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Authors: Obidziński, Artur, Pabjanek, Piotr, and Mędrzycki, Piotr

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Original article

Determinants of badger *Meles meles* sett location in Białowieża Primeval Forest, northeastern Poland

Artur Obidziński, Piotr Pabjanek & Piotr Mędrzycki

The aim of our research was to investigate the relative importance of food supply, geological conditions, human activity and neighbouring badger *Meles meles* territories for location of badger setts in Białowieża Primeval Forest (BPF) within the boundaries of Poland (595 km^2). In our study, we included 67 badger setts surveyed in the field as well as 7,563 pseudo-absence points located randomly in each subcompartment of the forest. For each point, 18 habitat and landscape variables were assessed. The data were analysed using the Random Forest model in two stages, i.e. feature selection and variable importance assessment. Our results indicate that the human-related variables for location of badger setts in BPF (strong avoidance of main roads, bimodal reaction to open and built-up areas) were of highest importance. The second most important variable was the distance to neighbouring active main setts (preference of the distance of 2 km from the nearest active main sett). The least important variables were habitat conditions affecting digging possibility and food availability, such as the presence of cambisols or fresh entic podzols made of loamy sands on ablation moraine or aeolian dunes with potential vegetation of thermophilous oak *Quercus robur*-hornbeam *Carpinus begulus* forest of fresh pine *Pinus sylvestris*-oak mixed forest. We conclude that large intact forest complexes function as refuge areas for badger populations if badger mortality is high in open areas relative to the benefits of wide food availability in open areas.

Key words: badger, habitat selection, low-density population, Meles meles, Random Forest model, sett location

Artur Obidziński, Department of Forest Botany, Warsaw University of Life Sciences, 159 Nowoursynowska Street, 02-776 Warsaw, Poland - e-mail: artur_obidzinski@sggw.pl
Piotr Pabjanek, Department of Geoinformatics and Remote Sensing, University of Warsaw, 30 Krakowskie Przedmieście Street, 00-927 Warsaw, Poland - e-mail: p.pabjanek@uw.edu.pl
Piotr Mędrzycki, Laboratory of Applied Plant Ecology, University of Ecology and Management in Warsaw, 14 Wawelska Street, 02-061 Warsaw, Poland - e-mail: piotr.medrzycki@pser.pl

Corresponding author: Artur Obidziński

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The distribution of organisms in the environment constitutes one of the basic elements of their ecology (e.g. Krebs 1994, Macdonald & Rushton 2003). The distribution of species with wide ecological niches often depends on many factors, and different factors may play the main role in different environments (e.g. Gaston & Blackburn 1999, Guisan & Zimmermann 2000). The identification of these factors and the understanding of their importance are crucial for species management or protection (e.g. Kaiser 1997, Krebs 2002).

The European badger *Meles meles* is a medium-sized carnivore from the Mustelidae family. Its range extends across the temperate zone of Eurasia, from Portugal and Ireland to Russia (west of the Volga River) and northern Afganistan (Wozencraft 2005). It inhabits many types of habitat, i.e. forests, agricultural areas, steppe and even suburbs (Griffiths & Thomas 1993). Because of its wide range of occurrence, both in geographical and environmental space, as well as its territorialism and environmental adaptability, the badger has become a subject of numerous studies on species-habitat relationships (review in Newton-Cross et al. 2007).

The Resource Dispersal Hypothesis (RDH; Macdonald 1983) is often applied to explain badger sett settling behaviour. It states that many aspects of the badger's ecology, e.g. social structure, are affected by the accessibility of certain limited resources. A version of the RDH is the Sett Dispersion Hypothesis (Doncaster & Woodroffe 1993). This hypothesis states that badger distribution and abundance is limited by accessibility of areas suitable for sett digging (Thornton 1988, Neal & Roper 1991, Roper 1993, Virgós 2001, Rosalino et al. 2005, Kaneko et al. 2006), determined by: geomorphological units, altitude a.s.l., slope orientation and inclination, soil type and cohesivity, accessibility of food, water and bedding material, type of vegetation cover, anthropogenic impact and many more (e.g. Dunwell & Killingley 1969, Thornton 1988, Neal & Roper 1991, Bičík et al. 2000, Hammond et al. 2001, Virgós 2001, Mickevičius 2002, Jepsen et al. 2005, Prigioni & Deflorian 2005, Kaneko et al. 2006). Both of the mentioned hypotheses have been strongly criticised (Revilla & Palomares 2002, Revilla 2003, Macdonald et al. 2004), and more habitat properties may be proposed as determinants of badger population density, e.g. the level of wilderness of available habitat. Badgers live in high density populations on small territories in agriculture or suburb landscapes intensively utilised by humans (e.g. Kruuk 1978, Roper 1992, Woodroffe & Macdonald 1993, Rogers et al. 1997, Tuyttens et al. 2000, Macdonald et al. 2004). Badgers also occur in low density populations on less disturbed lowlands in northeastern Poland (Kowalczyk et al. 2000, 2003), the Iberian Peninsula (Revilla et al. 2001b, Rosalino et al. 2005) and in Scandinavia (Brøseth et al. 1997, Kauhala et al. 2006). However, few studies have provided evidence for the importance of direct or indirect human-related habitat features for the badger population density or sett location (Revilla et al. 2001a, Jepsen et al. 2005, Kurek 2011, Mysłajek et al. 2012a). Studies from Białowieża Primeval Forest (BPF), situated on the borderland of Poland and Belarus, are particularly important for the investigation of wild animals' living patterns due to its long-term wilderness, uncommon in European lowlands (Faliński 1986, Jędrzejewska & Jędrzejewski 1998). Distribution of badger territories and sett location have so far only been studied in terms of habitat selection for sett excavation (Kowalczyk et al. 2003) and in terms of territory use and energy saving (Kowalczyk et al. 2006), but the importance of human pressure has not yet been analysed. Therefore, it is not clear whether data on the preferred forest habitat (i.e. English oak *Quercus robur*-hornbeam *Carpinus betulus* forest) from BPF can be extrapolated to other areas (e.g. Thornton 1988, Macdonald et al. 1996, van Apeldoorn et al. 1998, Wright et al. 2000, Hammond et al. 2001, Jepsen et al. 2005). Better understanding of the relative importance of the many determinants of badger sett location may be useful in the management of the badger population in more transformed lowland landscapes, e.g. in the vicinity of BPF, where badgers have been noted in secondary forests on abandoned fields (A. Obidziński, pers. obs., W. Kojło, Forestry Administration, pers. comm.).

Recent advances in methods of statistical modelling of distribution and abundance of organisms in geographic and environmental space may be helpful in such a study (Elith & Leathwick 2009). So far, most analyses of badgers' habitat preferences have used multiple regression models (Thornton 1988) or logistic regression models (e.g. Progioni & Deflorian 2005, Rosalino et al. 2005, Newton-Cross et al. 2007), sometimes coupled with ordination methods like DECORANA (Macdonald et al. 1996). Despite their wide use, these methods have many common disadvantages shared by all parametric statistical methods, e.g. they require satisfying assumptions on the shape of the relationships between predictors and dependent variable, as well as the independence of error terms (Franklin & Miller 2010). Some statisticians claim that parametric methods are not well suited for analysing data of natural experiments that cannot be fully controlled (Breiman 2001b), and propose more robust, non-prametric modelling methods, e.g. ensembles of classification and regression trees (Breiman 2001a, Cultler et al. 2007), possible to use for both regressive and classification purposes. Despite the complexity of the background algorithms, their use is growing in biogeographical modelling (Elith & Leathwick 2009, Franklin & Miller 2010).

The aim of our paper was to find natural and anthropogenic features important for sett habitat selection in BPF within the boundaries of Poland (595 km^2), and specifically, to investigate the relative importance of food supply, geological conditions, human activity and the neighbouring badger territories for sett location. Our hypothesis was that in the low-density badger population in BPF, geological conditions allowing digging and supply of earthworms in the habitat are more important than the level of human intervention or social neighbourhood.

Material and methods

Study area

BPF, located on the Polish-Belarusian border (52°30'-53°N, 23°30'-24°15'E) is considered to be the best preserved natural forest of European lowlands. Currently, it occupies an area of ca 1,450 km^2 (595 km^2 in Poland and 855 km^2 in the Republic of Belarus; Fig. 1). The exceptional value of the BPF, expressed by high species diversity with numerous species endangered elsewhere in Europe (Faliński 1986, Jędrzejewska & Jędrzejewski 1998), derives from certain tree stands that have never been exploited for timber, despite exploitation that started during World War I and was continued to a limited extent recently (e.g. Jędrzejewska & Jędrzejewski 1998, Sokołowski 2004). Local climate displays continental-maritime characteristics. Annual average temperature (1955-2001) is 6.8°C, with an average temperature of -4.2°C and 17.7°C in January and July, respectively, and the average annual precipitation (1955-2001) is 633 mm (Pierzgalski et al. 2002). The vegetation season lasts 208 days, while snow cover lasts 92 days (Faliński 1986). The geological substrate of BPF is formed mainly by moraine upland, made of glaciofluvial sands, gravels and silts and divided by marshy river valleys. The ablation moraine has a prevalence of cambisols, the ground moraine either cambi- or luvisols and the eolic accumulation plains mainly podzols. River valleys are filled with hydrogenic soils (Kwiatkowski 1994). BPF is situated within a mixed forest zone. Its main forest-forming species are hornbeam, English oak, Norway spruce *Picea abies,* Scots pine *Pinus sylvestris* and alder *Alnus glutinosa* (Faliński 1986). Potential natural vegetation covering the greatest area is composed by oak-lime *Tilia cordata*-hornbeam forests (65%), alder wet forests (15%) and mixed pine-oak forests (10%; Kwiatkowski 1994). BPF is inhabited by four denning predators, i.e. wolf *Canis lupus*, badger *Meles meles*, red fox *Vulpes vulpes* and raccoon dog *Nyctereutes procyonoides* (the last-mentioned predator colonised BPF in the early 1950s; Jędrzejewska & Jędrzejewski 1998). Density of badgers in BPF (0.21 individuals/km^2) and of their setts (0.055 setts/km^2) is one of the lowest in Europe while territories of the groups (12.8 km^2) are among the largest in Europe (Kowalczyk et al. 2003). The Polish part of BPF includes Białowieża National Park (BNP; with a strictly protected area of 57 km^2 and a partially protected area of 48 km^2), nature reserves of partial protection (outside BNP) of 118 km^2 and managed forests of 372 km^2.

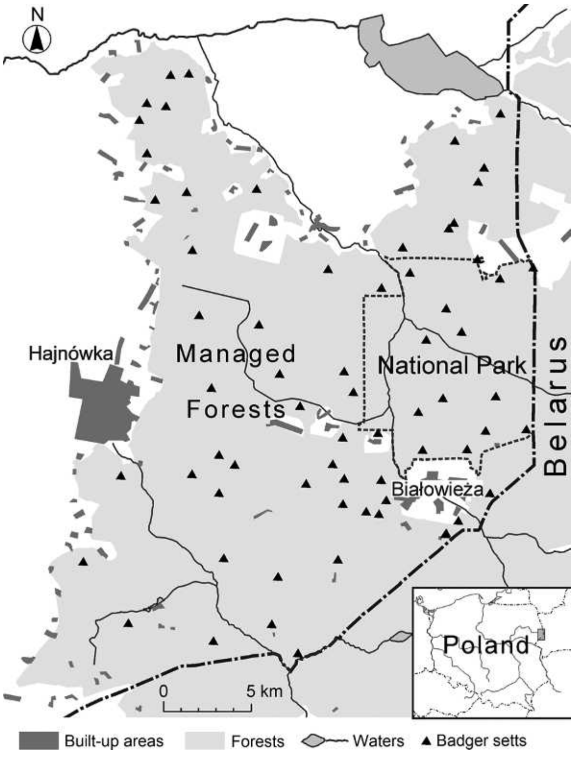

Figure 1. Locations of analysed badger setts in the Białowieża Primeval Forest, Poland. Triangular markers indicate presence points of analysed badger setts.

Data collected in the field

Habitat and landscape features were assessed for two kinds of locations. One set of points called presence points were all places where setts were found. Locations of these points were obtained from the literature (Kowalczyk et al. 2000, 2003), Forest Administration (pers. comm.) and own field surveys. Field data were collected in the years of 2006-2009. Setts were surveyed 4-6 times within our study period, usually by one person with up to two aids. Out of 128 dens found, 67 were recognised as badger dens, based on direct observation of animals (R. Kowalczyk and Forest Administration, pers. comm.) and their traces or were determined on the basis of morphometry of setts according to the criteria of Thornton (1988). All 67 badger setts were divided into three categories: main, secondary or occasional according to the categorisation of Matyáštík & Bičík (1999). This classification was based on former observations by Kowalczyk et al. (2000, 2003) and personal observations by Forest Administration crew and then verified by A. Obidziński (pers. obs.). All the found setts were included in the habitat analyses because they often change their function (Neal & Cheeseman 1996, Wilson et al. 1997, Ostler & Roper 1998), and besides, it is sometimes impossible to distinguish between the main and other kinds of setts (Revilla et al. 2001b, Remonti et al. 2006). In some cases, no differences of habitat features were detected between setts of different categories (Macdonald et al. 2004). Moreover, the fact that a sett of any kind has been created indicates that habitat conditions of the location also enable digging of a main sett (Jepsen et al. 2005). Additionally, in our case, habitat properties of small setts did not diverge from habitat properties of the main setts either. Whether a small sett can change into a main sett depends on many other factors, e.g. presence of other badger groups or human activity in the neighbourhood. Field measurements were taken between May and October during 2006-2009. Surface area, height of spoil heaps, number of entrances as well as slope orientation and inclination, congruence between canopy and habitat and anthropogenic impact (e.g. settling setts in places transformed by humans, such as gravel pits) were determined for each sett in the field. Boundaries of sett areas were determined in the field on the basis of extent of earth relief distorted by the animals digging out soil. The maximum height of spoil heaps for each sett was measured with an optical lever. Geographic coordinates were measured with a GPS (GARMIN eTrex Vista) with an accuracy of at least 15 m.

The second set of points called pseudo-absence points, consisted of random points situated all over the Polish part of BPF. Coordinates of the pseudo-absence points were generated randomly with ArcGIS, four for each basic unit of Forest Administration net of 0.25 km^2 each, which made a total of 8,163 points. After elimination of points with no or incomplete predictor data, 7,630 points remained. This way there were 7,563 pseudo-absence and 67 presence points.

Habitat and landscape data

Data on geomorphologic units, soil type and texture, thickness of surface layers and habitat moisture were taken from forest numeric maps, obtained from the Regional State Forest Directorate and BNP. The GIS layers obtained from these two institutions were standardised and the number of categories was generalised. Four groups of variables were established: 1) conditions suitable for sett digging, 2) food supply (i.e. presence of habitats abundant in earthworms), 3) presence of other badger groups and 4) human pressure. Variables for each group were measured based on or taken directly from numeric maps. The first group, i.e. conditions favourable for digging setts, was geomorphological unit, soil texture, depth of soil layer, ground cohesivity and distance from surface waters. The second group, i.e. the availability of food, included type of soil, soil fertility, habitat moisture and potential vegetation. The third variable group, presence of other badger groups, included the distance to the neighbouring active main setts and the intensity of their use. Variables in the fourth group, linked with human pressure, were: a) protection status with four levels: strict reserves, partial reserves, forest of canopies congruent with habitat and forest of canopies incongruent with habitat, b) distance from open areas, c) distance from human settlements and d) distance from transportation lines.

Distances from open areas, built-up areas, transportation lines and surface waters were established according to topographic maps of scale 1:10,000 and according to an updated orthophotomap. The Belarussian frontier zone was taken from the orthophotomap and topographic maps of scale 1:50,000. Thickets and young forests on abandoned fields adjacent to BPF oldgrowth were included in delimiting the boundary of open areas. Buildings permanently inhabited were considered as built-up areas. Public roads and railways in use were considered as transportation lines. Permanent streams marked on the topographic map of 1:10,000 were included under the category of surface waters. Potential natural vegetation was adopted after Kwiatkowski (1994). Habitat moisture was taken from forest numeric maps with the following ranks assigned to the following classes: dry = 1, moderately fresh = 2, strongly fresh = 3, moderately wet = 4, strongly wet = 5, moderately swamp = 6 and strongly swamp = 7. Soil fertility was defined according to the trophy index of forest soil (ITGL; Brożek & Zwydak 2003). Ground cohesivity was defined according to civil engineering measures (Kostrzewski 1988) based on texture of surface deposits assessed for a depth of 3 m taken from a geological numeric map. Availability of earthworms, the main food resource, was estimated for soil and vegetation types on the basis of results by Kowalczyk et al. (2003). Presence of other badger groups was assessed as: a) distance from the given point to the nearest active main setts and b) intensity of use of the nearest active main setts. Both of these measures were calculated as an average of

2nd, 3rd, 4th and 5th closest active main setts, which may be interpreted as a measure of the influence on neighbouring territories. The first nearest active main sett was omitted because it should represent the active main sett of a given territory, and it should not be attributed to neighbouring social groups. Additionally, in all presence points representing active main setts, this measure would always be equal to zero. The indices for the intensity of sett utilisation were based on sett surface size and relief. It is assumed that the time spent by badgers in a certain place is linked to their preference for the conditions of that place (Balestrieri et al. 2009).

In case of setts, it causes a growth of their size, both area and height of spoil heaps. Because of that, we used the product of multiplication of the surface of each sett and maximum height of its spoil heaps divided by 100 as a measure of utilisation intensity. In total, 18 habitat features were applied, including five based on field measurements and 13 based on data acquired from maps. Nine out of them were categorial and nine numerical (Tables 1 and 2).

Statistical analyses

The robust Random Forest (RF) method (Breiman 2001a) was used for modelling the distribution of setts, because it had no requirements of variables distribution, was resistant to multicollinearity, was well suited for the analysis of factor variables and had a good ability to detect non-linear relationships among variables, even if sharp changes in response curves occurred. The RF method was implemented in a Random Forest (version 2.6.7) package from the R statistical environment (R Development Core Team 2012). We consider it well suited for analysis of complex data from a not fully controlled natural system (Breiman 2001b, Franklin & Miller 2010). We are aware that high prevalence, i.e. high dominance of pseudo-absence point numbers over presence point numbers may decrease the predictive accuracy of the RF model by 0.1 and may increase the model specificity (Barbet-Massin et al. 2012). It may result in a more conservative prediction, i.e. the model will tend to predict fewer places where badger sett location is highly probable.

While using a robust modelling method, in order to facilitate clearer modelling results, we performed a pre-analysis by eliminating non-informative and potentially problematic variables with R package caret, version 5.15-023 (Kuhn 2008) with default settings. The initial data set, which we call a factor data set elsewhere in the article, was tested against the presence of Near Zero Variance (NZV) variables, multicollinearity and the presence of linear combination of traits (Linear Combos). The pre-analysis revealed that there were: a) no NZV variables, b) no possibility of investigating the level of correlation of all variables as a part of them had a factor form and c) no Linear Combo variables as there were no factors divided into single variables of binary type. Therefore, all habitat factors were used in the RF analyses.

In order to further eliminate non-relevant variables from the data set and to increase the precision of the models, factor variables from the initial data

Table 1. Abbreviations and mean values (± SD) of numeric variables in sett pseudo-absence and presence points in Białowieża Primeval Forest, Poland. The variables of geomorphological unit, soil texture, soil type, potential vegetation and naturalness level are presented in Table 2.

Variable	Abbreviation	Absence of setts (N = 7630)	Presence of setts (N = 67)
Habitat moisture	HABIT_MOIS	3.72 ± 1.74	2.34 ± 0.64
Ground cohesiveness	GROU_COHE	7.18 ± 11.55	8.44 ± 9.96
Soil fertility	SOIL_FERT	33.55 ± 1.29	34.7 ± 0.00
Distance from creeks (km)	DIST_CREE	0.796 ± 0.614	0.879 ± 0.576
Distance from rivers (km)	DIST_RIVE	1.241 ± 0.873	1.03 ± 0.812
Distance from four nearest setts (km)	DIST_SETS	4.63 ± 1.44	4.28 ± 1.40
Mean intensity of use of four nearest setts	INT_SET_US	4.12 ± 1.89	4.38 ± 1.89
Distance from open areas (km)	DIST_OPEN	1.200 ± 0.871	1.340 ± 0.959
Distance from built-up areas (km)	DIST_BUILT	1.201 ± 1.245	1.76 ± 1.17
Distance from transportation lines (km)	DIST_TRAN	0.709 ± 0.651	1.499 ± 1.293
Geomorphological unit	GEOM_UNIT		
Soil texture	SOIL_TEXT		
Soil type	SOIL_TYPE		
Potential vegetation	POTE_VEGE		
Naturalness level	NATU_LEVE		

set were converted to indicators, i.e. to the binary form. We call this data set an indicator data set elsewhere in the article. Mean distance to and mean intensity of use of nearest active main setts were separated into single distances and intensities. The indicator data set was initially processed in R caret package. Among 65 variables, 18 NZV variables were found and eliminated (abbreviations are found in Tables 1 and 2). These included the following geomorphological variables: EOL_DUNE, DELUVIA and TER_PR_VAL; the following types of soils: ALB_PODZ, ENT_PODZ, GLPODZ, GRWA_GLE, MUD_SO, MUCKSOL and STAG_GLE; the soil texture SILTS and the following plant communities: BOG_ALD, FR_PIN, P-W_FLO, WT_MX_S-O, SPR_BOG, BIR_BOG and PIN_BOG. There were eight pairs of variables with correlation values > 0.75, but we decided not to exclude them from the analysis mainly because of sequential correlation of distances to the nearest active main setts, i.e. 2nd with 3rd, 3rd with 4th and so on. Other variable pairs that correlated at a level > 0.75 were: PEATS vs HISTOS, MUCKSOL vs MOO_SO, HABIT_MOIS vs BI_AC_PLA and GROU_COHE vs LOAMS. We were aware that leaving those highly correlated variables in the analysis may weaken the importance measure of traits. No Linear Combos were found in this data set. Finally, there were 45 predictors left for analysis.

The importance of variables for both data sets was assessed in a two-stage procedure. The first stage was feature selection. Its goal was to eliminate all predictors that were not relevant for the model of sett habitat. Feature selection procedure from R Boruta package, version 1.6 (Kursa et al. 2010, Rudnicki & Kursa 2010) with default settings was applied for this sake. The procedure is based on the RF model. It uses Z-score parameters calculated as the quotient of Mean Accuracy Loss and Standard Deviation of Mean Accuracy Loss. Its value is high when the variable importance is high and invariant among all RF runs. Therefore, it is useful for elimination of variables that do not have a strong and constant impact on the distribution of analysed phenomenon. Comparative analysis of Z-score values of predictors and random variables generated by their reshuffling determines which predictors have Z-scores at random level enabling their elimination, and which of them have Z-scores significantly higher than random, enabling their classification as confirmed. In that way, only habitat predictors with non-random importance for sett distribution were selected for further analysis. The Boruta algorithm is an example of the 'all-relevant, even weak' feature selection strategy, and is well suited to the aim of seeking possible explanations for the distribution pattern of badger setts.

The importance of relevant variables was determined by the RF model implemented in R BIOMOD package, version 1.1-7.03 (Thuiller at al. 2009) with default settings, in the second (main) stage of the analysis. BIOMOD package provides: a) measurement of quality of the model with the Set-Aside method, for which we selected the Area Under ROC Curve (AUC) parameter, b) calculation of Variable Importance (called elsewhere in this article BIOMOD Variable Importance; BVI) as 1-correlation coefficient between the values of modelled phenomenon predicted by the model with the use of a given predictor and predicted after its randomisation, which is easy for biological interpretation and c) generation of Partial Response Plots for predictors that present changes in value of Y variable in relation to changes of value of a single X predictor, which is an implementation of the 'evaluation strip' procedure, described by Elith et al. (2005). The simple way to calculate BVI enables the calculation of average variable importance for different groups of predictors.

Results

Out of 67 setts found, 48 were defined as main, seven as secondary and 12 as occasional setts. Main setts were 66-970 m^2 in size, usually with spoil heaps > 1 m high, with 5.8 functioning entrances and 12 visible entrances on average. Secondary setts mostly did not exceed 100 m^2, their spoil heaps were not > 1 m and the average number of all entrances was 6.6. Occasional setts usually did not exceed 50 m^2, their spoil heaps were not > 1 m and the average number of all entrances was 4.2 (Table 3). Of the main setts, 33 were used continuously during our period of research while the remaining 15 were either permanently abandoned or used sporadically.

The soils at sett locations were of low cohesivity, strongly fresh moisture and mezo-eutrophic fertility. Mean distance ± SD of setts from small creeks was 0.9 ± 0.6 km, while it was 1.0 ± 0.8 km from main rivers, 1.3 ± 1.0 km from open areas, 1.8 ± 1.2 km from built-up areas and 1.5 ± 1.3 km from roads. The mean distance from four nearest active main

Table 2. Abbreviations and frequencies of sett pseudo-absence and presence points (where categories of indicator variables' value is '1') and distances and use intensity indices of the n-th nearest active main sett. Variables that were later excluded are indicated by *.

Variable	Abbreviation	Absence of setts (N = 7630)	Presence of setts (N = 67)
Geomorphological unit			
Deluvia*	DELUVIA	75	0
Ablation moraine	ABLA_MOR	526	15
Ground moraine	GRND_MOR	4275	41
Plains of biogenic accumulation	BI_AC_PLA	1791	0
Plains of eolic accumulation	EOL_PLAIN	779	7
Proglacial valley terrace*	TER_PR_VAL	191	0
Eolic dunes*	EOL_DUNE	60	4
Soil texture			
Loams, clays	LOAMS	684	9
Light loams	L_LOAMS	421	0
Mucks	MUCKS	1050	0
Loamy sand	LO_SA	603	15
Loose sand	LS_SA	874	8
Light loamy loose sand	LLO_LS_SA	1101	13
Light loamy sand	L_LOA_SA	2136	22
Silts*	SILTS	88	0
Peats	PEATS	740	0
Soil type			
Albic podzols*	ALB_PODZ	3	0
Entic podzols*	ENT_PODZ	211	18
Cambisols	CAMBIS	1988	33
Chernozems	CHERNOZ	392	0
Gleyic podzols*	GLPODZ	50	0
Umbri-gleyic podzols	UM_GLPODZ	951	6
Groundwater gleys*	GRWA_GLE	371	0
Mud soils*	MUD_SO	2	0
Moorsh soils	MOO_SO	843	0
Muck soils*	MUCKSOL	91	0
Stagnogleys*	STAG_GLE	309	0
Luvisols	LUVISOL	827	10
Arenosols	ARENOS	1021	0
Histosols	HISTOS	638	0
Potential vegetation			
Bog alder forest*	BOG_ALD	160	0
Alder-flood forests	ALD_FLO	900	0
Termophilous oak-hornbeam forest	TER_O-H	1639	25
Wet pine forest	WT_PIN	452	2
Fresh pine forest*	FR_PIN_	141	5
Fresh mixed pine-oak forest	FR_MX_P-O	513	6
Wet mixed spruce-oak forest*	WT_MX_S-O	324	0
Poplar-willow flood forest*	P-W_FLO	18	0
Spruce bog forest*	SPR_BOG	127	0
Birch bog forest*	BIR_BOG	116	0
Typical oak-hormbeam forest	TP_O-H	1679	24
Wet oak-hormbeam forest	WT_O-H	1541	5
Pine bog forest*	PIN_BOG	87	0

Table 2. Continued.

Variable	Abbreviation	Absence of setts (N = 7630)	Presence of setts (N = 67)
Naturalness level			
Strict reserves	NATU_LEV_1	1195	17
Partial reserves	NATU_LEV_2	3517	24
Canopies congruent with soil	NATU_LEV_3	2218	18
Canopies incongruent with soil	NATU_LEV_4	628	8
Distance from nearest setts (km)			
Distance from nearest 2nd sett	DIST_SET_2	3.61 ± 1.35	3.20 ± 1.39
Distance from nearest 3rd sett	DIST_SET_3	4.73 ± 1.60	4.25 ± 1.46
Distance from nearest 4th sett	DIST_SET_4	5.75 ± 1.73	5.39 ± 1.68
Distance from nearest 5th sett	DIST_SET_5	6.58 ± 1.81	6.25 ± 1.74
Intensity of nearest sett use			
Intensity of use of nearest 2nd set	INT_SET_U_2	1.01 ± 1.49	1.71 ± 2.02
Intensity of use of nearest 3rd sett	INT_SET_U_3	0.86 ± 1.33	1.05 ± 1.51
Intensity of use of nearest 4th sett	INT_SET_U_4	1.25 ± 1.66	1.50 ± 1.76
Intensity of use of nearest 5th sett	INT_SET_U_5	0.98 ± 1.29	0.54 ± 0.10

setts was 4.3 ± 1.4 km and the mean intensity of use of four nearest setts was 4.4 ± 1.9 (see Table 1).

Setts were recorded mainly on ground moraine (61.2%) and ablation moraine (22.4%), on cambisols (49.3%) and podzols (26.9%), made of light loamy sand (32.8%) and loamy sand (22.4%), in the habitat of potential vegetation of thermophilous oak-hornbeam forest (37.3%) and typical oak-hornbeam forest (35.8%). Setts were found in forests of all forms of protection (38.8%) as well as managed forests (61.2 %). Within BNP, 20.9% of setts were recorded out of which 11.9% were within the area of strict protection and 9.0% were in the area of partial protection. In reserves outside of BNP, 17.9% of setts were found. Out of these setts, 61.2% were located in managed forests and 25.4% were situated under planted pine canopies not congruent with the habitat. Traces of human activity were recorded in 28.4% of the setts, out of which 19.4% were created in gravel pits, ditches, shell pits, storage pits for tree seedlings or potatoes and 9% were recolonised setts formerly dug out by poachers (see Table 2).

After 130 RF runs performed by the Boruta package, 14 of 15 analysed variables were found important. The DIST_TRAN variable proved to have the highest Z-score (25.6) and predominantly more so than all other variables. It was followed by a group of three other variables: DIST_SETS, DIST_BUILT and NATU_LEVE (Z-score from 12.3 to 15.2) and subsequently by a uniform group comprising the variables: DIST_OPEN, INT_SET_US, SOIL_TYPE, GEOM_UNIT, POTE_VEGE, HABIT_MOIS and DIST_CREE (Z-score from 8.6 to 10.7). A group of lesser importance included three variables: DIST_RIVE, GRND_COH and SOIL_FERT (Z-score from 5.8 to 7.2). Only one variable, SOIL_TEXT (Z-score = 2.9), remained with the status of 'tentative' (Fig. 2). Random

Table 3. Size and intensity of use of badger setts in the Białowieża Primeval Forest, Poland.

	Sett type					
	Main (N = 48)		Secondary (N = 7)		Temporary (N = 12)	
Measure of sett use	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Area (m^2)	313.7 ± 239.8	66.0-970.0	82.7 ± 52.4	40.0-180.0	37.5 ± 23.6	10.0-100.0
Denivelation (m)	1.1 ± 0.4	0.25-1.75	0.9 ± 0.2	0.5-1.0	0.7 ± 0.2	0.5-1.0
Area x denivelation x 10^{-2}	3.8 ± 3.4	0.5-15.0	0.7 ± 0.6	0.25-2.0	0.2 ± 0.2	0.1-0.6
All entrances	12.0 ± 6.8	4-28	6.6 ± 2.2	4-9	4.2 ± 2.2	2-8
Entrances in use	5.8 ± 4.0	0-18	5.4 ± 1.7	3-7	2.9 ± 1.3	1-6

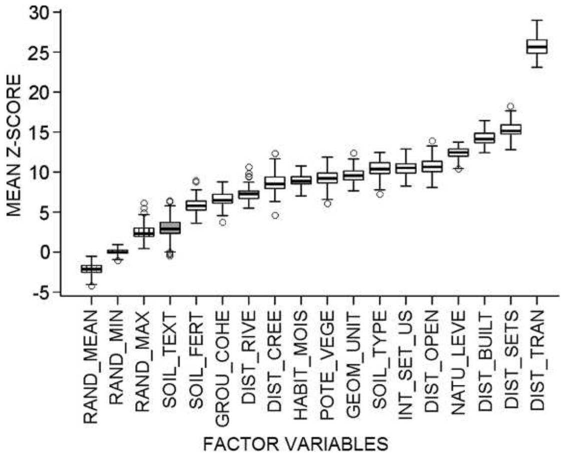

Figure 2. The distribution of Z-score values for Random Forest (RF) models run on the factor data set in R Boruta package. Vertically hatched boxes indicate importance level of random variables generated by Boruta package: white boxes indicate variables significantly more important than random variables and grey box indicate variable with unresolved status after 130 RF runs.

variables generated and tested with the RF model of the Boruta package had Z-score values below all real predictors, as RAND_MIN, RAND_MAX and RAND_MEAN boxes show (see Fig. 2). Finally, the variable SOIL_TEXT was classified as important after an additional Tentative Rough Fix Procedure by Boruta package. Thus, no attributes were deemed unimportant.

The model obtained with the RF algorithm from the BIOMOD package may be regarded as good because the highest AUC value for five repetitions of the model reached higher than 0.87, and the mean AUC value reached the level of 0.86 (Table 4), which falls within the range of AUC 0.8-0.9 and thus can be considered as good model performance (Thuiler et al. 2009). The analysis of BVI of the sett presence vs pseudo-absence sites in the RF model indicates that distance from roads has the highest impact on badger distribution (BVI = 0.725), followed by distance from human settlements (BVI = 0.295) and distance from the neighbouring active main setts (BVI = 0.206). Slightly lower values (BVI from 0.054 to 0.065) are connected with soil texture, distance from creeks and rivers, geomorphological landform, level of forest wilderness, habitat humidity and distance from open areas. These factors are followed by potential vegetation, intensity of neighbouring sett utilisation and soil type (BVI from 0.033 to 0.038). The lowest importance was connected with soil fertility and ground cohesivity (BVI from 0.006 to 0.012; Table 5).

Human pressure variables turned out to be the most important among variable groups (mean BVI = 0.283). They were followed by, with BVI lowered by half, neighbouring badger territories (mean BVI = 0.122), and then geological conditions impacting digging of dens (mean BVI = 0.049). Soil features that determine the food supply of habitats occurred to be the least important factor (mean BVI = 0.037). This order of the factors' importance was a consistent result of both mean value of BVI as well as mean rank of BVI values of variables from analysed groups (Table 6).

Detailed distribution of probability of sett occurrence predicted by the RF model as a function of different values of particular predictors obtained in a form of BIOMOD Partial Response Plots indicated strong and evident avoidance of transportation lines by badgers. The best model predicted almost complete lack of setts within a distance < 2 km from the nearest transportation line, and sharp increase in the probability of setts at distances > 4 km. Predicted occurrence of setts across the distance to the built-up areas had a bimodal distribution, with slightly higher values predicted by the model in the close vicinity of built-up areas (< 0.5 km) and far from it (> 6 km). Predicted distribution of dens with regard to open areas was intermediate between the two previous ones. It had a weak peak at 0.25 km and a strong peak at 4 km from the forest boundary. Distribution of

Table. 4. Predictive performance of Random Forest model for the factor data set run in R package BIOMOD. Area Under ROC Curve (AUC) values are cross validation values in lowest row. An overall model performance in the last column and row is the arithmetic mean of AUC values for all five repetitions (1-5).

	Repetition					
Performance measure	1	2	3	4	5	Full
Total score	0.97	0.98	0.98	0.99	0.98	1
Cut-off	13.69	12.84	12.61	13.68	19.54	600.7
Sensitivity (true positive fraction)	92.54	92.54	92.54	92.54	94.03	100
Specificity (true negative fraction)	93.24	92.22	92.67	92.98	94.99	100
Cross validation	0.812	0.862	0.871	0.877	0.867	0.858

Table 5. BIOMOD Variable Importance (BVI) for factor and numeric variables from different variable groups in factor data set.

Variable abbrieviation	BVI	Rank of BVI	Variable group
DIST_TRAN	0.725	15	Anthropic pressure
DIST_BUILT	0.295	14	Anthropic pressure
DIST_SETS	0.206	13	Neighbouring badger territories
SOIL_TEXT	0.065	12	Feeding conditions
DIST_RIVE	0.064	11	Denning conditions
DIST_CREE	0.061	10	Denning conditions
GEOM_UNIT	0.057	9	Denning conditions
NATU_LEVE	0.057	8	Anthropic pressure
HABIT_MOIS	0.055	7	Denning conditions
DIST_OPEN	0.054	6	Anthropic pressure
POTE_VEGE	0.038	5	Feeding conditions
INT_SET_US	0.037	4	Neighbouring badger territories
SOIL_TYPE	0.033	3	Feeding conditions
SOIL_FERT	0.012	2	Feeding conditions
GRND_COH	0.006	1	Denning conditions
Mean	0.118	7	-

setts with reference to the neighbouring active main setts indicated the highest predicted probability of sett occurrence at a mean distance of 2 km from the first four neighbouring setts. Other factors, i.e. geomorphological landforms including ablation moraines and aeolian dunes, habitat moisture including moderately fresh habitats, soil type including cambisols and entic podzols, soil texture including loamy sands as well as potential vegetation including fresh pine-oak mixed forest and thermophilous oak-hornbeam forest appeared to have hardly any partial impact on the predicted probability of sett locations, obtained in the form of Partial Response Plots.

In the feature selection performed on the indicator data set, 30 variables proved to have a Z-score higher than random variables. DIST_TRAN had the highest Z-score value (25.4), by far higher than any other variable. It was followed by six other variables: HABIT_MOIS, DIST_SET_2, DIST_BUILT, DIST_OPEN, DIST_SET_3 and INT_SET_U_3 (Z-score from 11.2 to 14.9), and by a group of 23 variables with steadily diminishing values, including: INT_SET_U_2, DIST_SET_5, DIST_SET_4, DIST_CREE, ABLA_MOR, INT_SET_U_5, NATU_LEV_4, INT_SET_U_4, ARENOS, LLO_LS_SA, DIST_RIVE, NATU_LEV_1, NATU_LEV_2, CAMBIS TER_O-H, GRND_COHE, NATU_LEV_3, SOIL_FERT, GRND_MOR, LS_SA, EOL_PLAIN, FR_MX_P-O and UM_GLPODZ (Z-score from 3.1 to 9.4). Two variables: TP_O-H and LUVISOL (Z-score = 2.6) acquired the status of 'tentative'. Lack of even weak relevance was found for 13 variables: L_LOA_SA, WT_O-H, L_LOAMS, LOAMS, BI_AC_PLA, ALD_FLO, MOO_SO, WT_PIN, CHERNOZ, MUCKS, HISTOS, PEATS and LO_SA (Z-score from -1.4 to 2.2). Finally, the LUVISOL variable was categorised as important and the TP_O-H variable as non-important as result of application of an additional Tentative Rough Fix Procedure by the Boruta package based on the last 100 RF runs. Thus, 31 variables were considered important (Fig. 3).

The predictive performance of models built with the indicator data set can be considered as good because cross validation AUC values for the best of five repetitions of the model reached values > 0.9 and the mean value of cross validation reached 0.87 (Table 7), which was slightly higher than mean AUC values for the RF model for the factor data set (0.86).

Table. 6. Mean BIOMOD Variable Importance (BVI) values for different variable groups in factor data set.

Variable group	Mean BVI	Mean rank of BVI	Variable group importance rank
Anthropic pressure	0.283	10.8	I
Neighbouring badger territories	0.122	8.5	II
Denning conditions	0.049	7.6	III
Feeding conditions	0.037	5.5	IV

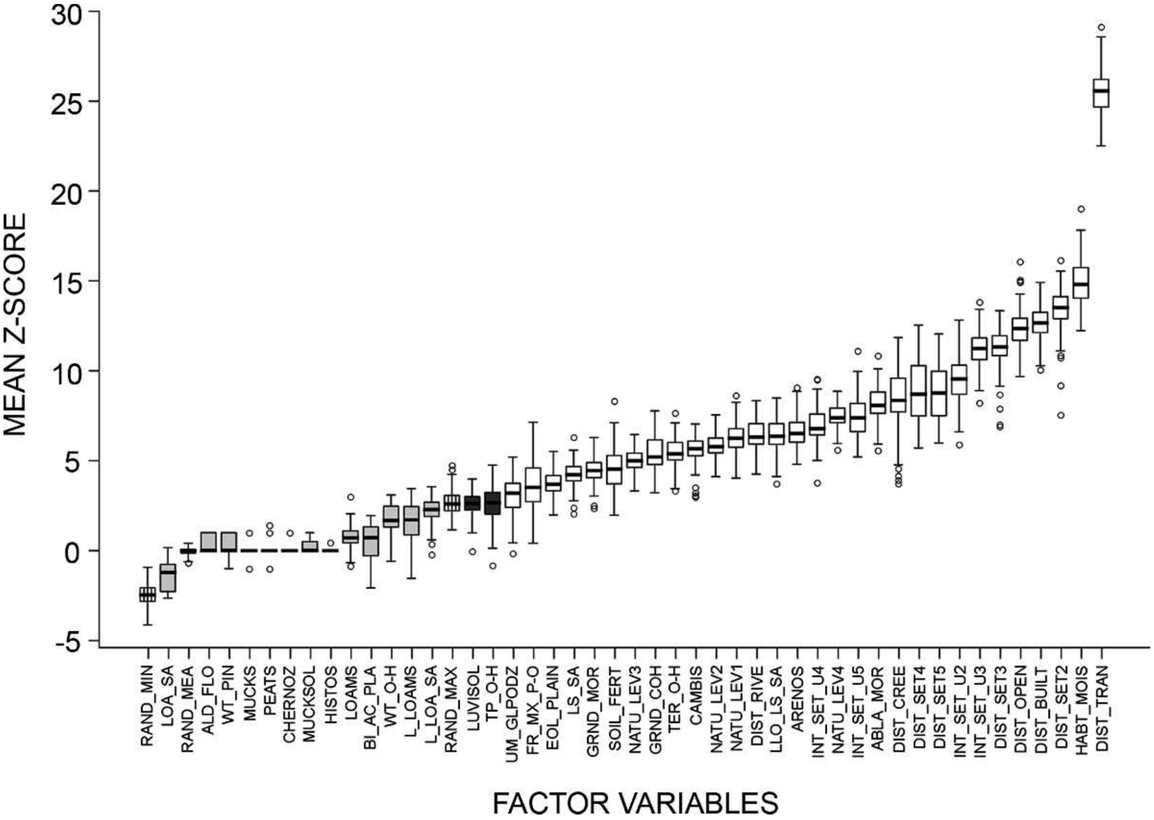

Figure 3. The distribution of Z-score values for Random Forest (RF) models run on the indicator data set in R Boruta package. Vertically hatched boxes indicate average, mean and max of Z-score for random variables generated by Boruta package. White boxes indicate variables significantly more important than random variables. Light-grey boxes indicate variables with importance not significantly higher than random ones and dark-grey boxes indicate variables with unresolved status after 130 RF runs.

This indicated a slight increase in the model quality as a result of the elimination of uninformative factor levels.

The analysis of BVI of the sett presence vs pseudo-absence sites in the RF model for the indicator data set underscored again the importance of the distance from roads (BVI = 0.688), then the distance from human settlements (BVI = 0.272), habitat moisture (BVI = 0.139) and distance from the second nearest neighbouring active main sett (BVI = 0.097). Other factors, with lower importance, did not create distinct groups, but rather their BVI values diminished gradually (BVI from 0.001 to 0.065; Table 8).

Among four variable groups, the human pressure variable group (Mean BVI = 0.147) appeared as the most important determinant of badger sett locations. It was followed by variables of neighbouring badger territories that had three times lower mean impor-

Table 7. Predictive performance of Random Forest model for the indicator data set run in R package BIOMOD. Area Under ROC Curve (AUC) values are cross validation values in lowest row. An overall model performance in the last column and row is the arithmetic mean of AUC values for all five repetitions (1-5).

	Repetition					
Performance measure	1	2	3	4	5	Full
Total score	0.99	0.98	0.99	0.98	0.97	1
Cut-off	19.12	9.66	15.38	13.78	11.58	599.88
Sensitivity (true positive fraction)	95.52	92.54	94.03	94.03	92.54	100
Specificity (true negative fraction)	95.39	91.43	94.26	94.33	92.28	100
Cross validation	0.923	0.825	0.890	0.861	0.833	0.867

Table 8. BIOMOD Variable Importance (BVI) for numeric and indicator variables from different groups in the indicator data set.

Variable abbreviation	BVI	Rank of BVI	Variable group
DIST_TRAN	0.688	31	Anthropic pressure
DIST_BUILT	0.272	30	Anthropic pressure
HABIT_MOIS	0.139	29	Denning conditions
DIST_SET_2	0.097	28	Neighbouring badger territories
DIST_SET_5	0.065	27	Neighbouring badger territories
DIST_SET_4	0.052	26	Neighbouring badger territories
DIST_OPEN	0.047	25	Anthropic pressure
ABLA_MOR	0.038	24	Denning conditions
DIST_SET_3	0.036	23	Neighbouring badger territories
INT_SET_U_2	0.030	22	Neighbouring badger territories
INT_SET_U_3	0.030	21	Neighbouring badger territories
DIST_CREE	0.027	20	Denning conditions
DIST_RIVE	0.024	19	Denning conditions
INT_SET_U_5	0.019	18	Neighbouring badger territories
INT_SET_U_4	0.012	17	Neighbouring badger territories
NATU_LEV_2	0.011	16	Anthropic pressure
SOIL_FERT	0.009	15	Feeding conditions
ARENOS	0.009	14	Feeding conditions
NATU_LEV_1	0.007	13	Anthropic pressure
NATU_LEV_4	0.006	12	Anthropic pressure
TER_O-H	0.005	11	Feeding conditions
LLO_LS_SA	0.005	10	Feeding conditions
GRND_COHE	0.004	9	Denning conditions
FR_MX_P-O	0.003	8	Feeding conditions
CAMBIS	0.002	7	Feeding conditions
GRND_MOR	0.002	6	Denning conditions
NATU_LEV_3	0.001	5	Anthropic pressure
LS_SA	0.001	4	Feeding conditions
UM_GLPODZ	0.001	3	Feeding conditions
EOL_PLAIN	0.001	2	Denning conditions
LUVISOL	0.001	1	Feeding conditions
Mean	0.053	16	-

tance value (Mean BVI = 0.043), and then, with just a slightly lower value, by geological conditions impacting digging of dens (Mean BVI = 0.034). Lastly, soil conditions determining food supply of the habitat (BVI = 0.004) had only a smal impact on location of badger setts. This order of variable groups resulted mainly from mean values of BVI that indicated high differences between groups (Table 9).

Detailed distribution of probability of sett occurrence, predicted by the RF model as a result of change of one particular predictor's value, obtained in a form of BIOMOD Partial Response Plots, again indicated strong and unambiguous avoidance of transportation lines by badgers (clear preference of areas distant by > 2.5 km). The less strong, but also clear avoidance of open areas (preference of areas

Table 9. Mean BIOMOD Variable Importance (BVI) values for different variable groups in the indicator data set.

Variable group	Mean BVI	Mean rank of BVI	Variable group importance rank
Anthropic pressure	0.147	18.9	I
Neighbouring badger territories	0.043	22.8	II
Denning conditions	0.034	15.6	III
Feeding conditions	0.004	8.1	IV

distant > 4 km), and the bimodal distribution of setts in terms of distance from human settlements with two peaks of probability (one at 0.5 km and one at 6 km from human settlements) both resembled respective Partial Response Plots for the factor data set. The predicted probability values with regard to the distance to the 2nd, 3rd, 4th and 5th active main setts showed peaks in the distance of 1-2 km and a rise in the distance of ca 8-10 km. Other variables did not significantly affect sett location probability changes.

Discussion

It can be assumed that the active main badger setts analysed in our study constituted nearly all existing setts of this type in BPF. Such conclusion can be drawn both because setts were easy to find and because of the asymptotic increase in their number in consecutive seasons when the research was carried out. The 33 utilised main setts found during our research were a higher number than the previously reported number of 23 utilised main setts in BPF (Kowalczyk et al. 2003). This means that the density of setts, so far considered as the highest, acquired by the use of telemetry of seven setts distributed over the area of 130 km^2 in the central part of BPF (Kowalczyk et al. 2003), is in fact average for the whole of BPF. Therefore, our results change the established idea about density of setts in the whole of BPF from 0.039 to 0.055 setts/km^2. On the other hand, the number of abandoned setts, in particular those abandoned long ago, is probably recorded incompletely. This applies also to secondary and occasional setts as they were recorded by chance alongside the survey of the main setts.

Setts analysed in our study in terms of surface and number of entrances did not reach the sizes of setts described in England, where setts can have nearly 180 entrances and 50 chambers (Roper 1992), or in Holland, where setts can have > 100 entrances and 1 ha of surface (van Wijngaarden & van de Peppel 1964) or northern Italy with 29 entrances and 0.375 ha of surface (Remonti et al. 2006). They were, however, bigger than setts recorded in the Mediterranean scrubland areas of Spain with 2.6 entrances (Revilla et al. 2001b) or submountain areas with 1.8 entrances (Prigioni & Deflorian 2005). The setts in BPF were closest in size to setts from central Poland of 340 m^2 average surface and 11.4 entrances (Obidziński & Głogowski 2005) or setts from the Czech Republic with an average area of 100 m^2 and 3.6 entrances (Bičík et al. 2000). Differences can result from diverse sizes of badger family groups living in distinct areas. These in turn probably depend on food resources of occupied habitats, which are partially dependent on the climate (Kowalczyk et al. 2003, 2004, 2006).

Selection of places for location of setts by badgers depends on several factors with terrain configuration, geomorphological land forms, habitat fertility, vegetation cover and man-made disturbances most often explored by researchers (e.g. Thornton 1988, Neal & Roper 1991, Bičik et al. 2000, Revila et al. 2001b, Mickevičus 2002, Macdonald et al. 2004, Prigioni & Deflorian 2005, Rosalino et al. 2005, Santos & Beier 2008, Kurek 2011, Mysłajek et al. 2012a). Results published so far are difficult to compare due to a wide diversity of studied habitats and geographic localities. In our research, we attempted to include as many of these determinants as possible. We included four groups of factors: 1) habitat fertility that influences food accessibility, 2) geological conditions that influences possibility to dig dens, 3) presence of other badger setts that limits settlement by other family groups as well as 4) presence of anthropogenic land-use forms. We did not include the topography or present vegetation, because the topography of our study area was only slightly wavy and the vegetation of setts that had been actively used for > 50 years (Forest Administration, pers. comm.) may have changed since their creation.

Our results revealed very high importance of anthropogenic land-use forms for sett locations. Such factors as transportation lines, built-up areas and open areas turned out to be the most significant variables impacting localisation of badger dens in BPF. Avoidance of transportation lines was previously observed elsewhere (e.g. Skinner et al. 1991, Jepsen et al. 2005, Prigioni & Deflorian 2005, Mysłajek et al. 2012a). The probable general mechanism of road impact is due to traffic noise, human penetration and increased mortality (Bennett 1991). In BPF, the lack of setts in the neighbourhood of roads (railways are scarce there) may not only be a result of vehicle noise, but also due to the more intensive penetration into natural areas by berry, herb and mushroom pickers, tourists, hunters and forest workers. Man-induced mortality is a limitation in analyses of animal distribution as it is difficult to obtain the necessary information on which such parameter could be based (Thornton 1988). Direct measures of road mortality are the best data sources to assess its real impact.

Badger setts are sometimes recorded in the vicinity of built-up areas, especially in the suburbs (e.g. Wright et al. 2000, Kaneko et al. 2006, Davison et al. 2009). However, such locations result mostly from lack of woods and mid-field wood lots. Nonetheless, in general, badgers mostly avoid the vicinity of built-up areas (Hammond et al. 2001, Jepsen et al. 2005, Prigioni & Deflorian 2005, Kurek 2011, Mysłajek et al. 2012a). More precisely, they shun the presence of humans as settling of setts was recorded under derelict buildings (Revila et al. 2001a, Pavlačik et al 2004, Mysłajek et al. 2012a, A. Obidziński, pers. obs. from Kampinoska Forest, Central Poland). Our observation of avoidance of the vicinity of built-up areas is, therefore, congruent with the majority of observations of other researchers.

Distribution of setts with reference to open areas looks different. Badger setts have usually been recorded at the outskirts of forests (e.g. Bičík et al. 2000, Good et al. 2001, Obidziński & Głogowski 2005, van Apeldoorn et al. 2006, Mysłajek et al. 2012b) and sometimes even a majority of setts are observed at the outskirts of forests (e.g. Neal 1972, Stubbe 1965, Sumiński 1989, Do Linh San et al. 2007). It is generally explained by close access to meadows and pastures with high earthworm abundance, the common and preferred food of the badger (e.g. Kruuk 1978, Brown 1983, Kowalczyk et al. 2003, Mysłajek et al. 2012b). However, in other areas, a smaller proportion of setts is recorded at the outskirts of forests than inside the forest (Virgós & Casanovas 1999, Revila et al. 2001b, Mickevičus 2002, Bičik et al. 2000, Prigioni & Deflorian 2005, Kaneko et al. 2006). This aspect of distribution is usually explained by several kinds of man-made disturbances present close to the forest edge.

The high proportion of setts recorded inside BPF (away from open areas) may be explained by two causes: 1) higher anthropic pressure at the outskirts than inside of the forest due to more roads and human settlements outside than inside the forest, and 2) a small area of meadows in the neighbourhood of forests and a large area of fields and fallow fields that are not so abundant with earthworms (Kruuk 1978, Ryl 1984). On the other hand, limiting habitat properties such as swamping or poor soils are not present in the outskirts more often than inside BPF (Table 10).

It is interesting to note that the significance of forest naturalness was low compared to demonstrated avoidance of anthropogenic forms of terrain use for sett distribution in BPF. The bimodal character of badger sett distribution, located either in most natural or in most transformed forests, can show badger's tolerance to anthropogenic transformations of forests. This finding is supported by the settling of setts in small mid-field woods or hedgroves in agricultural areas elsewhere (e.g. Feore & Montgomery 1999, Baliestieri et al. 2009, Rosalino et al. 2004, Remonti et al. 2006) or in suburbs (e.g. Wright et al. 2000, Kaneko et al. 2006, Davison et al. 2009). A different situation was reported by Kurek (2011) in central Poland, where badgers preferred to settle their setts in protected parts of forests; however, it was due to a more limited human presence and large areas of pine monocultures there. Regardless of the above, the lack of importance of the level of forest transformation on sett location that we observed could have been partially caused indirectly by our forest naturalness classification, based on the forms of protection used in BPF (strict protection, partial protection and managed forests). It is possible that the importance of forest naturalness would be higher if based on field observation of biological features of the forest.

Distances between badger setts observed in diverse environments differ significantly from 0.3 to 0.5 km in England (Kruuk & Parish 1982, Clements, et al.

Table 10. Avoided habitat properties in relation to distances from open areas and built-up areas by badgers in the Białowieża Primeval Forest, Poland. Data did not match the assumptions for the χ^2-test for swamps and oligotrophy at a distance of 250 m from built-up areas.

Avoided habitat properties	In distance of	From	Area observed (km^2)	Area expected (km^2)	χ^2	df	P-value
Swamps	500 m	Open areas	36	29	2.21	1	0.1373
	250 m		20	15	2.46	1	0.1168
	500 m	Built-up areas	6	11	2.38	1	0.1230
Oligotrophy	500 m	Open areas	24	24	1.59	2	0.4522
	250 m		11	12	0.95	2	0.6233
	500 m	Built-up areas	5	9	4.49	2	0.1060

1988) and from 3.75 to 4.1 km in Poland (Bartmańska & Nadolska 2003, Kowalczyk et al. 2003). They depend on a number of factors, mostly abundance of food supply, climate, size of family groups and predator pressure (Kruuk & Parish 1982, Kowalczyk et al. 2003, Sidorovich et al. 2011). The distance found most often between setts was 2 km, and it was two times smaller than the mean distance of 4.28 km. Our results indicated the existence of a certain level of clumping of setts in the investigated area. There may be many possible explanations for this pattern. First of all, this can be a result of a patchy distribution of most suitable habitats. In BPF, the areas most suitable for digging setts are moraine areas and the least suitable are large swampy areas, and both habitat types are distributed in patches of a few square kilometres. In big suitable patches, many smaller territories may be placed and beside them there are larger territories containing less suitable landscape patches. This is supported by conclusions from another study of the badger population in BPF (Kowalczyk et al. 2004). There may be other causes of the low distance between setts and higher density of setts relating to the average distance between setts. In high density badger populations, some males and females migrate between groups and almost half of the young badgers have fathers from neighbouring territories (Dugdale et al. 2007). That may be a reason for neighbouring groups not to compete aggressively or outcompete the other group from suitable habitat patches. It is possible that the correlation between the genetic and physical distances between badger groups is high. While it was not tested in the badger population in BPF, as it was in other mammal species (Gliwicz & Dabrowski 2008), it could be an interesting additional explanation of the lower than the mean, most probable distance to the nearest active main sett.

Geological conditions are, beside food supply, the most frequently mentioned factor conditioning sett settling. Ground diggability (e.g. Dunwell & Killingley 1969, Neal 1972, Thornton 1988, Revila et al. 2001b, Macdonald et al 2004, Rosalino et al. 2005), exposition and slope inclination (Neal 1972, Macdonald et al 2004, Prigioni & Deflorian 2005) or moisture (Hammond et al. 2001, Mickevičus 2002, Kowalczyk et al. 2003, Macdonald et al. 2004, Remonti et al. 2006) have been indicated as significant most frequently to date. In our case, moderately fresh habitat moisture and ablation moraines were the most significant habitat conditions. Distance from creeks (0.88 km) and distance from rivers (1.03 km) were other geomorphologic factors observed as significant. Preference of fresh and avoidance of wet habitats when settling setts results from a high level of ground waters that can flood underground corridors. This phenomenon has been recognised widely by all researchers who have analysed setts settled in habitats with varied moisture (e.g. Hammond et al. 2001, Mickevičus 2002, Kowalczyk et al. 2003, Macdonald et al. 2004, Remonti et al. 2006). Observed distance from surface waters seems to be linked with a sufficiently deep level of ground waters allowing settling setts. Ground cohesiveness had minimum impact on localisation of setts in our case (> 30 times weaker than habitat moisture). It could have been caused by the fact that the entire range of ground cohesiveness observed in BPF, from loose sands to loams and clays, enables badgers to dig setts. Clays are less inhabited here, but they are not avoided. Perhaps a larger sample size might allow more exact correlation with respect to this habitat aspect.

Habitat fertility is also very often indicated as a factor conditioning sett distribution (e.g. Neal & Roper 1991, Bičík et al. 2000, Mickevičus 2002), reportedly connected with the abundance of earthworms (e.g. Kruuk 1978, Brown 1983, Da Silva et al. 1993, Kowalczyk et al. 2003, 2006). However, it had a rather insignificant impact on sett distribution in BPF. An average forest habitat patch in BPF is ca 20 ha (calculated on data from Kwiatkowski 1994) while an average badger family group territory measured as a 95% minimum convex polygon is 920 ha in BPF (Kowalczyk et al. 2003). This implies that one family group territory can include over 40 forest habitat patches. Therefore, setts could have been settled in places of any fertility. Habitats of high food supply were always available in badger family territories because fertile habitats prevail all over BPF. Hence, the observed weak correlation of sett distribution with habitat fertility does not contradict earlier results (Kowalczyk et al. 2003) indicating a strong correlation of badger territory distribution with fertility of habitats in BPF. Nonetheless, differences in habitat fertility can play a role in sett distribution in areas of large-scale habitat diversity (e.g. Neal & Roper 1991, Bičík et al. 2000, Mickevičus 2002).

Therefore, the hierarchy of factors impacting the distribution of setts that we observed is an interesting and new result. Only a few studies have defined this hierarchy so far. They indicated the following sequences of significance: geological structures suitable for digging setts > high quality feeding patches

(Rosalino et al. 2005), slope angle = boulder size > anthropogenic disturbances (Prigioni & Deflorian 2005), deciduous forests > cork oak *Quercus suber* plantations > pine plantations (Santos & Beier 2008). All of these works examined a wider scope of variables but only the factors mentioned were significant.

All factors impacting sett distribution taken into account in our study occurred to be significant; however, their hierarchic sequence was contrary to the one we had expected. Human pressure occurred as the most significant, followed by presence of other actively used setts, then, much less, geological conditions and lastly, habitat fertility. Even if the distinction between geological and soil factors may be considered somewhat contrived, the anthropogenic factor and space structure of badger populations will still occur as the primary habitat aspect, in comparison to other properties.

It is important to note, however, that while our model is a robust one, it also has some statistical limitations. Our data sets have very low prevalence, i.e. low number of presence points. While our models qualified as good in terms of predictive power (AUC > 0.8), it has recently been revealed that for best results, RF should have the same number of presence and pseudo-absence points (Barbet-Massin et al. 2012). In our cases, due to the high variability and low size of habitat patches, we decided to stay with the high number of pseudo-absence points. That probably lowered the predictive power, but drastically increased the accordance of results in subsequent model runs. Barbet-Massin et al. (2012) also warned that RF models with low prevalence would have higher specificity, i.e. in our case, they should have a weaker tendency to classify a given point as suitable for settling a sett. In other words, there may be more presence points than predicted, but all predicted presences are very probable to be true ones. However, relative importance of habitat features should not be affected by these methodological aspects of RF models. Another statistical limitation is an *a priori* assumption that absence points represent really unsuitable habitat forms. In a case of unsaturated habitat, it is difficult to determine whether the unoccupied areas are really unsuitable or whether the population is just not saturated (Schadt et al. 2002). This is another reason why we stayed with a more conservative sampling approach.

Demonstrated hierarchy of factors impacting badger sett distribution in BPF may result from: 1) the species' anthropophobia to presence of various man-made disturbances, 2) the species' territorialism, 3) diversification of the forest into fresh habitats (52%) that enable setts digging and moist or wet habitats (48%) not suitable for this purpose, as well as 4) prevalence of fertile habitats (48%) and medium fertile habitats (37%) over poor ones (15%). However, badgers' anthropophobia observed as the prime factor still remains unanswered. Levels of anthropophobia are diverse across the whole species range and they seem to depend on the level of transformation of the environment inhabited by a particular population. It has been observed that badgers avoid settling their setts close to human land-form use in areas with a high proportion of forest cover (Bičik et al. 2000, Mickevičus 2002, Kowalczyk et al. 2003, Prigioni & Deflorian 2005, Mysłajek et al. 2012a). On the other hand, badgers demonstrate distinct synanthropisation in agricultural areas or suburbs (Wright et al. 2000, Rosalino et al. 2004, Kaneko et al. 2006, Davison et al. 2009). A higher density of setts inside BPF can more likely result from higher pressure of poachers at the outskirts of the forest than from road kills as the traffic around BPF is low. Also traces of destruction of setts are present more often at the outskirts than inside of the forest (A. Obidziński, pers. obs.). Smaller numbers of badgers at the outskirts of the forest caused by the pressure of poachers and road kills was observed also in Doñana National Park, southwestern Spain (Revilla et al. 2001a) and by hunters in Beskidy Mountains, southern Poland (Mysłajek 2012a,b). It can, therefore, be assumed that the lack of or smaller numbers of badgers at the outskirts of BPF is caused rather by their physical extermination than aetiological anthropophobia.

It seems that there is a sort of balance of costs and benefits for badgers inhabiting the outskirts of forests. They have easier access to meadows abundant in earthworms, but a higher risk of mortality at the outskirts of forests. Traditional use of forests, including poaching, is more common in regions less developed in terms of economy and farming, such as BPF (Radecki 1996), than in developed regions (e.g. Wilfred & MacColl 2010). Therefore, inhabiting the outskirts of the forests is an advantage for badgers living in regions with well developed agriculture. Inhabiting the forests outskirts is dangerous or even impossible in regions of extensive agriculture (Revilla et al. 2001a, Wilfred & MacColl 2010). In some cases, badgers have developed a survival strategy where they live inside the forest and feed at the outskirts (Mysłajek 2012a).

Fortunately, poaching gradually disappears in BPF since the last poachers gradually pass away and new ones are not recruited (Forests Administration, pers. comm.). Only old traces of destruction of setts were observed during our research. Moreover, we recorded the creation of new setts and reinhabiting of formerly abandoned ones. Anti-rabies vaccines distributed in the forest may have an additional impact on the growth of the badger population. All this seems to have an influence on the current recolonisation of badger setts at the outskirts of the forest (A. Obidziński, pers. obs.). The regeneration of badger populations is recorded all over Europe (e.g. Griffiths & Thomas 1997, Macdonald et al. 2004, van Apeldoorn et al. 2006). It happens in Poland as well, e.g. the number of badgers increased from 386 to 1,361 individuals and the number of hunting harvest increased from 5 to 119 individuals/year during 2000-2011 in the Białystok Region where BPF is situated (Kamieniarz & Panek 2008, Research Station of Polish Hunting Association, unpubl. data).

Recognition of habitat properties shaping badger sett distribution in BPF may facilitate protection of this species through landscape management. Our results show that forest refuges for badgers should ideally represent mesotrophic deciduous canopies on cambisols, consisting of loamy sands, on moderately fresh habitats. Ecological corridors and road passes should be aimed at linking such places. Due to low importance of naturalness level, our results should be applicable to less natural areas with similar spatial extent of suitable habitats and the similar mean distance to roads and open areas as well as local badger population density. Our results may also be helpful in predicting recolonisation of the badger in areas of BPF that are still unoccupied by this species but which seem suitable for settling. The same applies to post-agricultural areas being overgrown with thickets and pole-timber woods adjacent to BPF as well as in other forest complexes. The obtained results may also be helpful for understanding the distribution of other taxa for which the badger plays the role of engineer species (*sensu* Jones et al. 1994), e.g. the raccoon dog, partially the red fox and occasionally the wolf (Kowalczyk et al. 2008) as well as a number of rodent species (Neal & Roper 1991) offering them shelter in abandoned burrows, and even several plant species usually considered as non-forest species may grow in the soil conditions offered by the digging activity of the badger (Obidziński & Głogowski 2005, Obidziński & Kiełtyk 2006).

Conclusions

- Random Forest models of good predictive power enabled us to calculate and rank the habitat feature importance (BIV) and possible impact for habitat features and their groups.
- Contrary to our expectations, human impact features with the distance to roads in the first place were the most important factor determining badger sett distribution, then the presence of neighbouring badger territories, then digging suitability conditions and the habitat fertility was the least important feature.
- Badgers in Białowieża Primeval Forest prefer cambisols or entic podzols of fresh moisture, made of loamy sands on ablation moraines or eolic dunes, with potential vegetation of thermophilous oak-hornbeam forest or fresh pine-oak mixed forest in the distance of 2 km from the nearest active main setts, and they avoid vicinity of roads, open areas or built-up areas for settling their setts.
- Our results emphasise the role of large, intact, not necessarily highly natural, forest preserves as the refuge areas for badger populations, when the mortality on the more open areas is higher than the benefits of easy food availability.

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References

Balestrieri, A., Remonti, L. & Prigioni, C. 2009: Habitat selection in a low-density Badger *Meles meles* population: A comparison of radio-tracking and latrine surveys. - Wildlife Biology 15(4): 442-448.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. 2012: Selecting pseudo-absences for species distribution models: how, where and how many? - Methods in Ecology and Evolution 3(2): 327-338.

Bartmańska, J. & Nadolska, M. 2003: The density of badger setts in the Sudety Mountains, Poland. - Acta Theriologica 48(4): 515-525.

Bennett, A.F. 1991: Roads, roadsides and wildlife conservation. - In: Saunders, D.A. & Hobb, R.J. (Eds.); Nature Conservation 2: The Role of Corridors. Surrey Beatty &

Sons, Chipping Norton, New South Wales, Australia, pp. 99-117.

Bičík, V., Foldynová, S. & Matyáštík, T. 2000: Distribution and habitat selection of badger *Meles meles* in Southern Moravia. - Acta Universitatis Palackianae Olomucensis Biologica 38: 29-40.

Breiman, L. 2001a: Random forests. - Machine Learning 45(1): 5-32.

Breiman, L. 2001b: Statistical modeling: the two cultures (with comments and a rejoinder by the author). - Statistical Science 16(3): 199-231.

Brøseth, H., Knutsen, B. & Bevangek, K. 1997: Function of multiple badger *Meles meles* setts: distribution and utilisation. - Wildlife Biology 3(2): 89-96.

Brown, C.A.J. 1983: Prey abundance of the European badger, *Meles meles* L., in north-east Scotland. - Mammalia 47(1): 81-86.

Brożek, S. & Zwydak, M. 2003: Atlas gleb leśnych Polski. - CILP, Warszawa, Poland, 467 pp. (In Polish).

Clements, E.D., Neal, E.G. & Yalden, D.W. 1988: The national badger sett survey. - Mammal Review 18(1): 1-9.

Cutler, D.R., Edwards, T.C., Jr., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J. & Lawler, J.J. 2007: Random forests for classification in ecology. - Ecology 88(11): 2783-2792.

Da Silva, J., Woodroffe, R. & Macdonald, D.W. 1993: Habitat, food availability and group territoriality in the European badger, *Meles meles*. - Oecologia 95: 558-564.

Davison, J., Huck, M., Delahay, R. & Roper, T. 2009: Restricted ranging behaviour in a high-density population of urban badgers. - Journal of Zoology (London) 277(1): 45-53.

Do Linh San, E., Ferrari, N. & Weber, J.M. 2007: Socio-spatial organization of Eurasian badgers *Meles meles* in a low-density population of central Europe. - Canadian Journal of Zoology 85(9): 973-984.

Doncaster, C.P. & Woodroffe, R. 1993: Den site can determine shape and size of badger territories: implications for group-living. - Oikos 66(1): 88-93.

Dugdale, H.L., Macdonald, D.W., Pope, L.C., Burke, T. 2007: Polygynandry, extra-group paternity and multiple-paternity litters in European badger (*Meles meles*) social groups. - Molecular Ecology 16(24): 5294-5306.

Dunwell, M.R. & Killingley, A. 1969: The distribution of badger setts in relation to the geology of the Chilterns. - Journal of Zoology (London) 158(2): 204-208.

Elith, J., Ferrier, S., Huettmann, F. & Leathwick, J. 2005: The evaluation strip: a new and robust method for plotting predicted responses from species distribution models. - Ecological Modelling 186(3): 280-289.

Elith, J. & Leathwick, J.R. 2009: Species distribution models: ecological explanation and prediction across space and time. - Annual Review of Ecology, Evolution, and Systematics 40: 677-697.

Faliński, J.B. 1986: Vegetation dynamics in temperate lowland primeval forests. Ecological studies in Białowieża forest. - Geobotany 8, W. Junk, Dordrecht, the Netherlands, 537 pp.

Feore, S. & Montgomery, W.I. 1999: Habitat effects on the spatial ecology of the European badger *Meles meles*. - Journal of Zoology (London) 247(4): 537-549.

Franklin, J. & Miller, J.A. 2010: Mapping species distributions: spatial inference and prediction. - Cambridge University Press, Cambridge, UK, 320 pp.

Gaston, K.J. & Blackburn, T.M. 1999: A critique for macroecology. - Oikos 84(3): 353-368.

Gliwicz, J. & Dabrowski, M.J. 2008: Ecological factors affecting the diel activity of voles in a multi-species community. - Annales Zoologici Fennici 45(4): 242-247.

Good, T.C., Hindenlang, K., Imfeld, S. & Nievergelt, B. 2001: A habitat analysis of badger *Meles meles* L. setts in a semi-natural forest. - Mammalian Biology 66(4): 204-214.

Griffiths, H.I. & Thomas, D.H. 1993: The status of the badger *Meles meles* in Europe. - Mammal Review 23(1): 17-58.

Griffiths, H.I. & Thomas, D.H. 1997: The conservation and management of the European badger *Meles meles*. - Nature and environment, No. 90, Council of Europe, Brussel, Belgium, 86 pp.

Guisan, A. & Zimmermann, N.E. 2000: Predictive habitat distribution models in ecology. - Ecological Modeling 135(2-3): 147-186.

Hammond, R.F., McGrath, G. & Martin, S.W. 2001: Irish soil and land-use classifications as predictors of numbers of badgers and badger setts. - Preventive Veterinary Medicine 51(3-4): 137-148.

Jędrzejewska, B. & Jędrzejewski, W. 1998: Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. - Ecological Studies 135. Springer-Verlag, Berlin, Germany, 450 pp.

Jepsen, J.U., Madsen, A.B., Karlson, M. & Groth, D. 2005: Predicting distribution and density of European badger *Meles meles* setts in Denmark. - Biodiversity and Conservation 14(13): 3235-3253.

Jones, C.G., Lawton, J.H. & Shachak, M. 1994: Organisms as ecosystem engineers. - Oikos 69(3): 373-386.

Kaiser, J. 1997: When a habitat is not a home. - Science 276: 1636-1638.

Kamieniarz, R. & Panek, M. 2008: Zwierzęta łowne w Polsce na przełomie XX i XXI wieku. (In Polish with an English summary: Game animals in Poland at the turn of the 20th and 21st century) - Stacja Badawcza OHZ PZŁ, Czempiń, Poland, 132 pp.

Kaneko, Y., Maruyama, N. & Macdonald, D.W. 2006: Food habits and habitat selection of suburban badgers *Meles meles* in Japan. - Journal of Zoology (London) 270(1): 78-89.

Kauhala, K., Holmala, K., Lammers, W. & Schregel, J. 2006: Home ranges and densities of medium-sized carnivores in south-east Finland, with special reference to rabies spread. - Acta Theriologica 51(1): 1-13.

Kostrzewski, W. 1988: Parametry geotechniczne gruntów budowlanych oraz metody ich oznaczania. - WPP, Poznań, Poland, 315 pp. (In Polish).

Kowalczyk, R., Bunevich, A.N. & Jędrzejewska, B. 2000: Badger density and distribution of setts in Białowieża Primeval Forest Poland and Belarus compared to other Eurasian populations. - Acta Theriologica 45(3): 395-408.

Kowalczyk, R., Jędrzejewska, B., Zalewski, A. & Jędrzejewski, W. 2008: Facilitative interactions between the Eurasian badger *Meles meles*, the red fox *Vulpes vulpes,* and the invasive raccoon dog *Nyctereutes procyonoides* in Białowieża Primeval Forest, Poland. - Canadian Journal of Zoology 86(12): 1389-1396.

Kowalczyk, R., Zalewski, A. & Jędrzejewska, B. 2004: Seasonal and spatial pattern of shelter use by badgers *Meles meles* in Białowieża Primeval Forest (Poland). - Acta Theriologica 49(1): 75-92.

Kowalczyk, R., Zalewski, A. & Jędrzejewska, B. 2006: Daily movement and territory use by badgers *Meles meles* in Białowieża Primeval Forest, Poland. - Wildlife Biology 12(4): 385-391.

Kowalczyk, R., Zalewski, A., Jędrzejewska, B. & Jędrzejewski, W. 2003: Spatial organization and demography of badgers *Meles meles* in Białowieża Primeval Forest, Poland, and the influence of earthworms on Badger densities in Europe. - Canadian Journal of Zoology 81(1): 74-87.

Krebs, C.J. 1994: Ecology: The experimental analysis of distribution and abundance. 4th edition. - Harper Collins College Publishers, New York, New York, USA, 801 pp.

Krebs, C.J. 2002: Beyond population regulation and limitation. - Wildlife Research 29(1): 1-10.

Kruuk, H. 1978: Spatial organization and territorial behaviour of the European badger *Meles meles*. - Journal of Zoology (London) 184(1): 1-19.

Kruuk, H. & Parish, T. 1982: Factors affecting population density, group size and territory size of the European badger, *Meles meles*. - Journal of Zoology (London) 196(1): 31-39.

Kuhn, M. 2008: Building predictive models in R using the caret package. - Journal of Statistical Software 28: 1-26.

Kurek, P. 2011: Spatial distribution of badger *Meles meles* setts and fox *Vulpes vulpes* dens in relation to human impact and environmental availability. - Acta Zoologica Lituanica 21(1): 17-23.

Kursa, M.B., Jankowski, A. & Rudnicki, W.R. 2010: Boruta - a system for feature selection. - Fundamenta Informaticae 101(4): 271-285.

Kwiatkowski, W. 1994: Vegetation Landscapes of Białowieża Forest. - Phytocoenosis N.S. Supplementum Cartographiae Geobotanicae 6: 35-87.

Macdonald, D.W. 1983: The ecology of carnivore social behaviour. - Nature 301: 379-384.

Macdonald, D.W., Mitchelmore, F. & Bacon, P.J. 1996: Predicting badger sett numbers: evaluating methods in East Sussex. - Journal of Biogeography 23(5): 649-655.

Macdonald, D.W., Newman, C., Dean, J., Buesching, C.D. & Johnson, P.J. 2004: The distribution of Eurasian badger, *Meles meles*, setts in a high-density area: field observations contradict the sett dispersion hypothesis. - Oikos 106(2): 295-307.

Macdonald, D.W. & Rushton, S. 2003: Modelling space use and dispersal of mammals in real landscapes: a tool for conservation. - Journal of Biogeography 30(4): 607-620.

Matyáštík, T. & Bičík, V. 1999: Distribution and habitat selection of badger *Meles meles* in northern Moravia. - Acta Universitatis Palackianae Olomucensis Biologica 37: 77-88.

Mickevičius, E. 2002: Distribution of badger *Meles meles*, fox *Vulpes vulpes* and raccon dog *Nyctereutes procyonoides* burrows in different habitats and soil types of Lithuania. - Acta Zoologica Lituanica 12(2): 159-166.

Mysłajek, R.W., Nowak, S. & Jędrzejewska, B. 2012a: Distribution, characteristics and use of shelters by the Eurasian badger *Meles meles* along an altitudinal gradient in the Western Carpathians, S Poland. - Folia Zoologica 61(2): 152-160.

Mysłajek, R.W., Nowak, S., Rożen, A. & Jędrzejewska, B. 2012b: Factors shaping population density, demography and spatial organization of the Eurasian badger *Meles meles* in mountains - the Western Carpathians (Southern Poland) as a case study. - Animal Biology 62: 479-492.

Neal, E. 1972: The National Badger Survey. - Mammal Review 2(2): 55-64.

Neal, E. & Cheeseman, C. 1996: Badgers. - T. & A.D. Poyser, Natural History, London, UK, 350 pp.

Neal, E. & Roper, T.J. 1991: The environmental impact of badgers *Meles meles* and their setts. - Symposium of the Zoological Society of London 63: 89-106.

Newton-Cross, G., White, P.L.C. & Harris, S. 2007: Modelling the distribution of badgers *Meles meles*: comparing predictions from field-based and remotely derived habitat data. - Mammal Review 37(1): 54-70.

Obidziński, A. & Głogowski, R. 2005: Changes of forest flora composition in vicinity of dens of red fox and setts of Eurasian badger. - Polish Journal of Ecology 53(2): 197-213.

Obidziński, A. & Kiełtyk, P. 2006: Changes in ground vegetation around badgers' setts and foxes dens in Białowieża Primeval Forest, Poland. - Polish Botanical Studies 22: 407-416.

Ostler, J. & Roper, T.J. 1998: Changes in size, status, and distribution of badger *Meles meles* L. setts during a 20-year period. - Zeitschrift für Säugetierkunde 63: 200-209.

Pavlačik, L., Literák, I., Klimeš, J. & Bojková, M. 2004: Use of human buildings by European badger in Moravskoslezké Beskydy Mountains, Czech Republic. - Acta Theriologica 49(4): 567-570.

Pierzgalski, E., Boczoń, A. & Tyszka, J. 2002: Zmienność opadów i położenia wód gruntowych w Białowieskim Parku Narodowym. (In Polish with an English summary: Variability of precipitation and ground water level in the Białowieża National Park). - Kosmos 51(4): 415-425.

Prigioni, C. & Deflorian, M.C. 2005: Sett site selection by the

Eurasian badger *Meles meles* in an Italian Alpine area. - Italian Journal of Zoology 72(1): 43-48.

R Development Core Team 2012: R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org/ (Last accessed on 25 June 2012).

Radecki, A. 1996: Rolnictwo w rejonie Puszczy Białowieskiej. (In Polish with an English summary: Agriculture in the region of Białowieża Primeval Forest) - Wydawnictwo SGGW, Warszawa, Poland, 135 pp.

Remonti, L., Balestrieri, A. & Prigioni, C. 2006: Factors determining badger *Meles meles* sett location in agricultural ecosystems of NW Italy. - Folia Zoologica 55(1): 19-27.

Revilla, E. 2003: What does the Resource Dispersion Hypothesis explain, if anything? - Oikos 101(2): 428-432.

Revilla, E. & Palomares F. 2002: Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles*. - Journal of Animal Ecology 2002(71): 497-512.

Revilla, E., Palomares, F. & Delibes, M. 2001a: Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Doñana National Park. - Conservation Biology 15(1): 148-158.

Revilla, E., Palomares, F. & Fernandez, N. 2001b: Characteristics, location and selection of diurnal resting dens by Eurasian badgers *Meles meles* in a low density area. - Journal of Zoology (London) 255(3): 291-299.

Rogers, L.M., Cheeseman, C.L., Mallinson, P.J. & Clifton-Hadley, R. 1997: The demography of a high-density badger *Meles meles* population in the west of England. - Journal of Zoology (London) 242(4): 705-728.

Roper, T.J. 1992: The structure and function of badger setts. - Journal of Zoology (London) 227(4): 691-698.

Roper, T.J. 1993: Badger setts as a limiting resource. - In: Hayden, T.J. (Ed.); The badger. Royal Irish Academy, Dublin, Ireland, pp. 35-56.

Rosalino, L.M., Macdonald, D.W. & Santos-Reis, M. 2004: Spatial structure and land-cover use in a low-density Mediterranean population of Eurasian badgers. - Canadian Journal of Zoology 82(9): 1493-1502.

Rosalino, L.M., Macdonald, D.W. & Santos-Reis, M. 2005: Resource dispersion and badger population density in Mediterranean woodlands: is food, water or geology the limiting factor? - Oikos 110(3): 441-452.

Rudnicki, W.R. & Kursa, M.B. 2010: Feature Selection with the Boruta Package. - Journal of Statistical Software 36: 1-13.

Ryl, B. 1984: Comparison of communities of earthworms (Lumbricidae) occurring in different ecosystems of agricultural landscape. - Polish Journal of Ecology 32(1): 155-165.

Santos, M.J. & Beier, P. 2008: Habitat selection by European badgers at multiple spatial scales in Portuguese Mediterranean ecosystems. - Wildlife Research 35(8): 835-843.

Schadt, S., Revilla, E., Wiegand, T., Knauer, F., Kaczensky, P., Breitenmoser, U., Bufka, L., Červený, J., Koubek, P., Huber, T., Staniša, C. & Trepl, L. 2002: Assessing the suitability of European landscapes for the reintroduction of Eurasian lynx. - Journal of Applied Ecology 39(2): 189-203.

Sidorovich, V.E., Rotenko, I.I. & Krasko, D.A. 2011: Badger *Meles meles* spatial structure and diet in an area of low earthworm biomass and high predation risk. - Annales Zoologici Fennici 48(1): 1-16.

Skinner, C., Skinner, P. & Harris, S. 1991: An analysis of some of the factors affecting the current distribution of badger *Meles meles* setts in Essex. - Mammal Review 21(2): 51-65.

Sokołowski, A.W. 2004: Lasy Puszczy Białowieskiej. - CILP, Warszawa, Poland, 363 pp. (In Polish).

Stubbe, M. 1965: Zur Biologie der Raubtiere eines abgeschlossenen Waldgebietes. - Zeitschrift fur Jagdwissenschaft 11(2): 73-102. (In German with an English summary).

Sumiński, P. 1989: Borsuk. - Wydawnictwo PWRiL, Warszawa, Poland, 128 pp. (In Polish).

Thornton, P.S. 1988: Density and distribution of badgers in south-west England - a predictive model. - Mammal Review 18(1): 11-23.

Thuiller, W., Lafourcade, B., Engler, R. & Araujo, M.B. 2009: BIOMOD - a platform for ensemble forecasting of species distributions. - Ecography 32(3): 369-373.

Tuyttens, F.A.M., Macdonald, D.W., Rogers, L.M., Cheeseman, C.L. & Roddam, A.W. 2000: Comparative study on the consequences of culling badgers *Meles meles* on biometrics, population dynamics and movement. - Journal of Animal Ecology 69(4): 567-580.

van Apeldoorn, R.C., Knaapen, J.P., Schippers, P., Verboom, J., van Engen, H. & Meeuwsen, H. 1998: Applying ecological knowledge in landscape planning: a simulation model as a tool to evaluate scenarios for the badger in the Netherlands. - Landscape and Urban Planning 41(1): 57-69.

van Apeldoorn, R.C., Vink, J., Matyáštík, T. 2006: Dynamics of a local badger *Meles meles* population in the Netherlands over the years 1983-2001. - Mammalian Biology 71(1): 25-38.

van Wijngaarden, A. & van de Peppel, J. 1964: The badger, *Meles meles*, in the Netherlands. - Lutra 6: 1-60.

Virgós, E. 2001: Role of isolation and habitat quality in shaping species abundance: a test with badgers *Meles meles* L. in a gradient of forest fragmentation. - Journal of Biogeography 28(3): 381-389.

Virgós, E. & Casanovas, J.G. 1999: Badger *Meles meles* sett site selection in low density Mediterranean areas of central Spain. - Acta Theriologica 44(2): 173-182.

Wilfred, P. & MacColl, A.D.C. 2010: Income sources and their relation to wildlife poaching in Ugalla ecosystem, Western Tanzania. - African Journal of Environmental Science and Technology 4(12): 886-896.

Wilson, G., Harris, S. & McLaren, G. 1997: Changes in the

British badger population 1988 to 1997. - People's Trust for Endangered Species, London, UK, 143 pp.

Woodroffe, R. & Macdonald, D.W. 1993: Badger sociality: models of spatial grouping. - Symposium of the Zoological Society of London 65: 145-169.

Wozencraft, W.C. 2005: Order Carnivora. - In: Wilson, D.E. & Reeder, D.A.M. (Eds.); Mammal species of the world: A taxonomic and geographic reference. 3rd edition. Jon Hopkins University Press, Baltimore, Maryland, USA, pp. 532-628.

Wright, A., Fielding, A.H. & Wheater, C.P. 2000: Predicting the distribution of European badger *Meles meles* setts over an urbanised landscape: a GIS approach. - Photogrammetric Engineering and Remote Sensing 66 (4): 423-428.