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Badger *Meles meles* spatial structure and diet in an area of low earthworm biomass and high predation risk

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Investigating the endangered badger *Meles meles* population in Belarus we aimed to find out in accordance with which model, i.e. bottom-up or top-down, it is structured and functions. Two important factors (low earthworm biomass and high predation risk) were considered with a view to explaining the specificity in badger spatial structure and diet. The study was conducted in a semi-natural terrain in north-eastern Belarus. We analysed 1188 scats, radiotracked seven badgers and assessed variations in earthworm biomass. In the conditions of low biomass and uneven distribution of earthworms badgers were found to act as generalist predators tending to specialize on the more readily available foods during short seasonal periods. The earthworm portion in the species diet was relatively low and correlated with earthworm biomass and we did not find any evidence of badger feeding selectivity. Data on badger distribution and activity suggest that avoidance of high predation risk forces badgers towards the security of utilising primarily straight-line routes between setts. Such tactics limit availability of earthworms and other food resources and so determine low density in badgers.

Introduction

While analysing a declining population, several questions directing research design arise. First of all, what is the optimal species density that respects habitat carrying capacity in the given terrain. An answer to this question provides an estimate of population size before the decline in case the population acts in the community within the bottom-up model (Krebs 1994, Krebs *et al*. 2001). Alternatively, the population may be limited by predators at the level of density lower than allowed by resources, i.e. the population belongs to the community functioning within the top-down model (Krebs 1994, Krebs *et al*. 2001). It is the second question to answer. Such a limitation of species population density by predation is a complicated process as possible population size is influenced by both variable resources and predators that, in turn, vary in numbers under own factors. Also, severe predation may affect population size not only directly, e.g. avoiding predation the species may reduce its reproduction efforts (Korpimäki *et al*. 1994, Sheriff *et al*. 2009). Furthermore, in vertebrate community, not only species on the prey level but predators themselves may be affected by functioning within the top-down model, that is a known phenomenon, especially for carnivores, called intraguild predation (Polis *et al.* 1989, Palomares & Caro 1999).

Taking into account that in Belarus the threatened population of badgers coexists with relatively dense population of large predators — wolf *Canis lupus*, lynx *Lynx lynx* and brown bear *Ursus arctos* (Sidorovich *et al.* 2003a, Sidorovich 2006a, 2006b) — functioning of the badger population in the vertebrate community may perform within the top-down model.

Our study in Belarus dealt with badger population because the species has been on the list of endangered species for more than 20 years, seemingly as a result of anthropogenic threats (Kozla 1993). Nevertheless, the implementation of protective measures appears to have been ineffective. One plausible reason for this failure to conserve badgers effectively is connected directly to a poor understanding of badger ecology in the area.

Detailed knowledge of the badger population ecology has been derived from a number of detailed studies conducted in western Europe (e.g. Kruuk 1989, Neal & Cheeseman 1996, Rosalino *et al.* 2002, 2004, 2005a, 2005b, Virgós *et al.* 2005, Macdonald *et al.* 2009). However badgers in Belarus experience quite different ecological niche conditions, severely limiting the utility of these studies for extrapolation. Firstly, their habitat has a relatively low earthworm biomass throughout Belarus (Hotko 1993). Secondly, there is a support to the idea that population size and socio-spatial organization in badgers in Belarus is considerably influenced by predation impact registered (Bunevich 1988, Rotenko & Sidorovich 2011), while large carnivores have been extirpated throughout much of western Europe.

These two factors appear to be crucial in determining the badger feeding strategy and socio-spatial population structure.

Earthworms are known to be a preferred food of badgers, and in such habitats badgers display high reproduction rate (Kruuk 1989, Neal & Cheeseman 1996, Johnson *et al.* 2001, Kowalczyk *et al.* 2003). Shortage of available earthworms induces badgers to switch to alternative food supplies; a phenomenon well established in Mediterranean ecosystems (Virgós *et al.* 2004). We hypothesise that in Belarus badgers may follow a similar foraging strategy, but that additionally their foraging tactics would be evidently modified by the high risk of being predated upon. Possible avoidance of predation risk in the absence of high earthworm abundance would thus result in a feeding strategy and socio-spatial structure different from that observed in western Europe. We investigate this hypothesis in a semi-natural terrain in north-eastern Belarus.

The study area in a semi-natural terrain was chosen because of the common co-occurrence of large carnivores in the area, which actively prey upon badgers. Moreover, the feeding strategy and socio-spatial structure of badgers in these semi-natural environmental conditions (that still prevail in Belarus) are far less well investigated than is the case in human-modified landscapes. Existing publications on badger ecology evidence that badger feeding habits in modified landscapes are markedly distinct from those in a semi-natural terrain. For example, in rural areas badgers can eat a lot of maize, other cereal seeds and cultivated fruits (e.g. Shepherdson *et al.* 1990, Martin *et al.* 1995, Marassi & Biancardi 2002, Fischer *et al.* 2005) that are all but absent in semi-natural conditions. Consequently our objectives with this study were focussed on establishing relationships between the badger population socio-spatial structure, diet and foraging regimes, earthworm biomass, and the effects of large predators in this semi-natural study area, which provides a model for badger ecology throughout north-eastern Belarus.

Study area

The study was carried out in north-eastern Belarus in the Paazerje extensive woodland (Garadok district, Vitebsk region, 55°45´N, 30°20´E, area about 330 km^2). Here forest habitats prevail, and intensive rural areas (agricultural fields, villages, etc.) comprise only a small proportion of the landscapes (0.8%). Abandoned, dry-land meadows are common in the area (10.7%) and these disused fields are gradually becoming reforested due to the decline in hay production. There are also numerous small, open, grassy marshes located on sites with a surface clay soil layer (6.8%). Residual glacial lakes are common, and the river network is extensive (about 0.7 km km^{-2}). The topography of the area is characterized by mostly hilly terrain that originated from the last glaciation (Matveev *et al.* 1988). The region lies in the extensive transitional forest zone between temperate deciduous (mostly broad-leaved) forests and boreal coniferous forests. The spruce *Picea abies* and pine *Pinus sylvestris* are the dominant coniferous trees. The black alder *Alnus glutinosa* and grey alder *Alnus incana*, birches *Betula pendula*, *Betula pubescens*, and aspen *Populus tremula* are the most common deciduous trees.

Surface soils are clay rich, resulting in a good water supply and abundant trace elements; constituting relatively rich soils in Belarus. Considering variations in biomass of earthworms and other soil invertebrates throughout Belarus, the highest values have been recorded in such clay soil (Hotko 1993). Nevertheless, these values are markedly lower than those for the majority of western European badger study sites (Neal & Cheeseman 1996, Goszczyński *et al.* 2000, Johnson *et al.* 2001). Thus, badgers in this study were in conditions of low earthworm biomass.

The study area was populated fairly densely by large predators: the wolf — 0.5–3.2 (mean = 1.8) indiv. per 100 km^2 (Sidorovich *et al.* 2003a), lynx — 1.0–5.4 (mean = 3.1) indiv. per 100 km^2 (Sidorovich 2006b), brown bear — 0.9–6.7 (mean = 3.6) indiv. per 100 km^2 (Sidorovich 2006a). The pooled density of large carnivores averaged 8.5 indiv. per 100 km^2. Other potential predators of young badgers in the study area include the eagle owl (*Bubo bubo*), golden eagle (*Aquila chrysaetos*), white-tailed eagle (*Haliaeetus albicilla*), and greater spotted eagle (*Aquila clanga*). The pooled density of these raptors is about 2 indiv. per 100 km^2 (Sidorovich *et al.* 2008a). Consequently, there is a much higher risk for badgers to be preyed upon here than in countries of western Europe, where large carnivores are rare or missing (Wilson & Mittermeier 2009).

The climate in northern Belarus is humid continental. Winters, characterized by snow cover with average air temperature below 0 °C, are variable, but usually snow cover persists for at least 1.5–2 months, with a maximum depth of 30–90 cm. Maximum duration of the snow period is around six months, i.e. from late October until mid-April. During winter, periods of severe frost (below –20 °C) alternate with thaws lasting for some weeks.

Material and methods

Dietary analysis

A total of 1188 badger scats were collected and analysed. The scats were mostly collected from latrines at setts. Latrines were rare (one latrine per about 40 active setts inspected) and principally located inside rather than along borders of badger group home ranges. Badgers defecated irregularly or sporadically in these monitored latrines. As a consequence scats were collected for this dietary study over a long period (between 1996 and 2007 inclusive) to acquire good sample size. We succeeded in collecting 100–150 scats of badgers per each month from mid-March until late November. Note, in north-eastern Belarus winter conditions are too harsh for badgers to be active, and thus badgers normally enter a period of torpor from first frost (normally in mid-November) until snowmelt (normally between the end of March and the beginning of April). Some badgers (especially large individuals), however, have been recorded to resume activity as early as late February.

Scats were analysed following the standard procedure given by Kruuk (1989), and Jędrzejewska and Jędrzejewski (1998). Firstly, a microscopic examination for earthworm chaetae was undertaken to establish earthworm remains and to estimate their consumption rate (Kruuk 1989). Scats were then washed through a mesh sieve, and undigested remains were dried. Identification of mammal remains in these faeces was based on: (1) teeth and jaw remnants (for small mammals) according to Pucek (1981); (2) ten hairs taken randomly from each scat examined microscopically according to Teerink (1991). Insects were distinguished by exoskeletal remains, birds by feathers and bones, amphibians by bones, reptiles by bones and skin scales (Böhme 1977, März 1987). Plant material was simply recorded as consumed matter, when a significant amount was found in the scat analysed.

Data on the diet composition are thus presented in terms of 15 food categories: earthworms, molluscs, insects (mainly beetles), crayfish, fish, amphibians, reptiles, birds, bird eggs, small rodents and insectivores, medium-sized mammals, ungulate and beaver carcasses, plant matter, fruits (mostly berries), cereal seeds.

Calculating the composition of badger diet

Percentage of frequency of occurrence of various food items consumed (hereafter %OC) was derived from the total number of scats analysed. Plant remains of a particular kind (fruits, seeds or plants) in a given scat were grouped as one occurrence.

To derive the diet composition as percentage biomass consumed (hereafter %BC), we followed the approach based on the coefficients of digestibility recommended by Jędrzejewska and Jędrzejewski (1998), i.e. the ratio of fresh weight of a given food item to the dry weight of its remains in scats. To compare the trophic niche breadth of badgers in different seasons, we used the Levins *B* index (Levins 1968), calculated for the 15 food categories. This *B* index thus varied from 1 (the narrowest niche) to 15, i.e. the maximum number of food categories included in these calculations (the broadest niche possible).

Earthworm availability

Earthworms have been established as the most influential food category in determining the success, density and socio-spatial organisation of badgers across western Europe (e.g. Kruuk 1989, Neal & Cheeseman 1996, Goszczyński *et al.* 2000, Kowalczyk *et al.* 2003, Virgós *et al.* 2004). To calibrate the environmental availability of earthworms within the study area, we actually used the method recommended by Johnson *et al.* (2001). During the warm season earthworms were taken from soil on unitary plots of 1 m^2 and up to 30 cm deep. These earthworms were then counted and weighed. The total weight of earthworms per unit volume of soil (0.3 m^3) was then used as a repeatable measure of earthworm biomass available to foraging badgers. This survey was stratified to include the five main habitat types that compose the majority of the study area — spruce old-growth, small-leaved deciduous medium-aged forest, old and medium-aged pine forest, black alder swamp and meadow on glade — each sampled monthly over three years from 1997 through 1999.

Each sampling procedure consisted of measuring ten unit plots located in the same habitat. Sampling plots for subsequent months were situated close to those that were sampled in a previous month (i.e. exact sites were not re-used, once excavated). Data on earthworm biomass in each 0.3 m^3 per habitat type were averaged and re-calculated per kg ha^{-1}. Thus mean-weighted earthworm biomass represented earthworm biomass in the study area relative to the proportions of the main habitat types (Sidorovich *et al.* 2003b).

Additionally, to reveal between-year variations in earthworms, in mid-July of each year from 1996 until 2002, we estimated earthworm biomass in the same 1-m^2 plots in two habitat types: one in the dry-land (i.e. small-leaved deciduous medium-aged forest), and one in the black-alder swamp, which was characterized by the highest earthworm biomass. For each summer, we recorded weather conditions that were categorized as 'hot and dry', 'cool and wet', 'warm and wet'. In order to check variations in earthworm abundance within each particular habitat type during the hot and dry summer in 1996, we estimated earthworm biomass in several 1-m^2 plots in the same place with similar soil conditions within the two habitats mentioned above.

Badger population density and social group size

In 1997, prior to commencing our radiotracking study, we conducted a detailed survey of the study area to find all possible badger setts. Both direct inspection of the area and snow-tracking of badgers in early spring were utilised. We thus established the location of all (active and inactive) setts across the study area. We then inspected all known badger setts each year and continued to add any new ones as they appeared by continuing to use the methods described above.

Between May and August in both 1998 and 2009 (the years when radiotracking studies were performed) we conducted detailed badger censuses based on three components: (i) knowledge of all badger sett locations; (ii) sett inspection in May; (iii) the frequency of visits to each sett by badgers and the number of badgers recorded at each main sett. All active setts were categorized as ‘main’ and ‘outlier’ setts, according to their frequency of use by badgers, i.e. presence and absence of signs of denning or use as a hibernation site. To reveal the social group size (i.e. number of badger counted at each main sett), multiple methods were applied, including live-trapping using cage box-traps, visual observation from a hide, filming with camera traps (TrailMaster TM550 passive infrared trail monitors and TM35-1 camera kits, Goodson & Associates, Inc.), and morning checks for tracks at sett entrances smoothing the ground afterwards. Methods were combined, as necessary, to provide us with data on sett occupancy, to include number of adults and the number of cubs in litter.

Radiotracking

Prior to radiotracking badgers, we estimated the possible telemetry error for the transmitter type used in the study. Receivers were provided by Telonics Inc. (Mesa, Arizona), and radio collars were made by ATS (Isanti, Minnesota). With a transmitter on the ground surface, or 1 m underground in a badger sett entrance, or being carried by a member of the tracking team, another researcher tried to fix its position from different distances. From experience of telemetry studies with other mustelid species (Sidorovich & Macdonald 2001, Sidorovich *et al.* 2008b), this protocol enabled us to calibrate relatively precise bearings during this study.

In 1998, throughout the whole warm season, radiotracking of breeding females was carried out to estimate the territory occupied by four badger social groups. All instrumented females were relatively large, and thus designated as putative breeding individuals. The home range of each tracked female, as established over the whole active period, was thus taken to present social group territory. In the warm season in 2009, we additionally radiotracked three lone individuals — all relatively large adult individuals that survived a depression in the numbers observed within these social groups in 2008.

Fixes were established using short-distance compass bearings, taken by one or two researchers that were familiar with the area. Positions were plotted on a detailed map of the area (1:25 000) using a GPS equipment. Whenever practicable, we established one radio fix per 15 min, accompanied by notes on coordinates, habitat type and activity (active or inactive).

The number of fixes for each of the seven radiotagged badgers averaged 1822, and totalled 12 754. Radiotracking was conducted intensively until the values of the home-range areas reached an asymptote with respect to the increasing number of locational fixes. Home-range areas were then estimated using convex polygons (White & Garrott 1990) with the RANGES V software (Kenward & Hodder 1996).

While undertaking radiotracking, special attention was paid to the way the badgers moved when active. There were only few studies analysing badger walking patterns (e.g. Kruuk 1989, Loureiro *et al.* 2007) that suggest that badger movements are adapted to the distribution and availability of preferred food resources. With regard to the avoidance of predation risk, we tested whether badgers remain in proximity of setts or follow paths between setts directly. The escape tactics to tend to a sett in case of emergency was confirmed for badgers by specially designed study (Butler & Roper 1995). A lot of habitats with high food supply may be located outside foraging routes established.

Statistical analyses

STATISTICA Analysis System (release 6.0) was used to calculate the Spearman rank correlation coefficients (r_s). A *G*-test was used to examine heterogeneity of percentages (Sokal & Rohlf 1995). Variation in data obtained was assessed by the coefficient of variation (hereafter CV).

Results

Badger home range and population density

In July–August 1998, our census recorded a relatively low density of badgers, with scattered and uneven distribution, despite badgers being at their national maximum of abundance in our study area in north-eastern Belarus. We established 30 individuals per 330 km^2, i.e. 9.1 badgers per 100 km^2, divided between four badger social groups, with the addition of two lone badgers, i.e. ca. 1.2 badger social groups per 100 km^2. Social groups consisted of 2–12 (average 7) individuals per group (Table 1). According to the radiotracking data, group territories were relatively large and covered 16–34 km^2, with an average of 23.5 km^2.

This distribution and regional abundance of badgers, as established in 1998, continued to be more or less stable until 2008, when we observed a marked decline in badger numbers. During the inspection of the six badger setts in the warm season of the previous year (2007) a badger group was observed (not lone individuals) in each sett, with litters in five setts. In July–August 2009, a detailed census of badgers revealed that only nine individuals persisted over the same 330 km^2 area, i.e. 2.3 badgers per 100 km^2, with only one badger social group and three lone badgers present (Table 2), i.e. ca. 0.3 badger family groups per 100 km^2. Thus, this remaining social group consisted of 6 individuals.

Radiotracking of three lone adult badgers revealed that these maintained relatively small home-range areas, with activity spaced mostly around their main setts. For two lone females, home ranges averaged 4 km^2. The home range of the lone male was similar (4.2 km^2), but expanded during June–August up to 13.3 km^2. During this period, the male badger often used outlier setts, which were reached by walking directly from the main sett.

Radiotracking studies in both years did not show any overlap in territory usage between neighbouring badger social groups and/or lone individuals.

Badger walking patterns

Several walking patterns were observed: (1) walking around setts; (2) walking slowly and directly to an outlier sett, resting there and returning to the main sett; (3) walking directly to one site and from that to another with some cursory exploration at each site; with an outlier within 250 m of these sites; (4) walking directly to one site and from that to another with some cursory exploration in each, but not within a 250m range of an outlier. These second and third walking patterns differed only by visiting or not visiting outlier setts along the way. Generally we thus noted radial walking directly between-sett routes (2–4) and circular routes around setts (1). We use the adjective ‘direct’ for walking patterns

Table 1. Badgers counted in the study area of 330 km^2 and their home ranges in north-eastern Belarus in warm season 1998.

Main sett locality	Barsuchyha	Kaverzy	Kavaliova	Dzyudzi	Prasimka	Sinyaki
Family-group size	12	9	2	5	1	1
Number of outlier setts used by badgers	7	7	3	3	1	2
Home range (km^2)	26	34	16	18	–	–

Table 2. Badgers counted in the study area of 330 km^2 and their home ranges in north-eastern Belarus in warm season 2009.

Main sett locality	Barsuchyha	Kaverzy	Kavaliova	Dzyudzi	Prasimka	Sinyaki
Family-group size	adult female	adult male	0	adult female	0	6
Number of outlier setts used by badgers	3	3	–	1	–	2
Home range (km^2)	2.5	13.3	–	5.5	–	–

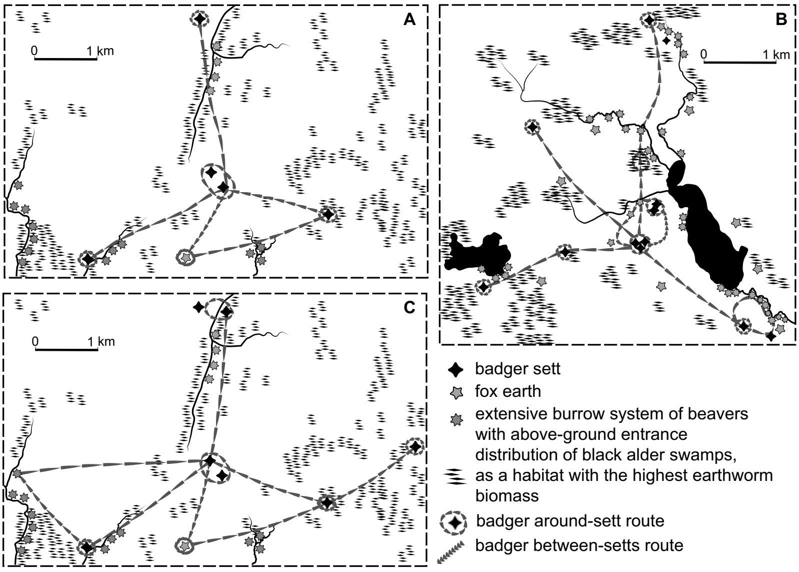

Fig. 1. Examples of foraging routes used by radio-tagged badgers in north-eastern Belarus. (**A**) adult female, Kaverzy locality, warm season 1998, (**B**) adult female, Barsuchyha locality, warm season 1998, and (**C**) adult male, Kaverzy locality, warm season 2009.

where fixes formed straight lines on the map.

Badgers that lived in social groups in the majority of cases were observed to walk slowly and directly either to outlier setts or to sites with setts nearby, while lone badgers tended to stay around their main setts more frequently or even in the majority (Table 3). Each radiotracked badger typically utilised from two to six permanent routes, which, in fact, created a network within each badger home-range (Fig. 1). Lengths of routes varied from 0.8 to 7.5 km (mean 3.7 km, $n = 11$). Badgers were recorded moving for 1.5–9.1 km (mean 4.1 km, $n = 38$) in a day.

Walking patterns with setts nearby, were found to occur in 91.3%–100%, mean 96.6%, of all routes examined (Table 3 and Fig. 1).

Seasonal changes in badger diet

Monthly data on badger diet (Fig. 2) show a pronounced seasonal variation in the consumption

Table 3. Walking patterns of adult badgers lived in family groups and alone recorded by radiotracking, warm seasons 1998 and 2009, north-eastern Belarus.

Walking pattern	Adult female lived in the family group in Barsuchyha locality, 1998	Adult female lived in the family group in Kaverzy locality, 1998	Lone adult female in Barsuchyha locality, 2009	Lone adult male in Kaverzy locality, 2009
Walking slowly and directly to an outlier sett, resting there and returning to the main sett	28 (48.3%)	10 (55.6%)	1 (6.3%)	5 (41.7%)
Walking around setts	7 (12.1%)	2 (11.1%)	15 (93.8%)	4 (33.3%)
Walking directly to one site and from that to another with some cursory exploration at each site; with an outlier within 250 m of these sites	20 (34.5%)	6 (33.3%)	0	2 (16.7%)
Walking directly to one site and from that to another with some cursory exploration in each, but not within a 250-m range of an outlier	3 (5.2%)	0	0	1 (8.3%)
Total number of walking patterns observed	58	18	16	12
Total number of fixes	3128	1892	1340	928

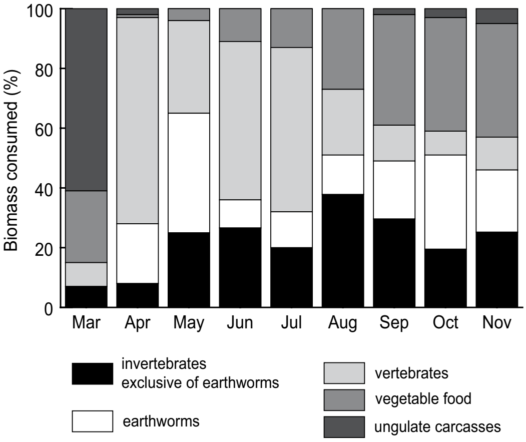

Fig. 2. Month-scale changes in badger diet in north-eastern Belarus.

of the four main food items: invertebrates (CV = 41.5%), vertebrates (CV = 74.9%), carrion (CV = 237.6%) and plant food (CV = 77.9%). The highest variation was found in the consumption of carrion that was taken mainly in early spring.

These dietary data suggest a pattern of five seasonally different diets of badgers (Table 4). These dietary variants are statistically significant when comparing the diet composition of badgers in adjacent seasonal periods (*G*-test = 56.2–185.1, $p < 0.001$).

In early spring, when snow cover still persisted (mid March–mid April), approximately during the first two post-dormancy weeks, badgers mainly scavenged for carrion of wild ungulates (58.4% BC). Snow-tracking revealed that badgers mainly searched for carcasses of wild boars *Sus scrofa*, many of which usually die from starvation by late winter. Also, in early spring, badgers ate cranberries which constituted an essential part of their diet (16.1% BC). Among vertebrate prey, only amphibians — mostly common frogs *Rana temporaria* — were consumed by badgers frequently in this season, when they comprised up to 5.5% BC.

In April, when snow cover had disappeared, badgers switched to predominantly feeding on amphibians (44.0% BC) and earthworms

Table 4. Diet composition expressed as percentage of occurrence of various food items in the scats analysed (%OC) and as percentage of food biomass consumed (%BC) in different seasons in north-eastern Belarus. The values were calculated from the data pooled across 1996–2007.

Food items	Early spring with snow cover (mid-March–mid-April)		April without snow cover		May		June–mid-July		mid-July–end of November	
	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC	%OC	%BC
Insects	9.2	6.3	19.3	7.4	67.4	24.2	50.3	24.1	70.1	31.3
Molluscs	6.7	2.0	2.3	0.4	3.7	1.0	–	–	–	–
Earthworms	–	–	46.1	20.2	78.6	40.0	33.1	10.4	52.2	19.0
Crayfish	–	–	–	–	–	–	–	–	3.6	1.7
Fish	0.8	0.5	3.2	1.0	0.9	0.4	–	–	0.9	0.4
Amphibians	16.0	5.5	53.9	44.0	13.0	12.7	4.6	2.1	4.8	2.1
Reptiles	3.4	1.0	11.1	6.3	7.4	3.3	4.0	1.7	1.8	0.5
Small mammals	4.2	3.1	4.2	3.9	6.5	4.4	9.9	11.2	9.0	6.8
Medium-sized mammals (mainly hedgehog)	–	–	3.2	5.7	3.7	6.8	2.7	5.4	0.9	1.6
Birds	0.8	0.7	4.2	3.9	6.5	3.8	28.1	29.5	2.1	1.5
Bird eggs	–	–	–	–	6.0	1.2	9.6	4.6	–	–
Ungulate and other carcasses	58.0	58.4	6.5	5.3	–	–	–	–	3.9	4.5
Fruits	14.3	16.1	1.4	0.7	–	–	6.6	2.1	55.2	16.7
Cereal seeds	–	–	–	–	–	–	–	–	38.8	10.2
Herbs	18.5	6.4	4.6	1.2	8.4	2.2	19.5	8.9	9.9	3.7
Number of scats analysed	119		217		215		302		335	
Index of food niche breadth (*B*)	2.63		3.95		4.1		5.48		5.50	

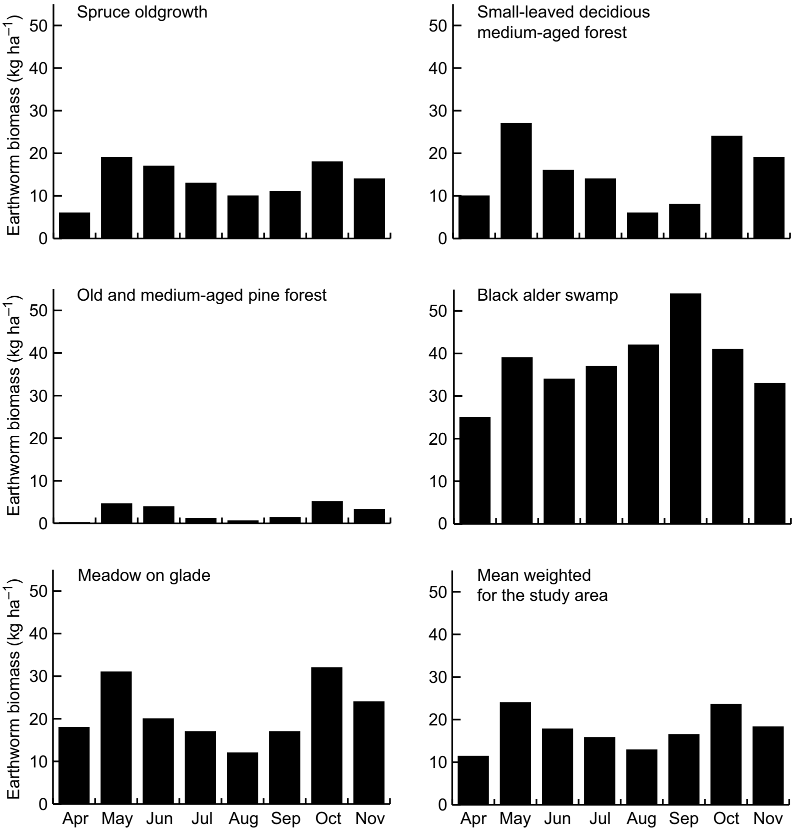

Fig. 3. Seasonal changes in earthworm biomass available for badgers (up to 30-cm deep in soil) in various habitat types in north-eastern Belarus. Each habitat type was sampled monthly over three years (1997–1999). The values presented were averaged.

(20.2% BC). Insects (mainly beetles) and reptiles (mainly lizards) were also important food categories consumed in this month. Other food categories (small rodents, birds, fish, carrion, fruits, seeds and vegetation) were of minor importance (Table 4).

In May, badger feeding was concentrated on invertebrates: earthworms (40.0% BC) and imago beetles (24.2% BC). The proportion of amphibians, which were important for badgers in April, declined markedly (Table 4).

In June, until the beginning of July, badger diet was more generalized and characterized by high consumption of birds (29.5% BC), insects (24.1% BC), earthworms (10.4% BC), and vegetation (8.9% BC). Other food items such as mammals (16.6% BC), amphibians (2.1% BC), and reptiles (1.7% BC) were also consumed frequently.

From mid-July onwards, badgers began feeding on more plant food: fruits (16.7% BC), cereal seeds (10.2% BC) and vegetation (3.7% BC). Simultaneously, badgers continued consuming many invertebrates: insects (31.3% BC), earthworms (19.0% BC).

Seasonal and habitat-related variations in earthworm biomass

The highest earthworm biomass was established in black-alder swamps (mean 38.1 kg ha^{-1}), while the lowest occurred in pine forests, usually growing on sandy soils (mean 2.5 kg ha^{-1}). Other main habitat types in the study area (mature spruce forest, seral small-leaved wood, meadow on glade) demonstrated medium levels of earthworm biomass (mean 13.5–21.4 kg ha^{-1}). Mean biomass of earthworms weighed for the habitat structure in the study area equalled 17.5 kg ha^{-1}. Between-month changes in earthworm biomass were characterized by two peaks occurring in May–June and in October, across all habitats sampled with some exceptions found in black-

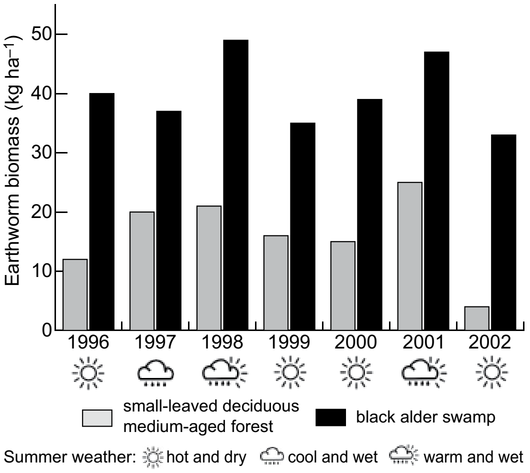

Fig. 4. Between-year variation in earthworm biomass available for badgers (up to 30-cm deep in soil) in two habitat types: small-leaved deciduous medium-aged forest as a dry-land habitat type that prevailed in the study area, and black-alder swamp as a habitat type characterized by the highest earthworm biomass. The same plots were sampled each correspondent year in mid-July.

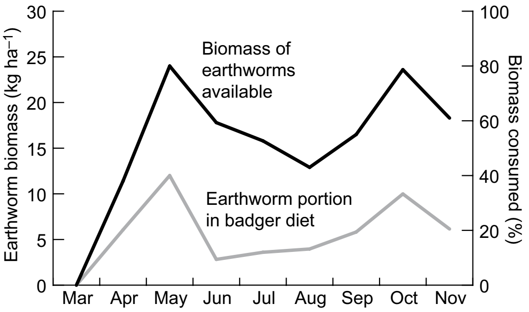

Fig. 5. Relationship between biomass of earthworms available for badgers (kg ha^{-1}) and portion of earthworms in badger diet (expressed as percentage of biomass consumed) in north-eastern Belarus. Estimates of erthworm biomass were averaged for the habitat types sampled over three years (1997–1999) and mean weighed for the study area. Eartworm portion in badger diet was calculated from the data pooled across 1996–2007.

alder swamps (Fig. 3). Despite the pronounced variation between habitat types we recorded, the coefficient of variation was not high and averaged 25.7%. There were positive correlations between earthworm biomass in various habitats throughout the warm season (r_s = 0.80–0.95, p = 0.0001–0.017) with exception of the black-alder swamp that showed a seasonal trend differing significantly from those in other habitat types (G-test = 54, $p < 0.001$). Between-month changes in earthworm biomass in black-alder swamps were less pronounced with only slight increase in May and September (CV = 22%).

Between-year variations in black-alder swamps were least defined (CV = 14.9%; Fig. 4). In contrast, in small-leaved deciduous medium-aged forest, earthworm biomass varied appreciably with years and weather conditions (CV = 42.5%; Fig. 4). Variations in earthworm abundance during the dry and hot summer in 1996 were especially well-defined in small-leaved deciduous medium-aged forest (2–21 kg ha^{-1}, n = 10; CV = 61.5%) but indistinct in black-alder swamps (33–49 kg ha^{-1}, n = 12; CV = 11.2%).

It is apparent that these values of earthworm biomass are relatively low as compared with those from other European countries, which range from 50.3 to 556.2, with a mean 272.0 kg ha^{-1} (Kowalczyk *et al.* 2003), with exception of stony habitat in Ardnish in Scotland, with only 8.7 kg ha^{-1} (Kruuk & Parish 1982). Importantly, however, within our study area in north-eastern Belarus about 10% of black-alder swamps (each tenth sampling plot) had earthworm biomass in excess of 300 kg ha^{-1}, and black-alder swamps comprised a substantial part of the area, ca. 12% (Sidorovich *et al.* 2003b). Thus, despite predominantly low earthworm biomass, at least 1% of badger habitats in this study area had high earthworm abundance, i.e. earthworm abundance was locally highly heterogeneous.

Of importance in terms of relating earthworm abundance to availability, and thus to the volume actively consumed by badgers, we found significant positive correlation between earthworm biomass per month and the proportion of earthworms in the species diet (r_s = 0.72, p = 0.03; Fig. 5).

Discussion

Feeding strategy in badgers under conditions of low earthworm biomass and high predation risk

From our analyses of walking patterns we postulate that badgers follow foraging routes that represent a network within the occupied territory, with little use of the majority of the apparent territory, as represented by MCPs. Moreover, foraging along narrow and direct between-sett routes exposes badgers to a limited variety of habitat types, perhaps at the expense of habitats with rich food supply that may be located out-of-the-way. Indeed, there is high biomass of earthworms in only around 1% of habitats, thus for every 10 km of badger foraging route there are about 100 m of habitat with high earthworm abundance. As badgers covered on average only 4.1 km per day, it is evident that their opportunity to feed on earthworms is thus restricted, or constrained. In black-alder swamps, badgers are further limited in their opportunity to feed on earthworms by the lack of suitable sites where they can dig setts in the swampy habitat. Thus topographic data is informative with regard to the restrictions incurred by a tendency to follow between-sett routes (Fig. 1).

These features of foraging behaviour affect diet markedly. Looking at the diet composition, badgers appear to act as a generalist predator, with a tendency to be an omnivore scavenger in this semi-natural terrain in north-eastern Belarus. Badgers relied mostly on the available variety of non-mobile prey, both vertebrate and invertebrate, to include beetles, earthworms, amphibians, lizards, young mammals and bird fledglings. Also, badgers consumed a large proportion of carrion and plant food.

Seasonal changes in the badger diet demonstrate pronounced opportunistic feeding adaptations, i.e. predominantly and opportunistically eating the most available food types that results in the appearance of short-term dietary specialization. Indeed, in early spring in the conditions of forested terrain still covered by snow, badgers, being already active, mostly feed on wild boar carcasses and cranberries, which are actually only two available nutritious foods for badgers (Sidorovich *et al*. 2000). Then, almost in two weeks remnants of wild ungulate carcasses and last year's cranberries usually decay under spring warm weather. At the same time, common frogs and other amphibian species gather in relevant wetlands to spawn, creating concentration from hundreds to thousands of individuals (Pikulik 1985). Spawning places are spaced along waterways at the distance of no more than one kilometre apart and their noisy lekking may be easily detected far away. While spawning, amphibians are easily available for badgers, so the predator can get its daily food intake in a short time. Across the above changes in food supply during early spring badgers dramatically switch to utilizing amphibians (mainly common frogs) that appear to be highly available. Simultaneously, badgers begin to eat a lot of earthworms that appear in unfrozen soil in numbers and frequently creep onto the surface at night (Hotko 1993). A few weeks later, from the beginning of May badgers give up frequently eating amphibians perhaps due to their disappearance from spawning places and an equal distribution of them in the surrounding habitats with average density 0.1–2.3 individuals 10 m^{-2} (Pikulik 1985, Sidorovich *et al*. 2001). In contrast, biomass of earthworms (Fig. 5) and their night activity on the surface markedly increase, and many relatively big beetles (cockchafer *Melolontha melolontha* and dung beetles *Scarabeidae*) appear in numbers (Hotko 1993) — on average about one per one m^2 (in some habitat types markedly more). Therefore, badgers start to specialize in feeding on these invertebrates. High biomass of dung beetles continues to be stable until mid-autumn (Hotko 1993), which, in turn, conditions frequent eating of the beetles by badgers and forming a quarter of the species diet until entering torpor (Table 4). In June–July, earthworms become less available (Fig. 5), and badgers switch their diet to mammals and birds (50.7% BC), presumably mainly taking young individuals with poor escape tactics. Then, a month later when young mammals and birds can more easily escape from the relatively clumsy badger; the badgers reduced their dependence on them as prey species. From mid-July they are more and more attracted by mature fruits and seeds, and the consumption of plant food increases three fold. So, indeed, the results on seasonality in badger diet gained in north-eastern Belarus suggest that, first, seasonally badger feeding mainly concentrates on a few food items from the wide variety of existing foods and, second, the chosen food items are always the most readily available.

Such generalism combined with seasonal opportunism are well-established for badgers from many studies in different European regions (e.g. Kruuk 1989, Shepherdson *et al.* 1990, Rodriguez & Delibes 1992, Martin *et al.* 1995, Neal & Cheeseman 1996, Goszczyński *et al.* 2000, Madsen *et al.* 2002, Lanszki 2004, Fischer *et al.* 2005). However, the cases of seasonal specialization of badger diet have been less investigated (Rosalino *et al.* 2005b, Cleary *et al.* 2009).

Similar seasonal feeding switches, that are attributable to the badger in north-eastern Belarus, may be found in other European regions. For instance, in central Poland badgers specialize in eating earthworms from February to June — 75.9%–86.4% BC and afterwards change their feeding to consuming plant food — 43.6%–51.2% BC (Goszczyński *et al.* 2000). Another example comes from southern England, where in July and August badgers switch their diet, mainly consisted of earthworms, to predominantly foraging in wheat plantations (Shepherdson *et al.* 1990). In autumn in mid-mountain and lowland Switzerland, badgers stop their generalized foraging and specialize in eating maize — 68.4%–81.1% BC (Fischer *et al.* 2005).

The character of the badger to be an 'opportunistic specialist' within a generalist (even an omnivore) food niche revealed in seasonal dynamic of food supply appears on a regional scale as well. For instance, badgers specialize in eating earthworms in Great Britain (Kruuk 1989, Neal & Cheeseman 1996), fruits or insects in Italy (Marassi & Biancardi 2002 and references therein), rabbits or fruits in Spain (Martin-Franquelo & Delibes 1985, Martin *et al.* 1995), olives in Portugal (Rosalino *et al.* 2005b), maize or small rodents in Switzerland (Fischer *et al.* 2005). So, it appears that the generalized food niche of the badger tends to realize as feeding specialization on a few profitable food items in connection with specificity of food supply that varies seasonally, regionally and landscape-related.

Interestingly, how far the revealed seasonal changes in the diet of badgers in north-eastern Belarus are related to the species preference for a food. To examine correctly the preference for a food item it is not enough to record its high proportion in the diet. To prove that, the consumption of the food item in a markedly higher proportion than its relative availability (i.e. compared to other food items) should be find out (Krebs 1999). In these terms, we feel weak to calculate selectivity index for any food item used. First of all, because it is too hard to estimate plant-food biomass that varied greatly in terms of habitat types, seasons and years. Also, it is difficult to assess precisely earthworm biomass available for badgers, while they forage along straight directed routes. Selective feeding on earthworms was largely confirmed in many studies conducted in Europe (e.g. Kruuk 1989, Goszczyński *et al.* 2000, Virgós *et al.* 2004). Maybe in north-eastern Belarus the badger would take earthworms preferably as well, but low availability of earthworms along the limited foraging routes, perhaps, resulted in the relatively low portion of earthworms in the diet. Concerning other food items, amphibians and beetles are evidently abundant from the end of April until the end of October; bird fledglings — in June–July, berries — in July–October. Undoubtedly, if one of the above food items is preferred by badgers and is largely available, it would be taken by them almost exclusively in such feeding conditions. Actually badgers do not do this, and so there is no selective consuming of these seasonal foods. Conversely, carrion from wild ungulate carcasses looks like a food item used with positive selection. Definitely, in north-eastern Belarus carrion is strongly limited in early spring (Sidorovich *et al.* 2000). Badgers eat this food a lot in this harsh period; however it is the only food available in still snowy forest there. So, again we cannot state that the badger prefers this food.

From this observation it thus becomes even more apparent that the optimal foraging of badgers in north-eastern Belarus is apparently constrained by some further limiting factor, as badgers do not demonstrate any preference for any food. We hypothesise that under conditions of high predation risk, badgers will consume every edible food type along their foraging route to obtain sufficient daily food intake, by the most expedient means possible. In effect, the proportion of different food items in the badger diet should reflect food item availabilities within their habitat, i.e. pronounced opportunistic feeding (what we actually recorded in the study). Recorded walking patterns largely support the idea of predation risk avoidance.

Socio-spatial structure under conditions of low earthworm biomass and high predation risk

We found relatively large home ranges, focusing on a network of pathways, with a low average number of individuals occupying each sett, resulting in low population density. Low density is unlikely to be a simple result of low food availability as: (1) occasionally larger social groups are recorded in setts, while at another date only a lone individuals will be recorded at the same site, e.g. Barsuchyha and Kaverzy localities in 1999 and 2009 (Tables 1 and 2), evidencing that such territory can feed a relatively high number of badgers; (2) usually badgers display good body condition (thick subcutaneous fat) in autumn and cases of emaciated badgers in spring are rare (V. Sidorovich unpubl. data), thus badgers are able to forage efficiently in these food biomass and availability conditions.

If we thus rule out the lack of adequate food supply as a constraint on local badger density, high mortality may be an alternative limiting factor. Predation, especially by wolves and lynxes, is one of the most plausible mortality factors in semi-natural terrain in north-eastern Belarus. During 2006–2009, badger remains were recorded three times in 293 wolf scats analysed (1%) and once in 67 lynx scats analysed (1.5%). With a local population of around five wolves and lynxes (Rotenko & Sidorovich 2011) and 3–9 badgers per 100 km^2, even with simple mathematical extrapolation one can ascertain that these large carnivores have the capacity to exterminate about a half of the badger population. In other areas of Belarus, badgers have also been found in wolf and lynx diets: Naliboki woodland, central-western Belarus, wolf — 0.8% (n = 1401 scats analysed) and lynx — 1.4% (n = 142), where 0.7–2.6 badgers were censused per 100 km^2 (Rotenko & Sidorovich 2011); Belavezha forest, south-western Belarus — 2.7% (Bunevich 1988) with a badger density of 20 individuals per 100 km^{-2} (Kowalczyk *et al.* 2003). Feeding on carrion in early spring, when carcasses of wild ungulates and beavers are frequently visited by large predators (Sidorovich *et al.* 2000), seems to be a particularly dangerous situation for badgers. Although we did not find direct evidence of badgers predated upon in such situation, quite often we observed that badger and wolf fed on the same carcass during the same night. Also badger remains were found two hundred meters from elk carcass but without sure evidence that it was killed by a large predator.

According to a study by Olsson *et al.* (1997), in Sweden badgers occurred in 19% of wolf scats analysed, and thus constituted a relatively high percentage of wolf diet. Bevanger and Lindström (1995) also report extermination of wolves as one of the causes of badger expansion during second half of the 20th century in Scandinavia.

We postulate that avoidance of high predation risk forces badgers towards the security of utilising primarily straight-line routes between setts when foraging, remaining in close proximity to setts and other burrows in which to shelter (beaver burrows and red fox earths). Overall predation conditions, peculiar spatial structure in badger population in north-eastern Belarus characterized by low badger density (a few badgers in each sett), and networks of straight between-setts foraging routes spread within extended home ranges.

The predation risk hypothesis for feeding strategy of badgers in north-eastern Belarus characterized by pronounced opportunistic feeding without any food preference does not reject the presence of selective feeding of the species in other regions, principally, preference of earthworms as a very nutritious food providing demography success (Kruuk 1989, Kowalczyk *et al.* 2003). Indeed, the results obtained in Great Britain (e.g. Kruuk 1989, Silva *et al.* 1993, Neal & Cheeseman 1996) largely demonstrate such an importance of earthworms. There earthworm-specialized badgers show a very high population density, e.g. in different areas of Scotland it varies between 100 and 800 indiv. per 100 km^2 (Kruuk 1989); in England — 288–3800 indiv. per 100 km^2 (Kowalczyk *et al.* 2000, Macdonald & Newman 2002). In north-eastern Belarus, we faced a markedly lower population density of badgers in the conditions of semi-natural forested terrain, relatively low earthworm biomass and plausible absence of strong human-originated factors limiting badger population. There the badger density is approximately 100–1500-fold lower than the values recorded in Great Britain.

On the other hand, to explain the great difference in badger numbers in the same latitude, the specificity of badger habitat in Great Britain may be taken into account. Indeed, so high density of badgers was found in widely spread rural areas dominated by pasture and still having some woods (Silva *et al.* 1993, Neal & Cheeseman 1996). For hundreds of years, numerous cattle have grazed on the pasture resulting in rich soil with high humus content and huge earthworm biomass. In north-eastern Belarus, earthworm biomass mean-weighted for the habitat structure in the study area equals 17.5 kg ha^{-1} that is, at the least estimate, next lower to that in Great Britain: New Deer, Scotland — 147 kg ha^{-1} (Kruuk & Parish 1982), Speyside, Scotland — 441.5 kg ha^{-1} (Kruuk & Parish 1982), Wytham Woods, central England — 123–971 kg ha^{-1} (Silva *et al.* 1993). So, this comparison of badger density and food supply with earthworms in Great Britain and north-eastern Belarus situated at the similar latitude (at least, Scotland) suggests secondary feature of thriving character of badger population in Great Britain that dwells in manmade landscapes with artificially high earthworm biomass. Perhaps, the structure of badger population in north-eastern Belarus is characterized by more primary features in the conditions of the European forest zone, when it is more rarefied and unsaturated, while badger groups occupy markedly larger territories up to 10 or more km^2 with many setts. Similar situation in badgers is attributed to a semi-natural (almost primeval) terrain in Białowieża woodland in eastern Poland and western Belarus (Kowalczyk *et al.* 2003) and European regions of Russia (Geptner *et al.* 1967, Danilov & Tumanov 1976), which also supports our inference.

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