver × distance in Table 1b).

Habitat variability and beaver density on a large spatial scale

Comparison of the habitat composition between the 0–500 m buffers established in beaver territories and those in random sites showed substantial overlap between these two categories in DCA ordination space, indicating that they were quite similar (Fig. 3a, Supplementary material Appendix 1 Table A3). At the same time, according to the gradient length (Axis1 = 3.12, Axis2 = 3.02) the beaver territories were relatively diverse regarding the composition of land use types. The above results suggest that there were other factors, such as spatial autocorrelation and differences between distant water bodies (especially between Lake Drużno and the Vistula and Nogat river systems), that influenced both habitat selection and habitat composition (Fig. 3b). This geographical variation was tested in comparison with local beaver density (described as the percentage overlap of the 0–500 m buffer) by variation partitioning (VP) with the PCNM analysis, which was based
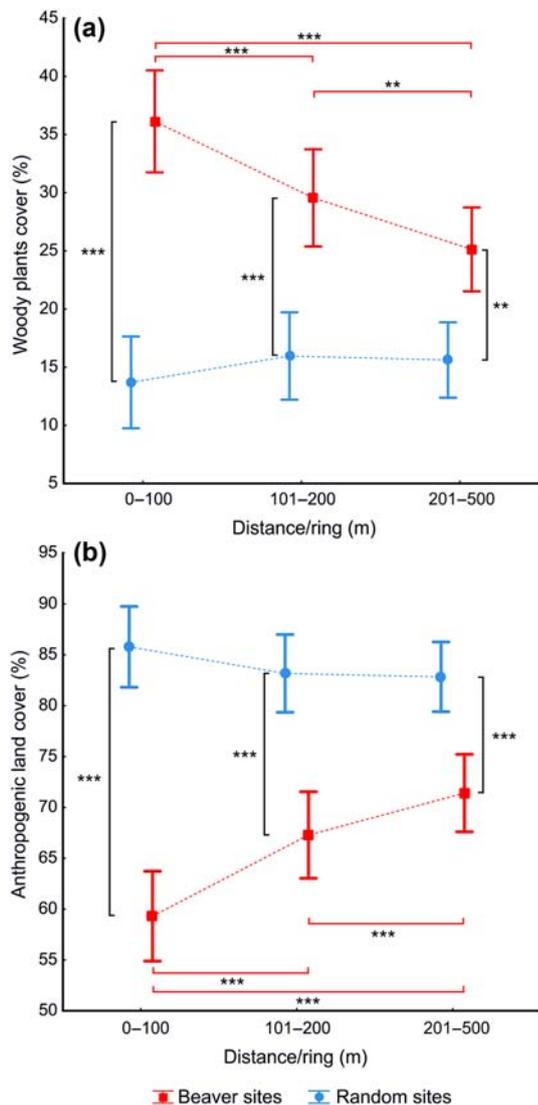
Figure 2. Land-use characteristics in sequential rings (0–100, 101–200 and 201–500 m) surrounding beaver sites (red) and non-occupied random sites (blue); (a) woody plant cover (combination of trees and shrubs, forests, and shrubs); (b) anthropogenic areas (combination of fallow land, arable land, grassland, urban area). Points represent mean values and the whiskers indicate the 95% confidence intervals (CI). Significant post hoc Tukey test comparisons are presented as vertical or horizontal brackets; $* = p < 0.05$, $** = p < 0.01$ and $*** = p < 0.001$. For a detailed description of the ANOVA results see Table 1b.

on data from beaver sites only. All tested variables (i.e., beaver density [pseudo-F = 9.9, df = 1, p = 0.001], geographical position of the colony [pseudo-F = 5.2, df = 16, p = 0.001], and joined variation [pseudo-F = 5.3, p = 0.001]) were significant. The geographical location of a colony explained the largest fraction of variability of land use composition in beaver sites (efficiency = 46.7%), while in the case of local beaver density the geographical location explained only 10.3% of the beaver habitat variability, and the shared variation explained 7.6% (Fig. 4a, Supplementary material Appendix 1 Table A5).

Among the spatial predictors from the 33 PCO eigenfunctions that were obtained, 16 were statistically significant (Monte-Carlo permutation test p < 0.042, Supplementary material Appendix 1 Table A5). Among these predictors, the largest portions of the spatial variability were explained by PCO.1 (14.2%) and PCO.4 (7.2%) (Fig. 4b, Supplementary material Appendix 1 Table A6). The CCA plot presents a clear separation between the beaver sites from the different water bodies within the spatial gradients, which were selected as most important (Fig. 4d, Supplementary material Appendix 1 Table A7). The first eigenvector (PCO.1) describes the differences in beaver territories at the broad scale, mostly between the Drużno Reserve and other water bodies, and this gradient showed no correlation with the local beaver density and percentage of woody plant cover ($r_s = -0.08$, p = 0.327 and $r_s = -0.05$, p = 0.517 respectively; Fig. 4e). PCO.4 illustrates fluctuations at the intermediate-scale within the main water bodies, clearly visible along the Vistula River but also within the Drużno Reserve, and it was significantly correlated with beaver density and woody plant cover ($r_s = -0.31$, p < 0.001 and $r_s = -0.20$, p < 0.016, respectively; Fig. 4f). This result implies that the differences between the habitats selected by beavers depended mostly on their broad-scale spatial distribution, while on a more local scale, they were related to the local density of beaver sites and availability of food resources.

In addition, we found a highly significant correlation between the local beaver density and habitat quality. The percentage of overlap of the 0–500 m buffers occupied by beavers was positively correlated with the proportion of woody plant cover ($r_s = 0.69$, p < 0.001, GAM $R^2 = 28.1\%$, p < 0.001; Fig. 5a) and negatively with anthropogenic land use type ($r_s = -0.74$, p < 0.001; GAM $R^2 = 40.7\%$, p < 0.001; Fig. 5b).

Discussion

In the Vistula River delta, European beaver preferred riparian habitats with large proportions of woody plants, such as shrubs, and lower cover by anthropogenic land use types, particularly arable lands. However, it is worth stressing that the variability of these habitats was dependent on both local (family territory) and ecoregion scales, which has not been previously reported in this species. Our results imply that the ideal despotic model of habitat selection (IDD) was affected not only by the density of these territorial animals but also through the spatial variation of the habitat (Fretwell and Lucas 1969).

Habitat selection

Habitat composition in beaver territories differed significantly from that of random areas. These differences resulted from the avoidance of arable lands and the clear preference for areas covered by woody plants (Shrubs, Forest, Trees and shrubs land use types; Supplementary material Appendix 1 Table A2). The most substantial difference was observed in
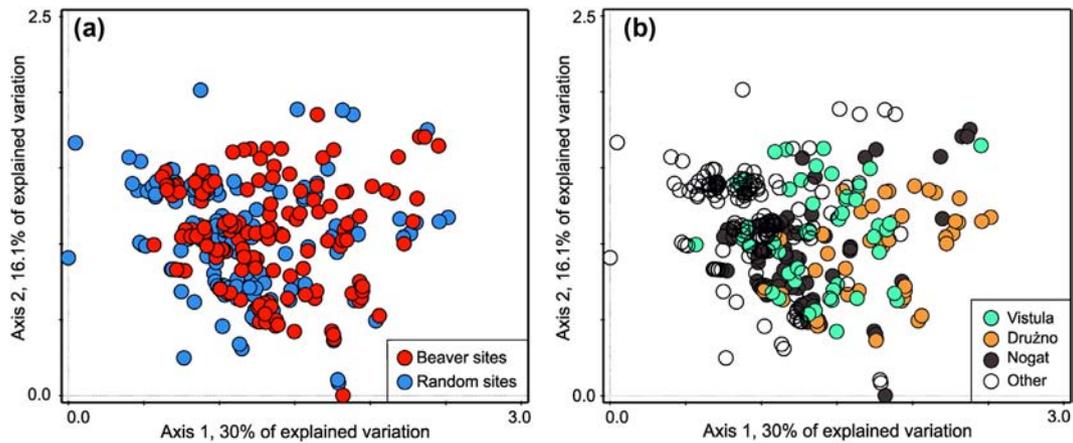
Figure 3. Detrended correspondence analysis (DCA) ordination plot based on the composition of all distinguished land cover types within the 0–500 m buffer for (a) the beaver sites (red points) and random sites (blue points) and (b) selected water bodies.

the average Trees and shrubs cover, which was up to 5 times higher in the centre of beaver territories (0–100 m ring) than in the centre of random sites. This result was not surprising, however, as many previous studies have reported similar observations (Hartman 1996, Fustec et al. 2001, John and Kostkan 2009, Pinto et al. 2009, John et al. 2010).

Both the beaver and random areas were covered primarily by fallow land, a remnant of high anthropogenic pressure. The two areas also showed similar average fallow land cover, which suggests that fallow lands could be treated as neutral habitat elements. Fallow land also corresponded to the second highest contribution to the dissimilarity measure between occupied and unoccupied areas. Such seemingly contradictory results could be because the preferences of beavers towards this land use type change with the proportion of preferred woody plants. These results agree with earlier work that showed how the importance of habitat variables may change during the colonization process (John et al. 2010). This result might also be related to the flexibility of beavers, which can inhabit and reproduce in different habitats, including semi-natural and cultivated landscapes (Nolet and Rosell 1998).

Urban areas provided some of the lowest proportions in both beaver and non-occupied habitats; however, this land use type was avoided by animals in all ranges, which also has been reported previously (e.g. from the Morava River basin; John et al. 2010). Some preferences could be observed for even the smallest land cover type, which was represented by small water bodies. The proportion of this land cover type was higher near colony centres, and the average values were higher in beaver territories at all distances. This could reflect the real preference of the species, and it may result from the engineering activities of beaver, such as digging canals. However, this result was not related to building dams because such constructions were observed in three beaver sites only.

At the end of the last century the beaver population in Sweden was still increasing and animals settled only in optimal habitats; therefore, beaver sites and non-occupied areas

differed significantly (Hartman 1996), in marked contrast to our study. The similarity in beaver and random sites, that we document for the Vistula River delta, was manifested by the large variation within both beaver sites and random areas (Fig. 3), and a large part of the variation was represented by the residuals in PERMANOVA (Table 1a). Beavers occupied a wide variety of habitats, from optimal (Drużno Reserve and Vistula River) and suboptimal (Nogat River) to marginal (other studied watercourses), which could reflect the fact that all preferred habitats had already been occupied, so colonization slowed or stopped. Additionally, the similarity between occupied and non-occupied areas may be related to the fact that the current food conditions in beaver territories has altered since settlement (Wright et al. 2002). Such a pattern is characteristic of a population that represents the number and density of animals close to the carrying capacity for the available area (John et al. 2010).

Beavers colonize the best habitats during the initial phase of population development, and as their numbers increase they switch to lower quality environments (Fustec et al. 2001, Pinto et al. 2009, John et al. 2010). Based on the results of this study, we conclude that the Vistula River delta beaver population was at, or near, carrying capacity. The densities of beaver sites between the water bodies we studied differed from 0.05 to 0.86 colonies km^{-1}, reaching relatively high values in the Drużno Reserve and the Vistula River when compared to other studies (0.12 km^{-1}, Fustec et al. 2003; 0.25 km^{-1}, Hartman 1994; 0.72 km^{-1}, Rosell and Hovde 2001; 0.76 km^{-1}, Rosell et al. 1998). The reason for such a high density may be due to the high quality of the riparian environment, which was mostly overgrown by willow scrub that is favored by beavers (Nolet et al. 1994, Fustec et al. 2001, John and Kostkan 2009, Buliński et al. 2013). Willow habitat may be an important predictive variable for beaver settlement in both optimal and suboptimal/marginal habitats during the expansion phases before a population reaches carrying capacity (Fustec et al. 2001, John et al. 2010).
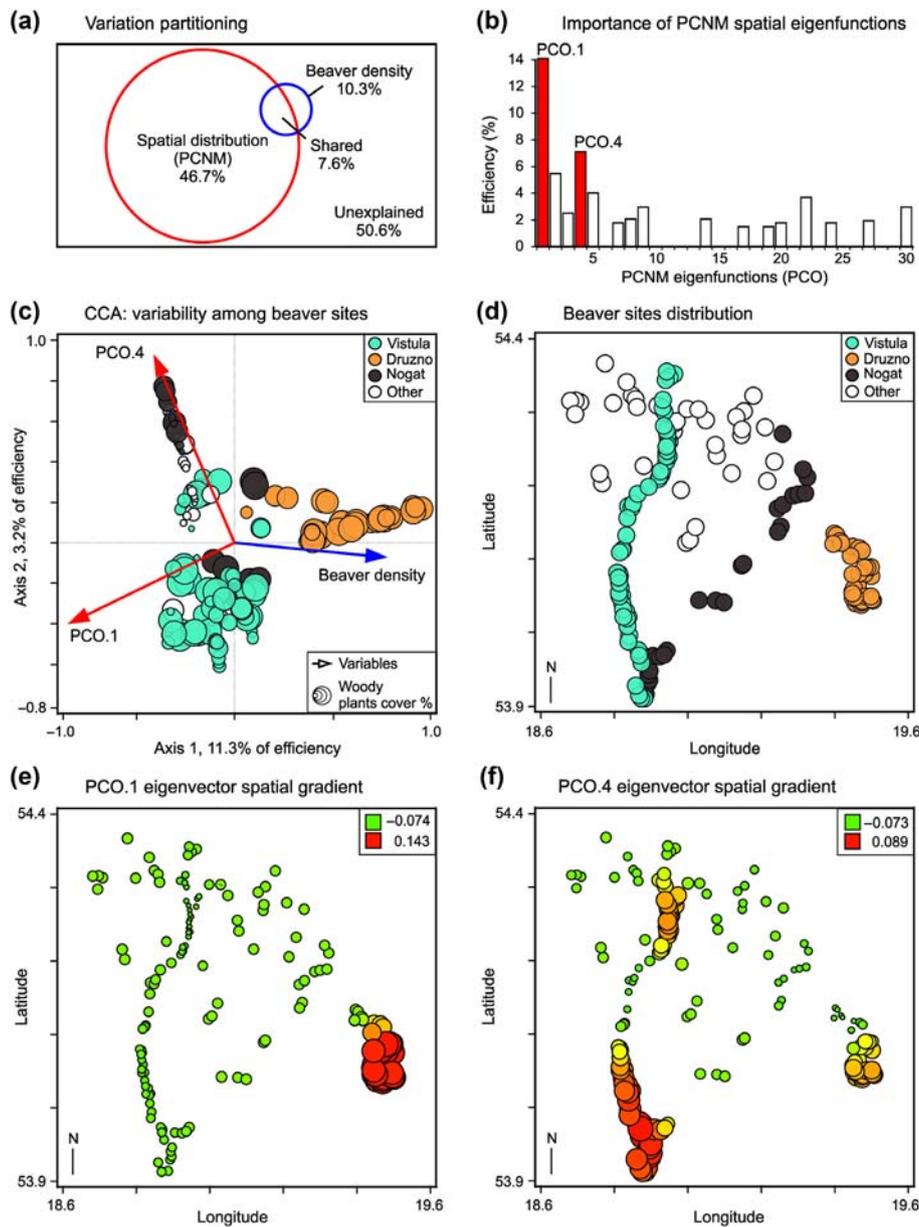
Figure 4. Results of variation partitioning (VP) with principal coordinates of neighbour matrices analysis (PCNM) and associated analyses. (a) Venn diagram of variation partitioning presenting unique and shared fractions of the total variation in beaver sites land use composition that are explained by both geographic location (using the PCNM method) and local density of beaver sites (all VP fractions, Monte Carlo permutation test p = 0.001, Supplementary material Appendix 1 Table A5). (b) Bar chart of significant eigenfunctions illustrating different spatial scales, derived from the PCNM analysis, which were used in the variation partitioning model (Monte Carlo permutation test p ≤ 0.042, Supplementary material Appendix 1 Table A6). (c) CCA plot presenting the variability of land cover composition among beaver sites (points) in relation to the main spatial gradients (PCO.1 and PCO.4 eigenfunctions from PCNM) and the local beaver sites density. (d) Spatial distribution of beaver sites along the main watercourses in the Vistula River Fens. (e) and (f) Values of key eigenfunctions (PCO.1 and PCO.4, respectively) as a function of their geographic location in the Vistula River Fens.

Spatial habitat structure within a family territory

Our study also indicated that the habitats preferred by beavers could be distinguished by the spatial distribution of favoured and avoided land use types along the shore of a watercourse. With increasing distance from a lodge, den, or winter food supply, the percentage of woody plants decreased while anthropogenic area increased. This preference was also confirmed by the decrease in the total dissimilarity between beaver sites and unoccupied areas within the subsequent 0–100, 101–200, and 201–500 m ranges from a colony centre, as indicated by the SIMPER analysis.

Such preferences for a clearly clumped distribution of woody plants within a beaver territory (3rd-order selection)
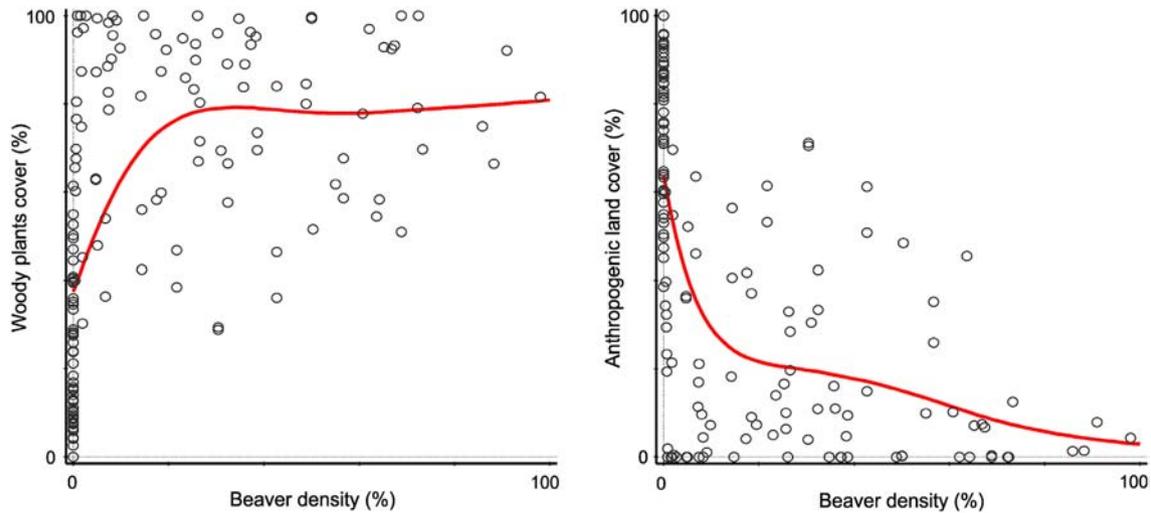
196

Figure 5. General additive models (GAM) between the local density based on the percentage overlap of the beaver sites and (a) the percentage cover of woody plants and (b) anthropogenic lands for the 500 m buffer from a colony centre.

may be beneficial from the optimal foraging theory viewpoint because the majority of food resources is localised in the vicinity of a family lodge (MacArthur and Pianka 1966). Our study shows that beaver prefers habitats where the most valuable, available, and abundant resources are located near a territory centre or in the direct vicinity of a family lodge or winter food supply to reduce the cost of food transportation. Beavers are well-known as central place foragers, and foraging time or size of food items decreases with increasing perpendicular distance from a riverbank or pond (Orians and Pearson 1979, Schoener 1979, Jenkins 1980, Fryxell and Doucet 1991, Fryxell 1992). Therefore, during the process of colonization or natal dispersal, a settlement decision should be based not only on the local abundance of food resources but also on the clumped spatial distribution of these resources within a home range, which may be especially important for the long-term occupation and utilization of a certain territory (Wright et al. 2002).

The importance of a large spatial scale in habitat selection

The ideal despotic model of habitat selection describes how the quality of selected habitats depends on population density, where a settlement decision is possible only in unoccupied areas (Fretwell and Lucas 1969, Fretwell 1972). Based on the GAM, we determined that the local beaver density was positively correlated with the abundance of woody plants and negatively with anthropogenic lands, which confirms previous findings (Fustec et al. 2001, Pinto et al. 2009, John et al. 2010). We believe that this is a consequence of larger territories in poorer-quality habitat, leading to lower densities (Fustec et al. 2001, Wright et al. 2002). The GAM plots (Fig. 5) also illustrate a large spread of points, which suggests that the dataset was influenced by other important variables,

one of which may be the spatial distribution of beaver sites at a broad ecoregion scale.

Our study suggests that the spatial scale for habitat selection is more important than the density of occupied territories. The results of the variation partitioning showed that the importance of spatial scale, represented by 16 significant eigenfunctions in the PCNM, explained over 14 times more of the habitat variation between beaver sites, compared to the local beaver density. The most influential spatial gradients, represented by PCO.1 and PCO.4, provided two completely different interpretations of spatial scale. The broad-scale spatial component, which could be attributed to the entire ecoregion level and was represented by the principal coordinate PCO.1, was independent of local beaver density and woody plant cover, whereas PCO.4 described a more local situation, in which the spatial gradient was correlated with both of these variables.

During habitat selection, which occurs at a local scale, animals assess the quality of food resources; as a consequence, the habitat differences at broader spatial scales are not considered by an animal during this selection stage (Mayor et al. 2009b). The habitats distributed along the water bodies of the Vistula River delta vary in quality, which could not be evaluated by a single beaver during dispersal. This factor likely is the reason why our results based on the PCNM showed that the composition of beaver territories differed mostly with the largest geographical distance between them, which was reflected by the highest proportion of variation explained by the first principal coordinate (Legendre et al. 2009). Moreover, the composition of beaver territories at the broad ecoregion scale was independent of beaver density and the proportion of woody plants. These findings showed that 2nd-order habitat selection by beavers was spatially limited and dependent on both local habitat quality and the development status of the population, the density of which was close to the carrying capacity.

Ecology in a human-dominated World

197

Based on the CCA biplot and the presentation of spatial gradients on a geographical axis (Fig. 4), we believe that beaver habitat selection occurs independently within large water bodies such as the Drużno Reserve and the Vistula or Nogat rivers. As a result, suboptimal habitat in one river or channel might be regarded as the best possible habitat in another water body. This difference likely reflects the fact that the distances between the above water bodies (mean distances: Drużno Reserve – Vistula = 42.94 km; Drużno Reserve – Nogat = 21.55 km; Vistula – Nogat = 22.76 km) is greater than the average dispersal distances of colonizing beavers in Europe (Sweden: averaged 12–19.7 km yr^{-1}, Hartman 1995; France: 8.8 ± 12.8 SD km yr^{-1}, Fustec et al. 2003). It is also important for the interpretation of spatial variability that the differences in habitat selection were not influenced by any migration barriers. In the Vistula River delta, distant water bodies are well connected through by rivers and drainage ditches (approximately 3500 km and 17 000 km of connections), which allows for beavers to disperse throughout the delta area with few constraints (Kondracki 2000).

Conclusions

Differences in habitat composition around beaver colonies in the Vistula River delta ecoregion mostly resulted from the large geographical distances between the territories, which were independent of the abundance of woody plants and beaver population density. Therefore, the behavioural decision to settle probably occurred independently at each site because the beavers were not able to compare the conditions between distant water bodies.

Within each watercourse, beaver habitat selection depended on habitat quality and was correlated with local population density, which may represent the scale of the beaver dispersal. This suggests that the ideal despotic model of habitat selection was limited by scale, and in the case of beavers it applies within restricted areas (e.g. a small watershed) but not at broader scales (e.g. between large watersheds).

The distribution of woody plants within a beaver family territory was clumped and non-random; the cover of woody plants declined with distance from a colony centre, while anthropogenic land cover increased. Therefore, settlement decisions had to be based on the assessment on both the total amount and the spatial distribution of resources at the potential future territory scale.

The results of our study also indicated that the beaver population from the Vistula River delta has reached carrying capacity. Moreover, we demonstrated that it was possible to study beaver habitat preferences even in the climax population phase when both the spatial distributions of resources and population densities are taken into account.

References

Anderson, M. et al. 2008. Permanova+ for Primer: guide to software and statistical methods. – PRIMER-E, Plymouth.

Aszyk, K. 1994. Bobry gdańskie. – DJ, Gdańsk.

Aszyk, M. and Kistowski, M. 2002. Monitoring bobra w województwie pomorskim. Wyd. Uniwersytet Gdański, Gdańsk – Poznań.

Bartak, V. et al. 2013. Spatial spread of Eurasian beavers in river networks: a comparison of range expansion rates. – J. Anim. Ecol. 82: 587–597.

Beier, P. and Barrett, R. H. 1987. Beaver habitat use and impact in Truckee River basin, California. – J. Wildl. Manage. 51: 794–799.

Borcard, D. and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. – Ecol. Model. 153: 51–68.

Buliński, M. et al. 2013. The vegetation of the Lake Drużno Nature Reserve. – In: Nitecki Cz. (ed.) Druzno Lake – Natural Monograph. Mantis Olsztyn., pp. 33–81.

Campbell, R. D. et al. 2005. Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? – Behav. Ecol. Sociobiol. 58: 597–607.

Cassini, M. H. 2013. Distribution ecology: from individual habitat use to species biogeographical range. – Springer.

Ciechanowski, M. et al. 2013. The Mammalian fauna of 'Jezioro Drużno' Nature Reserve. – In: Nitecki, C. (ed.), Druzno Lake – Natural Monograph. Mantis Olsztyn. pp. 33–81.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. – Aust. J. Ecol. 18: 117–143.

Clarke, K. R. and Gorley, R. N. 2006. User Manual/Tutorial. – Primer-E, Plymouth.

Collen, P. and Gibson, R. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review. – Rev. Fish. Biol. Fisher. 10: 439–461.

Donkor, N. T. and Fryxell, J. M. 1999. Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. – For. Ecol. Manage. 118: 83–92.

Dupke, C. et al. 2017. Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. – Ecography 40: 1014–1027.

Dzięciołowski, R. and Gozdziewski, J. 1999. The reintroduction of European beaver, *Castor fiber*, in Poland. – In: Busher P. E. and Dzięciołowski R. (eds), beaver protection, management, and utilization in Europe and North America. Springer, pp. 31–35.

Fretwell, S. D. 1972. Populations in a seasonal environment (no. 5). – Princeton Univ. Press.

Fretwell, S. D. and Lucas, H. L. Jr. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. – Acta Biotheor. 19: 16–36.

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

Fryxell, J. M. 2001. Habitat suitability and source–sink dynamics of beavers. – J. Anim. Ecol. 70: 310–316.

Fryxell, J. M. and Doucet, C. M. 1991. Provisioning time and central-place foraging in beavers. – Can. J. Zool. 69: 1308–1313.

Fustec, J. et al. 2001 Colonization, riparian habitat selection, and home range size in a reintroduced population of European beavers in the Loire. – Freshwater Biol. 46: 1361–1371.

Fustec, J. et al. 2003. Beaver lodge location on the upstream Loire River. – CR Biol. 326: 192–199.

Gromadzka, J. 1996. Na wyspie Sobieszewskiej zamieszkały bobry. – Echa Wyspy 14: 10–11.

Hartman, G. 1994. Long-term population development of a re-introduced beaver (*Castor fiber*) population in Sweden. – Conserv. Biol. 8: 713–717.

Hartman, G. 1995. Patterns of spread of a reintroduced beaver *Castor fiber* population in Sweden. – Wildl. Biol. 1: 97–103.

Hartman, G. 1996. Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. – J. Zool. 240: 317–325.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. – Scand. J. Stat. 6: 65–70.

Jenkins, S. 1980. A size distance relation in food selection by beavers. – Ecology 61: 740–746.

Jenkins, S. H. and Busher, P. E. 1979. Castor canadensis. – Mamm. Species 120: 1–8.

John, F. and Kostkan, V. 2009. Compositional analysis and GPS/GIS for study of habitat selection by the European beaver, *Castor fiber* in the middle reaches of the Morava River. – Folia Zool. 58: 76–86.

John, F. et al. 2010. Habitat selection of an expanding beaver (*Castor fiber*) population in central and upper Morava River basin. – Eur. J. Wildl. Res. 56: 663–671.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. – Ecology 61: 65–71.

Kondracki, J. 2000. Geografia regionalna Polski. – Wydawn. Naukowe PWN.

Legendre, P., et al. 2009. Partitioning beta diversity in a subtropical broadleaved forest of China. – Ecology 90: 663–674.

Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. – Ecology 73: 1943–1967.

MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. – Am. Nat. 100: 603–609.

Mancinelli, S. et al. 2015. Roe deer summer habitat selection at multiple spatio-temporal scales in an Alpine environment. – Hystrix It. J. Mamm. 26: 132–140.

Mayer, M. et al. 2017. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. – Anim. Behav. 123: 375–382.

Mayor, S. J. et al. 2009a. Habitat selection at multiple scales. – Ecoscience 16: 238–247.

Mayor, S. J. et al. 2009b. The spatial structure of habitat selection: a caribou's-eye-view. – Acta Oecol. 35: 253–260.

Morris, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. – Evol. Ecol. 1: 379–388.

Morris, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. – Evol. Ecol. 6: 412–432.

Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. – Oecologia 136: 1–13.

Morris, D. W. and Davidson, D. L. 2000. Optimally foraging mice match patch use with habitat differences in fitness. – Ecology 81: 2061–2066.

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

Nolet, B. A. and Rosell, F. 1998. Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. – Biol. Conserv. 83: 165–173.

Nolet, B. A. et al. 1994. Selective foraging on woody species by the beaver *Castor fiber*, and its impact on a riparian willow forest. – Biol. Conserv. 70: 117–128.

Orians, G. H. and Pearson, N. E. 1979. On the theory of central place foraging. – In: Horn D. (ed.), Analysis of ecological systems. Ohio State Univ. Press, Columbus, pp. 155–177.

Økland, R. H. and Eilertsen, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. – J. Veg. Sci. 5: 117–126.

Peres-Neto, P. R. and Legendre, P. 2010. Estimating and controlling for spatial structure in the study of ecological communities. – Global Ecol. Biogeogr. 19: 174–184.

Pinto, B. et al. 2009. Habitat selection of the Eurasian beaver (*Castor fiber*) near its carrying capacity: an example from Norway. – Can. J. Zool. 87: 317–325.

Pruszak, Z. et al. 2005. Hydrology and morphology of two river mouth regions (temperate Vistu la Delta and subtropical Red River Delta). – Oceanologia 47: 365–385.

Rosell, F. and Hovde, B. 2001. Methods of aquatic and terrestrial netting to capture Eurasian beavers. – Wildl. Soc. B 29: 269–274.

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

Rosell, F. et al. 2006. Use of dawn and dusk sight observations to determine colony size and family composition in Eurasian beaver *Castor fiber*. – Acta Theriol. 51: 107–112.

Rosell, F. et al. 2012. More genetic data are needed before populations are mixed: response to Sourcing Eurasian Beaver *Castor fiber* stock for reintroductions in Great Britain and western Europe. – Mammal Rev. 42: 319–324.

Rosenzweig, M. L. 1981. A theory of habitat selection. – Ecology 62: 327–335

Schaefer, J. A. et al. 2008. The spatial scale of habitat selection by red deer. – Can. J. Zool 86: 1337–1345.

Schneider, D. 2001. The rise of the concept of scale in ecology. – Bioscience. 51: 545–553.

Schoener, T. W. 1979. Generality of the size-distance relation in models of optimal feeding. – Am. Nat. 114: 902–914.

Simunkova, K. and Vorel, A. 2015. Spatial and temporal circumstances affecting the population growth of beavers. – Mamm. Biol. 80: 468–476.

Steele, J. H. 1991. Marine ecosystem dynamics: comparison of scales. – Ecol. Res. 6: 175–183.

Swinnen, K. R. R. et al. 2017. Reintroduced Eurasian beavers (*Castor fiber*): colonization and range expansion across human dominated landscapes. – Biodivers. Conserv. 26: 1863–1876.

ter Braak, C. J. F. and Šmilauer, P. 2012. Canoco 5, Windows release (5.00). Software for mutivariate data exploration, testing, and summarization. – Biometris, Plant Research International, Wageningen.

Tyurnin, B. N. 1983. Factors determining numbers of the river beaver (*Castor fiber*) in the European North. – Sov. J. Ecol. 14: 337–344.

Weydmann, A. et al. 2014. Shift towards the dominance of boreal species in the Arctic: inter-annual and spatial zooplankton variability in the West Spitsbergen Current. – Mar. Ecol. Prog. Ser. 501: 41–52.

Wiens, J. A. 1989. Spatial scaling in ecology. – Funct. Ecol. 3: 385–397.

Wright, J. et al. 2002. An ecosystem engineer, the beavers, increasing species richness in the landscape scale. – Oceologia 132: 96–101.

Żurowski, W. and Kasperczyk, B. 1986. Characteristics of a European beaver population in the Suwałki Lakeland. – Acta Theriol. 31: 311–325.

Supplementary material (Appendix ECOG-03621 at <www.ecography.org/appendix/ecog-03621>). Appendix 1.