Bears among people:

Human influence on diet, daybed selection, habitat selection, and road crossing behaviour of the brown bear (*Ursus arctos*) in central Slovakia

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Michaela Skuban
München, den 27.11.2017

List of Abbreviations

CF	Coniferous Forest
CT	Clearcut
DF	Deciduous Forest
DOP	Dilution of Precision
EDC	Estimated Dietary content
EDEC	Estimated Dietary Energy Content
F	Field
FCOY	bear Female with cubs of the year
Fx	Female bear No x
GIS	Geographical Information System
GP	Grassland and Pastures
GPS	Global Positioning System
GSM	Global System for Mobile communication
hrs	hours
km	Kilometre
LPIS	Land Parcel Information System
m	metre
Mx	Male bear No x
MCF	Mostly Coniferous Forest
MDF	Mostly Deciduous Forest
MF	Mixed Forest
MCP	Minimum Convex Polygon
OEAS	Older even-staged forest stand
OT	Other land around human settlement
OUAS	Older uneven-aged forest stand
PAFS	Predictable Anthropogenic Food Resources
PCA	Principle Component Analysis

PM	Pastures and Meadows
SMx	Sub-adult Male bear No x
TC	Traffic Category
TRI	Terrain Ruggedness Index
USSR	Union of Soviet Socialistic Republics
UV	Urban
W	Waterbodies
WWF	World Wildlife Fund for Nature
YF	Young Forest/thicket

and the following combinations:

D_Field	Distance to fields
D_R_paved	Distance to paved roads
D_R_unpaved	Distance to unpaved roads
D_settl	Distance to settlements

List of Publications:

Paper 1:

Human impacts on bear feeding habits and habitat selection in the Poľana Mountains, Slovakia. Skuban M, Finďo S, Kajba M.

Eur J Wildl Res (2016) 62:353–364. DOI 10.1007/s10344-016-1009-x

Paper 2:

Bears napping nearby: Daybed selection by brown bears (*Ursus arctos*) in a human-dominated landscape. Skuban M, Finďo S, Kajba M.

Canadian Journal for Zoology. https://doi.org/10.1139/cjz-2016-0217

Paper 3:

Effect of roads on brown bear movements and mortality in Slovakia.

Skuban M, Finďo S, Kajba M, Koreň M, Antal V.

Eur J Wildl Res (2017) 63: 82. https://doi.org/10.1007/s10344-017-1138-x

Summary:

Bears living in a human-dominated landscape need to find a way to co-exist with people on a daily basis. People seriously alter their environment. Urbanization, agriculture, and road infrastructure actively change the natural environment of many wildlife species. Interestingly, especially omnivores and generalist species such as bears can even have a profit of habitat alternation mainly through adding of so-called “predictable anthropogenic food resources” (PAFS). These human-provided food resources are not only garbage or supplementary feeding stations, but also orchards or single fruit trees, agricultural crops, entrails left by hunters in the wood, and livestock animals. Bears can adapt to the availability of these foods and try to actively search for them. On the other hand in a human dominated landscape, animals are constantly disturbed by people. Many bears in cultural landscapes tend to be active during crepuscular or night-time hours in order to avoid people who are rather active during the day. Therefore, the relationship between Man and bear can be defined as ambivalent because the animals need to trade-off between feeding on PAFS and avoiding of human disturbance.

Bears in Slovakia had never been extinct and increased their population numbers during the last decades. However, till I started this work, scientific research of bears was nearly absent. By the help of smaller project, it was possible to catch bears and mark them by GPS/GSM telemetry. For this study, I could use the data of 22 bears in three different mountain ranges. My main interests were 1) to find out how important human-provided food resources for bears in Slovakia are and if bears are really dependent on supplementary feeding stations during winter time. I found out that bears indeed feed year round on cereals, but that the majority of their energy budget is provided by natural food resources. However, maize fields are an important new and temporal habitat feature where some bears even stay for several consecutive day. Exceptional activity of bears during winter months was rather triggered by a combination of warmer temperatures, less snow and seed years of beech nuts than just the availability of high caloric food at supplementary feeding stations for ungulates.

Second I wanted to know where bears can successfully retreat of human disturbance during the day and if the availability of PAFS can even influence the selection of a daybed. Most important driver for the selection of a daily resting site was the density of cover. Thus, bears selected for young regenerating forest, but also forest belts and thick shrubbery interspersed in agricultural land. This selection pattern was even more pronounced during late summer/autumn when bears need to fatten up for the upcoming winter and crops and fruits become available at the same time. Social structure (dispotic organization of the bear population) in bears as well as the reproductive status of females can significantly influence the choice of a daybed. Females with cubs of the year stay away from the other bear groups in order to minimize the risk of infanticide. These females and sub-dominant males can even approach human settlement in order to protect themselves or their offspring from dominant males. Further, habitat selection analysis showed that especially dominant males tend to monopolize attractive fields with maize. Sometimes, sub-dominant individuals even use people as a human shield. These results showed that non-protected areas could even need more protection because they are often very useful for wildlife including bears. Subsidies are paid for the reclamation of overgrown grazing areas which includes cutting of shrubs and small forest stands. Bears visible near villages are not necessary dangerous and often temporally restricted. Bear management should take this results more into account. However, people feel threatened if they have bears in close vicinity to their houses. Thus, education of people and working with public should be enhanced, too.

Third, bears need to move among patches with attractive foods and quiet refuges during the day. In a human dominated landscape, roads intersect wildlife habitat and bears need to undertake risky road crossings. Analysis of road crossing activity of the bears in Slovakia showed that especially the amount of daily traffic can seriously limit or even inhibit bear movements. Even secondary roads with more than 5 000 vehicles/24hrs can act as a habitat barrier. Further, analysis if road mortality pointed out that majority of killed bears are young males which are the dispersing element of the population and enhance genetic exchange among sub-populations. A scientifically based analysis of bear movement routes can help to define places where mitigation measures would be really useful. Slovakia is still in process to enhance their road infrastructure. So far, Slovakia has still prospective possibilities to influence road planning processes in order to keep the landscape permeable for bears and other wildlife. Studies on movement routes should be intensified in order to avoid irreversible habitat fragmentation and disruption of bear subpopulations.

Introduction:

Most parts of the world are seriously altered by human activities (Western 2001). People actively change and manipulate their environment with often negative lasting consequences for wildlife (Sanderson et al. 2002). Extensive habitat alteration takes place in agriculture, during urbanization, but also through building of road infrastructure (Mattson 1990; Forman et al. 2003). Further, recreational activities in pristine areas can pose another form of human disturbance (Kaczensky et al. 2006). Hunting aims directly at killing of animals. Yet, also so-called innocent outdoor activities like hiking, mountain biking, mushrooming or collecting of various plants and berries constitute a negative stimulus for many wildlife species including bears (Koreň et al. 2011). Many brown bear populations in North America and Europe are living in human dominated landscapes (McLellan et al. 2017). Thus, they are forced to cope with people nearly on a daily basis (Ordíz et al. 2011). Often, bears try to avoid direct confrontation with people by switching to a more crepuscular and nocturnal lifestyle (Kaszensky et al. 2006) which can be judged as a temporal avoiding strategy (Martin et al. 2010). Some authors even try to explain the relationship of people and bears similar to a predator-prey system in which bears attempt to stay away from people in any case (Ordíz et al. 2011; Huusko 2012). Contrary, some habitat alteration can harbour advantages for omnivorous and generalist wildlife species including bears (Beckmann and Berger 2003; Bino et al. 2010). The ability to adapt quickly to an anthropogenic environment has been defined as a form of "phenotypic plasticity" or resilience (Francis 2017). Especially coyotes (Canis latrans), racoons (Nyctereutes procyonoides), wolves (Canis lupus), and bears can recognize a potential benefit in mankind (Francis 2017). Through the availability of human provided food resources, bears are forced to trade-off between exploring high caloric food and avoiding of direct contacts with people (Beckmann and Berger 2003; Lamb et al. 2016). Bears living in urban or urban-interface landscapes often suffer from higher human-induced mortality either due to vehicle collisions or increasing human-bear conflicts (Beckmann and Lackely 2008; Can et al. 2014; Lamb et al. 2016).

It is all about food: anthropogenic food resources

People are adding anthropogenic food resources to the natural world through various activities. For example, agriculture, orchards, livestock farming, hunting, supplementary and diversionary feeding, garbage deposits, and composts all bring potential food sources for wildlife into the environment (Bateman and Fleming 2012; Oro et al. 2013). Moreover, anthropogenic food supply is often predictable in space and/or time. Thus, wildlife can rely on it and adapts its spatial behaviour in relation to the availability of man-made food resources (Oro et al. 2014). This food supply affects population dynamics of various wildlife species. Recent studies proofed the association between population size variation of animals and the availability of different human food resources especially in poor habitats or years (Oro et al. 2013; Baruch-Mordo et al. 2014). Further, a change in the population density in top predators can lead to cascading effects in many trophic levels and even the whole ecosystem (Oro et al. 2013). Recent studies showed that food input by people into ecosystems can increase the carrying capacity of habitats for some animal species (e.g. Brook et al. 2013; Newsome et al. 2015). Brown bears (Ursusarctos) and black bears (Ursusamericanus) successfully exploit a variety of human provided food resources (e.g. Paralikidis et al. 2010; Beckman and Lackey 2008; Lamb et al. 2016). These bears tend to be larger and show increased reproduction rates (Rogers 1987, Robbins et al. 2004, Peirce and Van Daele 2006). Increased population size in bears can harbour a potential for extended human-bear conflicts especially if bears are more visible (Rogers 2011; Newsome et al. 2015).

PRESENT STATUS OF WILDLIFE IN SLOVAKIA

Slovakia is a small and hilly country situated in the Central Europe, and harbours the most Western Part of the Carpathian Arc. With 90 inhabitants/km^2 in average (Statistical office of the Slovak Republic), Slovakia is relatively densely inhabited. About 41% of the country is forested (Koreň et al. 2010). Dominant tree species include European beech (Fagus sylvatica), European oak (Quercusrobor), Norway spruce (Piceaabies), silver fir (Abiesalba), and European larch (Larix decidua). Red deer (Cervuselaphus), roe deer (Capreoluscapreolus) and wild boar (Sus scrofa) are widespread across most of the country. Ungulate populations are steadily increasing which provides a food base for large predators (Slovak Hunting Statistics). All three large carnivore species of European interest, the wolf (Canis lupus), the lynx (Lynx lynx), and the brown bear (Ursusarctos) had never been extinct in Slovakia. However, due to intensive efforts to eradicate all large carnivores in the 19th century, bears went through a bottleneck at the beginning at the 20th century in which just around 30 individuals had been surviving (Finďo et al. 2007). As a consequence of hunters´ endeavour to save brown bears, the bear became protected species since 1932. From that time onward, the population has been steadily increasing. Stepwise, bears were able to re-settle many parts of their former distribution range. Nowadays, majority of bears are living in central Slovakia and few individuals in Eastern Slovakia at the border with Ukraine (Fig. 1). Based on expert opinion, around 900 bears live in Slovakia (State Nature Conversancy of the Slovak Republic). Yet, a recent study indicated that the central bear population genetically differs from the Eastern population (Straka et al. 2012). The main reason for this is the habitat fragmentation and destruction as well as the development of road infrastructure between western and eastern portion of the bear range (Koreň et al. 2010). Nevertheless, the study on habitat suitability for brown bears showed that some areas between these two sub-populations can fulfil habitat requirements of bears (Koreň et al. 2010) (Fig. 1). After population recovery, from the beginning of the 1960s the bears started to be hunted on exception in a small scale. Hunting of bears had been steadily increasing especially in the 1980s and 1990s. At that times, however mainly large adult males were hunted usually by foreign hunters from the West (Skuban 2011). Due to this hunting policy, the sex ratio has been biased in favour of females (59%:41%) (Paule 2015). Nowadays, the bear is protected species of European and national importance and managed by the Ministry of Environment. However, the State Nature Conservancy can issue exceptional permits for shooting of nuisancebears which cause damage on livestock and human property. Nuisance bears threatening human safety can be removed from the population any time (State Nature Conservancy: Action Plan for the brown bears 2016). According to expert opinions, illegal hunting is quite common in Slovakia.

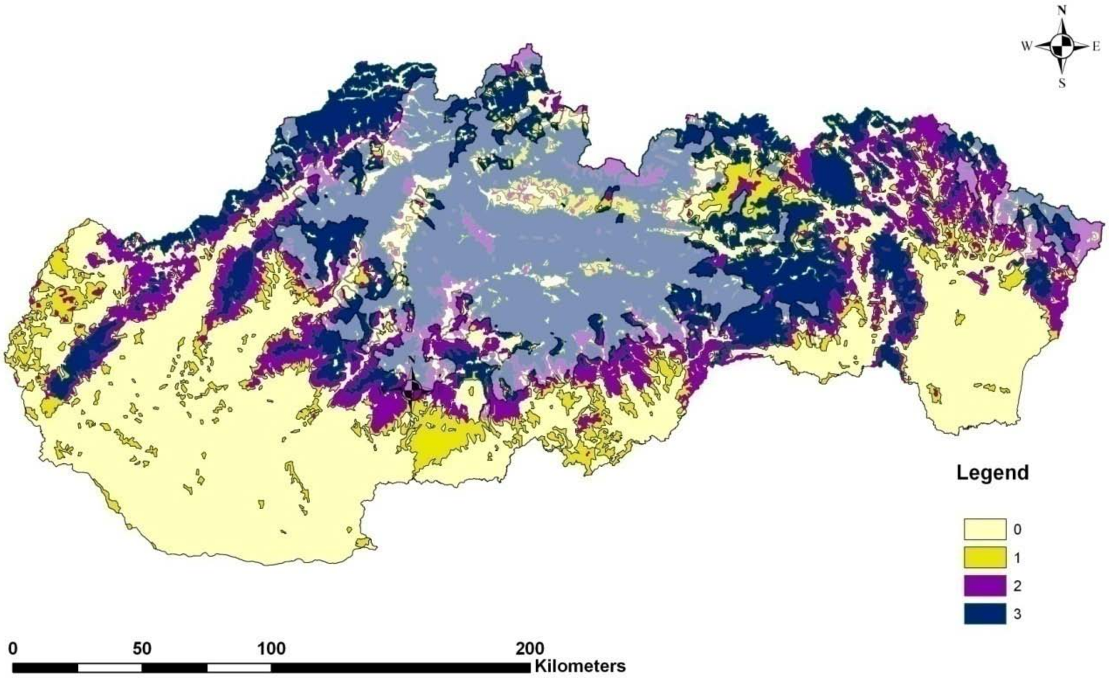

Fig. 1 : Habitat suitability model for the brown bear in Slovakia. Dark blue (3) indicates most suitable patches whereas light yellow areas (0) are not suitable for bears. The milky parts display present bear distribution mainly in central and Eastern Slovakia (Koreň et al. 2010).

WHICH “ANTHROPOGENIC FOOD” IS AVAILABLE FOR BEARS IN SLOVAKIA?

Bears in Slovakia have several options to feed on man-made food resources. Beside garbage, they can exploit agricultural fields, supplementary feeding stations for ungulates, orchards, and entrails left by hunters in the wood during the hunting season, especially in autumn.

CRUNCH QUESTION: SUPPLEMENTARY FEEDING

Diversionary or supplementary feeding of brown bears is not employed in Slovakia. Supplementary feeding stations are established to support ungulates during winter. Moreover, hunters have a legal duty to feed ungulates in order to increase their survivorship, trophy quality but also to reduce damage to forests (Slovak Hunting Act No. 23/1963, amended by Act No 99/193). Normally, feeding is practised from October/beginning of November until the end of March/beginning of April (Find́o and Skuban 2010). In the past, the fodder for wild ungulates was mainly composed of hay and sometimes grass silage. However during recent years, feeding policies changed mainly due to the assumption that high caloric food is increasing the weight of antlers. Supplementary feeding spots are regularly stocked with wheat (Triticum aestivum), oat (Avena sativa), apples (Malus domestica), soya (Glycine max), and especially maize (Zea mays). Since some years, we occasionally observe that various human food remains including cheese, biscuits, bread etc. are placed in increasing amount (see also Fig. 2). Thus, many omnivorous species including bears can utilize the fodder.

Fig 2: A GPScollared female with her cubs of the year feeds at an illegal feeding spot installed for photographing of bears. The provided fodder includes watermelons and remains of biscuits. This photo was taken at the 13th of August when feeding of wildlife is not allowed.

In order to reduce the incidence of the swine fever disease (Pestis suum) among wild boars, according to the Slovak hunting law it is possible to enhance hunting possibilities by luring wild boars by maize in summer time (Finďo and Petraš 2011). Bears in the Eastern Carpathians regularly consume cereal baits (Štofik et al. 2013) likewise in Slovenia (Kavčič et al. 2015), Poland (Bojarska and Selva 2012), and Estonia (Vulla et al. 2009).It was observed that after emergence from dens in spring, some bears are searching for supplementary feeding stations provided for ungulates (Skuban 2011; Štofik et al. 2013). It is supposed that feeding stations can affect the spatial behaviour and reduce home range sizes in bears as in case of ungulates (e.g. Peterson and Messmer 2007; Milner et al. 2014). However, studies on the effect of diversionary feeding on black bears indicated that fed bears indeed were more concentrated around feedings spots during feeding time but had similar home range sizes then non-fed bears (Fersterer et al. 2001).

Yet, feeding stations can increase intra- and inter-specific conflicts among animals (Oro et al. 2013). Sub-adult black and brown bears are more vulnerable to intra-specific predation at aggregated food sites (Stringham 1989, Mattson and Reinhart 1995). Information acquired from hunters and wildlife photographers confirmed conflicts among bears at feeding stations including physical fights. Moreover, the cascade effect of presence of bears and other scavengers at feeding sites in relation to ground-nesting birds was just recently described for the Polish Carpathians (Selva et al. 2014). In order to reduce human-bear conflicts or damage to forests and agriculture, in some areas of Japan (Sato et al. 2004) and North America (black bears; Ziegltrum and Nolte 2001; Rogers et al. 2011) diversionary feeding of bears is employed. This challenging research question should be more intensively investigated in the future.

BEARS AND FIELDS

Agricultural policy in Slovakia considerably changed after the country entered the EU in 2004. Until the end of the 20th century, main crops cultivatedin Slovakia were oat (Avena sativa), wheat (Triticum vulgare), barley (Hordeum vulgare), and potatoes (Solanum tuberosum). Due to the high EU subsidies for cereals production and market demand, the farmers have started to grow maize extensively after 2004. Maize is mainly used as a fodder for domestic animals, but also to fuel biogas plants. During 1999-2014, the area of maize fields nearly doubled (Fig. 3; Slovak University of Agriculture, Nitra).

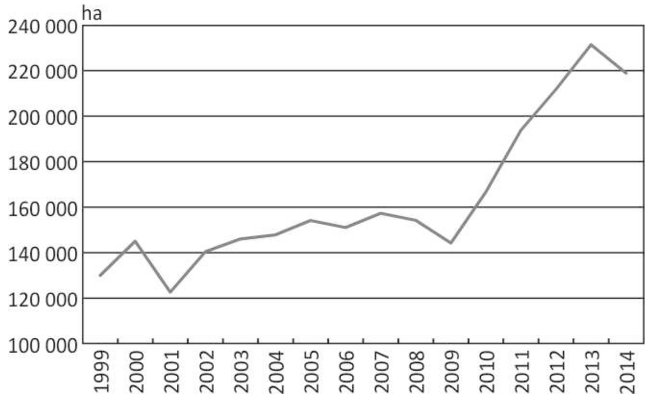

Fig. 3: Development of maize cultivation (in ha) during 1999 - 2014 in Slovakia

Animals can consume maize already after the “milk ripening” of the starches which starts at the end of July/beginning of August (Zadoks et al. 1974; Mattson 1990). After harvesting in October/November, remains of corn on stubble fields are still available for wildlife until the next spring (Oro et al. 2014). Agricultural fields do not remain unnoticed by many wildlife species. Especially ungulates are known to profit from crops and especially from maize (Rosell et al. 2010). Population numbers of ungulates can substantially increase which is additionally favoured by climate change and milder winters (Vetter et al. 2015). However, feeding of ungulates on fields causes damage to agriculture and is therefore of great concern in many European countries (Apollonio et al. 2010).

How bears react on this new, high caloric food resource remains so far not fully understood. Bears raiding fields with oat are known from Japan (Sato et al. 2004), Belarus (Sidorovich 2006), European Part of Russia (Pazethnov 1999), and Slovakia (Škultety 1967). In North America, black and brown bears are frequently visiting cereal fields including maize (Mattson 1990; Shivik et al. 2011). Just few studies stressed the contribution of wheat (Paralikidis et al. 2010) or maize fields (Skuban 2011, Kalamarová 2012) to bear diet in Europe.

FRUIT-EATING BEARS

Domesticated forms of fruit trees provide another anthropogenic food for bears (Mattson 1990; Lamb et al. 2016). Single fruit trees scattered across farmland and abandoned orchards occur near contiguous woodland areas. Bears can utilize this easily accessible source of food because they do not need to move across an open landscape.

"FAST FOOD" - MEAT FOR BEARS

By-product of hunting ungulates is a large amount of entrails that hunters leave in the woods as waste (Wilmers and Getz 2004; Oro et al. 2013).Average gut weight of a red deer or wild boar is estimated at around 12 kg (Slovak Hunting Statistics). Studies in North America demonstrated that bears search and consume gut-piles, too (Haroldson et al. 2004; Mowat and Heard 2006). Yellowstone grizzly bears adjust their distribution in fall in relation to hunters´ activities (Haroldson et al. 2004). In Europe, utilization of ungulate entrails is poorly studied. Based on anecdotic observations from Slovakia it is known that at least some bears dine on entrails left in the wood.

THE DOWNSIDE OF THE MEDAL: HUMAN DISTURBANCE ON DAILY BASIS

Bears living in a human dominated landscape face the problem of being frequently disturbed by people (Cristescu et al. 2013). Home ranges of bears often overlap with areas used by humans (Moe et al. 2007). Thus, bears need to adapt their daily needs including search for food or daily resting places to the activities of people (Martin et al. 2010). It is a relatively new idea to compare the relationships between people and bears to a predator-prey-system (Frid and Dill 2002; Ordíz et al. 2011). Consequently, bears contrive not to meet people in any case (Ordíz et al. 2011; Huusko 2012). However, expanding human land-use reduces wildlife areas. Therefore, the world of bears is shrinking and bears will have fewer possibilities to retreat from people (McLellan et al. 2017).

SELECTION OF DAYBED SITES UNDER THE ASPECT OF HUMAN DISTURBANCE

During the day when people are most active, bears need to find quiet refuges where they can rest (Garcia et al. 2007). It was already demonstrated that a lack of daily hiding places can pose a population limiting resource for carnivores in human dominated landscapes (Sunde 2006; Ross et al. 2010). So far, just few studies dealt exclusively with daybed selection by bears in relation to human disturbance (e.g. Akthar et al. 2007; Ordíz et al. 2011; Huusko 2012; Cristescu et al. 2013). Main driver for selection of a daybed by bears is the amount of cover, especially horizontal cover which makes the bear invisible (Akthar et al. 2007; Ordíz et al. 2011; Huusko 2012; Cristescu et al. 2013). How bears select daily resting sites in relation to attractive feeding grounds was mentioned but so far not completely clarified (Akthar et al. 2007; Cristescu et al. 2013).

Slovakia is densely inhabited (Statistical office of the Slovak Republic). Further, forest fragmentation is seriously enhanced (Koreň et al. 2011). Therefore, the possibilities for bears to retreat far away from people are limited. By adding anthropogenic food resources into natural habitats of bears, people create an ambivalent situation for the animals (Beckman and Berger 2003; Lamb et al. 2016). On the one side, bears are lured to spots with high caloric food, but consequently repelled by human presence. How bears select daily resting sites can be crucial for their further survival.

HUMANS AS A SHIIELD AGAINST PREDATORS OR DOMINANT CO-SPECIFICS?

Human activities can influence the distribution of and interactions among wildlife species (Muhly et al. 2011; Nowak et al. 2014). In particular, high-human disturbance can displace large carnivores. This situation indirectly offers a benefit for some prey species (Muhly et al. 2011). Ungulates are known to utilize people as a shield against predators (Berger 2007; Atickem et al. 2014). Often, they stay in close vicinity to people and their structures in order to reduce the risk of being killed by predators (Berger 2007; Muhly et al. 2011).

Human presence can also influence intra-specific relationships in wildlife. In concrete, vulnerable individuals such as subdominant, or young individuals start to approach human settlements in order to avoid dominant conspecifics in their primary habitat (Mattson 1990; Bateman and Fleming 2012). Similar relationships have been just recently reported for European brown bears (Elfström et al. 2014; Steyaert et al. 2016). Especially subdominant individuals or females with cubs of the year occur near villages (Elfström et al. 2014). During mating season when infanticide takes place (Pazethnov et al. 1999), females with dependent cubs can search for human presence as a shield against unknown adult males (Elström et al. 2014). Intra-specific conflicts among bear males for mating possibilities with females can increase in the mating season (Elfström et al. 2014) and subdominant males sometimes take advantage of human presence (Gibeau et al. 2002; Rode et al. 2006). These bears can explore attractive food resources in the vicinity of people without antagonistic conflicts with more dominant conspecifics (Mattson 1990).

BEARS AND ROADS: HOW TO MOVE IN A FRAGMENTED LANDSCAPE?

Roads are fragmenting wildlife habitat into small patches (Forman et al. 2003). Many wildlife species need to adapt their daily travel routes, long distance migration, but also lifestyle to the presence of roads (Forman et al. 2003; Bateman and Fleming 2012). So far, science just starts to understand the impact of roads on the behaviour and movement or dispersal routes of bears (e.g. Chruszcz et al. 2003; Kaczensky et al. 2003; Northtrup et al. 2012). The road-crossing likelihood in bears is determined by availability of food, diel periods, sex, and season (Beringer et al. 1990; Nielsen 2011; Northtrup et al. 2012).

1. Why and when do bears cross roads?

Majority of road crossings of bears are motivated by either search for food or breeding partners (e.g. Graves et al. 2006; Guthrie 2012). Especially in the bear mating season is spring, males increase their crossing frequency which is motivated by search for females (Chruszcz et al. 2003; Procter et al. 2008; Guthrie 2012). In autumn, bears need to fatten up in order to survive the upcoming winter (Hilderbrandt et al. 1999; Graham et al. 2010). Thus, bears cross roads more frequently to reach various food patches (Nielsen 2011; Sawaya et al. 2014). Food patches with anthropogenic food resources are often located in the vicinity of settlements with higher road densities (Nielsen 2011). Bears exploiting these attractive feeding grounds are under higher risk of traffic-related mortality (Beckman and Lackely 2008; Robertson et al. 2012). Therefore, these human-made feeding grounds in the vicinity of roads can act as an attractive sink-habitat when the mortality for the population is higher than the benefits (Nielsen 2011; Robertson et al. 2012; Lamb et al. 2016). In order to avoid collisions with vehicles, bears often cross at night when human activities are reduced (Graves et al. 2006; Northtrup et al. 2012).

2. Barrier effects of roads.

Roads can act as a complete barrier for dispersing bears. The noise and light pollution on busy roads can deter bears from crossing on the other side of a road (Kaszensky et al. 2003; Northtrup et al. 2012). This barrier effect often starts from 5000 vehicles/24hrs onward (Graves et al. 2006; Guthrie 2012). Bears attempting to cross roads with high traffic volume are under an increased risk of being killed in a traffic collision (Kaszensky et al. 2003; Kusak et al. 2009). In particular, young inexperienced individuals are exposed to danger (Kaszensky et al. 2003; Sawaya et al. 2014). Often, young dispersing males are struck by vehicles (Sawaya et al. 2014, Boulanger and Stenhouse 2014). Roads are suspected to act as sexual filters and reduce the gene flow among sub-populations (Sawaya et al. 2016; Boulanger and Stenhouse 2014). Many studies analysed the impact of highways on bear behaviour. (Kaczensky et al. 2003, Kusak et al. 2009). Only few studies surveyed the responses of bears to roads of lower categories which were not defined as a serious barrier for moving bears (Graham et al. 2010; Northtrup et al. 2012).

After Slovakia joined the European Union, traffic has been increasing rapidly. Up until now, the country is still in the process of enhancing its road infrastructure (Finďo et al. 2007). As a consequence, secondary roads serve as main transportation routes for national and international trade or travel. Thus, the traffic intensity can reach up to 27 000 vehicles/24hrs (Slovak Road Administration, E-Road Traffic Census 2015).

Every year, thousands of animals are killed on Slovak roads. Traffic mortality is especially high in roe deer, red deer and wild boar. Several individuals of protected large carnivores (bear, wolf and lynx) are also killed by vehicles (Slovak Hunting Statistics). Compared to traffic related mortality of lynx and wolves, bears are most often killed in traffic accidents. Wildlife-vehicle collisions can threaten driver´s safety. Collisions with wildlife often lead to economic damage on cars, human injuries or occasionally human fatalities (Finďo et al. 2007). Analysing the crossing behaviour of bears in relation to roads of lower categories but also availability of anthropogenic food resources can bring some new insights into the special situation in Slovakia and elsewhere.

MAIN RESEARCH QUESTIONS ADDRESSED IN THIS STUDY:

Paper I: Human impacts on bear feeding habits and habitat selection in the Poľana Mountains, Slovakia

The aim of this studywas to analyse if human provided food resources are an important part of the bear diet (1). Further, I evaluate how surrounding maize fields in the Poľana Mountains impact the habitat selection of bears (2). Additionally, I assess the seasonal variation in bear diet (3), and quantify the energetic distribution of major food items (4).

Paper II: Bears napping nearby: daybed selection by brown bears (*Ursusarctos*) in a human dominated landscape

Daybed selection in animals is a special form of habitat selection. Especially human disturbance is a great obstacle for resting bears. In this article I assess which habitat and bear characteristics influence the selection of a daybed in Slovakia. I hypothesize that bears can select a daybed outside the contiguous woodland in farmland if suitable hiding options are present (1). Further, I predict that females with cubs-of-the year ~~will~~ avoid resting in areas occupied by adult males (2). Last, I surmise that crops, orchards and scattered fruit trees in agricultural landscapes can attract bears to select daybeds near human settlements (3).

Paper III: Effects of roads on brown bear movements and mortality in Slovakia

Bears in Slovakia are living in a mosaic of patches with more or less suitable habitat. This mosaic is interspersed by a dense network of roads which bears need to overcome. The aim of this paper was to analyse road crossing behaviour and road mortality of bears in Slovakia. My intention was to reveal the impacts of secondary roads with various traffic intensities on the behaviour and movement of brown bears. In particular, I analysed brown bears’ road-crossing behaviour as well as temporal and daily patterns of cross-road movements and road mortality.

Discussion

In this study, I analysed how predictable anthropogenic food subsidies (PAFS) affect behaviour of brown bears in Slovakia. I focused on feeding ecology, habitat selection during ripening of wheat/oat/barley or maize, daybed selection, road-crossing behaviour and road mortality of bears. This study is the work analysing the impact of human presence on bear behaviour in Slovakia. The results of the 3 papers indicate that providing resource subsidies by people can clearly influence the behaviour of bears

INFLUENCE OF ANTHROPOGENIC FOOD ON BEAR BEHAVIOUR:

1. Diet composition: anthropogenic foods versus natural fodder

The diet of bears in Poľana Mts was clearly influenced by the availability of anthropogenic food resources. The intake of cultivated plants throughout the year was virtually the same. Occurrence of maize in bear faeces during summer times indicates that some bears do exploit fields which was confirmed by the analysis of habitat selection of 7 bears (Paper 1). However, the majority of estimated dietary energy content was still derived from natural food items prevailingly mammals, but also mast. Protein is known to be favourable an important nutritional component (Hilderbrand et al. 1999). During spring, consumed protein is transformed into muscle mass whereas in autumn, it is converted into fat (Hilderbrand et al. 1999). This could possibly explain the result that bears in Poľana prefer animal protein over cultivated plants which are composed by starch (Paper 1). Bears can gain animal protein either by scavenging, searching for the remains of wolf prey, active hunting of ungulates, or alternatively via consumption of insects. In fact, large mammal remains in bear scat during autumn could originate partially through hunting activities of people. It is quite common to leave entrails of ungulates in the wood which constitute an easy available source of animal protein.

Interestingly, mast was the most important energy source in autumn (Paper 1). Mast contains up to 80% fat and is of high caloric value (Hilderbrand et al. 1999). Even during the next spring, bears can eat beech nuts and acorns until they start to germinate. In general, I can conclude that cultivated plants in bear diet were less important than I expected. Thus, I may reject the hypotheses of some other authors that bears could become depended on cultivated plants if they have possibilities to achieve them in great amounts (Bojarska and Selva 2012; Kavčič et al. 2015). Habitat selection analysis of 7 brown bears in the Poľana Mountains additionally point out, that exploiting of maize fields is individually different. Especially two large, adult males were strongly selecting for maize fields (Paper 1). Yet, is worth to mention that by avoiding attractive feeding grounds like maize fields, females with depended cubs or subdominant males avoid agonistic interactions with dominant males (Elfström et al. 2012).

2. Crunch question supplementary feeding stations: Advantages and disadvantages

Supplementary feeding stations in Slovakia are established to support ungulates during harsh winter conditions. Feeding time starts at the end of October and lasts until end of March. It is employed every year and therefore predictable (Oro et al. 2014). Thus, in poor food years and/or crop failure of beechnuts or acorns, bears can compensate the lack of food by exploiting artificial feeding stations.

In extreme cases, feeding spots could even endanger human safety. In many parts of the former USSR, so-called “Shatun-bears” occur during winter in years when seed of the

Siberian pine (Pinussibirica) are lacking (Pazhetnov 1999). “Shatun” bear can be translated as a “desperately roaming or wandering” bear. These bears cannot accumulate enough fat resources in order to survive the winter (Pazhetnov 1999). Hungry bears threaten human safety, kill domestic animals in the villages and even people in the forests or in their houses (Formosov 1976; Chestin 2007). In case that bears in Slovakia could not accumulate enough fat resources from natural food to survive the winter, they can always find food at artificial feeding stations. The availability of plenty natural or anthropogenic food throughout the year can prevent dangerous human - bear encounters. However, it is doubtful if the climate conditions in temperate Europe can be compared directly with the boreal conditions in Siberia where Shatuns sometimes appear during severe winters and lack of pine nuts.

Better survival rates during the winter?

Winter is a selection factor for the surviving of many animal species. For ungulates it was successfully proved that artificial feeding stations can increase survivorship of individuals and increase the number of offspring (Appollonio et al. 2010; Vetter et al. 2015). If bears exploiting artificial feeding stations have better survivorship than non-fed bears remains unclear, yet. In North America, black bears are artificially fed by pellets in order to reduce damage to forest (Ziegltrum et al. 2008). Studies on the body composition of fed and non-fed bears confirmed that both groups of bears had similar proportions of fat (ca. 28%) and lean body mass (72%) (Patridge et al. 2001). Thus, it was not possible to conclude that fed bears have better body conditions to survive the winter than non-fed bears (Welch et al. 1997).

Higher reproduction rates of females?

Wild boar females feeding on cultivated plants have often higher reproduction rates and greater litter sizes (Vettel et al. 2014). The assumption that the reproduction rate will also increase in female black bears was not confirmed (Welch et al. 1997). Nevertheless, we occasionally observed in Slovakia that an increasing number of bear females have litter sizes with 4 bear cubs and more. Survival rate of these cubs has not been studied, so far. However, fed black bear females had the first litter at the age of 3,3 years which is significantly earlier than non-fed females (6,3 years) (Rogers 2011). Bear numbers are discussed emotionally in Slovakia, and a further growth of the bear population could worsen the attitude of people towards bears.

It has not been clarified if feeding spots can result in nuisance bears which can jeopardize human safety. Rogers (2011) showed that fed black bears did not threaten human safety. Moreover, he stated that feeding spots can reduce nuisance activity of bears either by preventing them to search for food near villages or to feed on livestock or beehives (Rogers 2011). Similar results were reported for brown bears in Japan (Sato et al. 2005). New results from Poland indicated that during exploitation of artificial feeding spots, scavengers negatively affect ground nesting birds (Selva et al. 2014). Further we observed intraspecific conflicts among bears. The relationship of bears and artificial feeding spots is of great general interest and warrants further research.

Can supplementary feeding change the lifecycle?

Feeding stations established for ungulates provide attractive food for bears in winter. The majority of bears belonging to a local population usually store or decode positions and attributes of feeding stations in their cognitive maps. Hibernation in bears is defined as part of the defending behaviour in order to avoid inclement weather in combination with lack of high caloric food (Pazhetnov et al. 1999). Some European studies assumed that winter activity of bears is mostly related to the availability of feeding spots (Štofik et al. 2013; Kavčič et al. 2015). Indeed, I found samples of bear scats in winter, but they mainly contained beechnuts, red deer remains, and to a lesser extent cultivated plants (Paper 1). Thus, I cannot confirm the general conclusion that bears roaming in winter are exclusively dependent on feeding places (Štofik et al. 2013; Kavčič et al. 2015). After analysing seed years of beech (Fagus sylvatica) and average temperature of the winter when scats were found, I conclude that winter activity of bears in Poľana is rather explained by a combination of mild winters and seed years of beech than the presence of feeding stations for ungulates (Paper 1). Additionally, activity data of GPS tracked bears indicated that the interruption of hibernation depends on the particular individual.

Fig. 4: Bear family at artificial feeding spot in the Poľana Mountains, Slovakia

Climate change and supplementary feeding stations

Global warming has been demonstrated to prolong snow-free periods and increase average temperatures during winter months (Wallace et al. 2014). By snow-tracking, camera traps, and by direct observations, we occasionally recorded signs and sightings of bears during winter. Additionally, we found fresh scats (Paper 1). I may surmise that shorter and milder winter could reduce the amount of fat resources needed to survive the winter. Further, it could be expected that the survival rate of bear cubs could increase which had been already successfully demonstrated in wild boars (Vetter et al. 2015). The effect of global warming in combination with artificial ungulate feeding spots on the population dynamics of bears is an important research question for many years to come.

Fig. 5: This bear mother with her cubs was roaming during January when brown bears are known to hibernate. Bear managers should react on non-sleeping bears and inform public about them.

3. Can we consider maize fields as a new habitat feature?

My results showed that some bears do select maize fields during ripening either for feeding purposes or even for resting during the day (Paper 1 and 2). Also, other animal species including birds and ungulates show selection of maize fields either during ripening or after harvesting on the stubble field (Bengtsson et al. 2014; Oro et al. 2014). Stalks of maize can reach heights up to 2.5 – 3m. Thus, they provide animals not only with high caloric food but also shelter against inclement weather and even human disturbance. Additionally in summer, water remains longer in the small puddles which supplies animals with another important resource. Especially during autumn when mushrooming and hunting by people takes place in the forest, animals could even retreat into fields in order to avoid human disturbance. We recorded several times that GPS tracked bears, but also red deer, stayed in the maize fields during the day and even for several consecutive days (Paper 1 and 2). Anecdotic knowledge of Slovak farmers and hunters regarding ungulates´ and bears´ presence in fields confirm these findings. Thus, maize fields can serve as a temporal habitat for wildlife which wildlife management should take more into account than nowadays.

Behavioural adaption and inter-or intra-specific interactions on maize fields could be an interesting scientific question in the future. Animals adapt on the presence of maize fields in various ways and utilize them. Heavy utilization of oat fields by bears was described for the European part of Russia. Moreover, bears feeding on oat fields even changed their social behaviour and were able to tolerate the presence of other conspecifics (Pazhetnov 1991). Pazhetnov (1991, 1999) compared these behavioural peculiarities to the unique situation on salmon streams in North America (Ben-David et al. 2003). The rich availability of food allows bears to reduce antagonistic relationships and tolerate presence of other bears. Further, he observed the establishment of a particular hierarchy in space and time of the visiting bears (Pazhetnov 1991). Every bear set up his feeding place and preferred time. Interestingly, sub-dominant individuals and bear mothers with cubs retreated from dominant males by engaging less profound feeding spots with less amount of oats in order to avoid dominant males (Pazhetnov 1991).

It is worth to mention that bears recently appeared in Western parts of Slovakia where the habitat offers just few forest stands but extended maize cultivation So far, it remains speculative if maize fields could “pave for bears the way” into former and more Western habitats. Presence of bears near Bratislava were confirmed in 2012 by a road kill on the highway D2 (WWF Slovakia) and by a mobile video in 2015 (www.aktuality.sk). How these bears reached the main capital city of the Slovak republic remains open up until now.

Last, I we even observed hunting of wild boars not only by bears in maize fields but also by wolves (Paper 1). Wild boars roaming among high maize starches are unable to detect predators. Vice versa, predators do have a change to hide among the plants and utilize easy hunting possibilities.Thus, agricultural activities of people can significantly affect not only the animal's feeding habits but also their overall life history.

Potential conflicts around maize fields

Damage on fields by ungulates including bears is a socio-economic topic and leads to increased conflicts (Amici et al. 2012). Damage to fields by bears in Slovakia is compensated by the State (The Nature and Landscape Protection Act 1932). In order to receive compensation, the farmer has a duty to prove preventative measures against wildlife damage. Hereby, the most recommended tool is electric fencing (Program starostlivosti o medveďahnedéhonaSlovensku 2016 (Action Plan for the Brown bear in Slovakia), ANNEX 5.2). However, fencing of large grain fields can enhance habitat fragmentation. To sustain habitat connectivity, it would be reasonable not to intersect movement paths of animals by electric fences.

Extended effects of crops standing on fields and offered at artificial feeding stations:

Human dominated landscape are often characterized by high nutrient and energy input (Western 2001). Bears in Slovakia consume great amounts of field crops, hereby especially maize, after the milk ripening started (Paper 1 and Paper 3). It is to expect that by defecation bears carry large quantities of remains of grain into the forest ecosystem; similar relationships have already been demonstrated for ungulates (Oro et al. 2014).

The analysis of grizzly bear and salmon interaction demonstrated that bears actively contribute to re-distribution of nutrients by leaving decaying salmon carcasses in the forest (Reimchen 2000). By this, important nutrients like nitrogen are brought into the forests which are essential for fertilizing the vegetation (Ben-David et al. 1998; Reimchen 2000). Finally, remains of marked nitrogen were found in herbivore faeces who consume this forest vegetation (Bed-David et al. 1998). Faeces containing grain are especially rich in starch and can be used by various other wildlife species including beetles, and small scavengers. However, the effect of increased amount of starch into the forest ecosystem remains so far poorly understood. It can be concluded that the influence of growing maize may have more far-reaching effects than just changing of diet composition and adjusted habitat selection by the particular wildlife consumers including ungulates and bears. This important subject should be more accurately investigated in order to avoid further speculations.

INFLUENCE OF HUMAN PRESENCE ON BEAR BEHAVIOUR

1. Human disturbance and bears

Human- dominated landscapes indeed offer increased feeding possibilities, but bears need to deal with human disturbance on a daily basis. Especially during the day, when people are most active, bears need undisturbed shelter areas (Kaczensky et al. 2006; Martin et al.

2010). Slovakia, with 90 inhabitants/km^2, is a densely inhabited country (Statistical Office of the Slovak Republic 2016). Therefore, bears face a challenging task to find quiet refuges. By analysing more than 3 800 daybeds of brown bears, I demonstrated that the most predictive driver for selecting a daily resting site is the availability of dense cover which is in agreement with other studies (Paper 2) (e.g. Ordíz et al. 2011, Cristescu et al. 2013). Dense cover in Slovakia can be provided by young regenerating forest, rugged terrain, but also shrubbery and small thick forest-belts interspersed across farmland (Paper 2). Slovak bears are able to rest not only in dense young stands intermingled in continuous forest stands, but also outside in agricultural land if dense groups of trees or shrubs provide enough horizontal cover. The selection for agricultural land for a daybed by bears was even more pronounced from July to October. This is the time of the year when bears need to gain fat in order to survive the winter. Many of the shrubs provide food through offering berries in autumn. Additionally, predictable anthropogenic food subsidies are available including grain fields and orchards. Thus, many daybeds were located in relatively close vicinity to human settlements. Some of the daybeds of females without dependent cubs or of sub-adults were located less than 100m away from settlements or houses. Analysis in the field showed that dense thickets are often attached to the edges of villages which provide suitable cover for resting bears enriched with prosperous feeding possibilities (Paper 2). Similar results are reported for sloth bears in India (Akhtar et al. 2007). My findings suggest that availability of food could be a more important factor for selection of daybeds than it had been known so far (Ordíz et al. 2011; Huusko 2012).

During autumn, many people regularly visit forests for hunting, mushrooming or berry picking. Thus, it is questionable if bears in many woodland areas in Slovakia can avoid human disturbance during the day. For daily resting, bears often select daybeds in farmland, especially in dense shrubbery belts or maize fields. Such places are usually not visited by people till crop harvest. Bears often rested outside protected areas in thick shrubbery or small forest corridors (Paper 2). However, unprotected areas are not preserved by nature conservation laws. Thick shrubbery or small forest stands in open landscapes can be removed at any time because they are not considered important for large mammals so far. More research will be necessary to discover the real needs of wildlife in a human-dominated landscape. I could not confirm the hypothesis that bears perceive human presence exclusively as predation risk and try to retreat from people whenever possible (Ordíz et al. 2011; Huusko 2012). Some studies on daybed selection of bears were carried out in Scandinavia (Ordíz et al. 2011; Huusko 2012) where bears still have better possibilities to withdraw from people than in Slovakia. My findings rather support studies from North America which defined human-bear relationships as ambivalent (Beckman and Berger 2003; Bateman and Fleming 2012). Yet, if bears are more visible near human settlements, people feel threatened and demand for removing of these animals. This situation is an ongoing problem in Slovakia and should be better managed in the future.

2. Humans as a shield for bears against conspecifics

Predators often try to avoid people (Nowak et al. 2014; Berger 2007). Thus, prey species can increase their survivorship by approaching human settlements and other human structures (Berger 2007). Even so, subdominant individuals of wildlife species with a strict hierarchical organization behave similarly and try to utilize people ´s presence as a protection against dominant conspecifics (Bateman and Fleming 2012). Comparable relationships has been demonstrated for black and brown bears (Mattson 1990; Elfström et al. 2012).

The analysis of daybed selection in brown bears showed that females with dependent cubs try to avoid other bear groups in spring by resting in rugged terrain and in closer vicinity to human settlements (Paper 2). During spring, mating season of bears takes place and males sometimes kill the offspring of unknown females (Bellemain et al. 2006). Adult males keep away from humans and the females can reduce the risk of infanticide for their new born cubs by resting closer to human structures (Paper 2). Moreover during the second season, all bears shifted closer to human settlements most probably to explore food resources in farmland (Paper 2). Especially the daybeds of subdominant males were situated in close vicinity to villages (Paper 2). By approaching people´s presence, subdominant individuals could have an additional benefit by exploring attractive food resources which are often monopolized by dominant males in the wild (Mattson 1990; Beckman and Berger 2003). However, on a long term scale, bears near villages are threatening people through their presence. Thus, villagers often demand to remove them. Additionally near human settlements, bears are under increased risk of being killed in accidents with cars, truck or trains (Paper 3). Thus, it remains doubtful if bears approaching human settlements do really have better surviving changes then their wilder counterparts.

HOW TO MOVE IN A PATCHY LANDSCAPE: INFLUENCE OF ROADS ON BEARS

In bear habitat, the distribution of resources like food and shelter is patchy (Belant et al. 2010). Thus, bears have to move through their habitats in order to reach them. In a human-dominated landscape, the distribution of resources in the landscape becomes even patchier. Human-made structures such as settlements and roads fragment the landscape (Forman et al. 2003). Human-made food resources can additionally add food patches into the fragmented landscapes. The intensity of traffic on secondary roads often exceeds the traffic on highways in Slovakia (Paper 3). Secondary roads often intersect bear habitat in Slovakia. Further, maize fields are preferably attached to local roads which can occasionally carry high traffic (Paper 3). Observations of individual animals showed that they clearly know about the presence of fields and walked during one day up to 35km in order to reach these highly attractive feeding spots (Paper 1). However, for reaching these fields, bears need to cross various roads. Thus, maize fields can increase the mortality rate among wildlife through wildlife vehicle collisions on roads and railways.

I could demonstrate for brown bears in Slovakia that the barrier effect of roads starts with an average traffic amount of 6000 vehicles/24 hours (Paper 3). Bear females are even more sensitive to high-use roads which supports the assumption that roads can act as a sexual filter (Sawaya et al. 2014). Interestingly, most of bear mortality happened on roads with much higher traffic. Despite the fact that I could observe site fidelity in the successful road crossings, the killed bears were more separated and on different localities (Paper 3). Especially in the decision making process where to place mitigation structures for wildlife, the different localities of successful and unsuccessful road crossings by brown bear should be taken into account. This strategy was already applied in case of moose (Neuman et al. 2014).

The majority of killed bears were younger than 3 years and males (Paper 3). I therefore support the postulation that especially young, dispersing males become victims in traffic accidents. However, young males represent the dispersing element of a bear population and would enhance genetic exchange among subpopulation (Boulanger and Stenhouse 2014; Sawaya et al. 2014). Bears in the central part of Slovakia show already genetic differences from bears in the Eastern part due to habitat fragmentation (Straka et al. 2012). In order to facilitate bear range re-connection, it could be reasonable to think about mitigation measures on busy secondary roads. The majority of stomachs of road-killed bears contained anthropogenic food, mainly maize, oat, plums, and apples. Most probably, bears needed to undertake a dangerous road crossing in order to reach attractive feeding grounds (Paper 3). I conclude that fields can, under special conditions function as an attractive sink-habitat (Nielsen et al. 2006). Attractive sink-habitats offer pronounced feeding possibilities, but at the same time an increased risk of mortality (Nielsen et al. 2006). Comparable relations were already demonstrated for bears in North America (Beckman and Lackely 2008; Lamb et al. 2016).

Main conclusion

In conclusion, I suggest that human provided food resources constitute an important part of bear diet, but are not the main source of energy (Paper 1). Bears in Slovakia need to trade-off between exploiting predictable anthropogenic food sources and human disturbance (Paper 2). Moreover, bears occurring near villages are not necessarily dangerous or threatening human safety (Paper 2). Especially females with dependent cubs can utilize human presence as a shield against dominant males (Paper 2). Bears are often living outside protected areas (Paper 1, 2 and 3) which is especially important for protecting of bear habitat in the future. Last, beside their advantages, human provided food resources can act as attractive sink habitats especially in the vicinity to busy roads and lure bears to undertake risky road crossing in order to reach them (Paper 3). Bears in Slovakia are so far just rarely scientifically studied. My study successfully demonstrated that research of bear behaviour can bring some real insight in their habitat requirements. Slovakia should continue with more scientifically based interpretation of bear behaviour. So far, decisions of the bear management are not based on scientific results in Slovakia. Management agencies should finally take scientific results into account in order to resolve problems between people and bears effectively.

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ORIGINAL ARTICLE

Human impacts on bear feeding habits and habitat selection in the Pol'ana Mountains, Slovakia

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Abstract Due to altered agricultural and hunting policies, anthropogenic food recently became more accessible for bears in Slovakia. Supplementary feeding of ungulates and cereal/maize crops in fields provide attractive food for bears. Although the influence of supplementary feeding on bear behaviour has been partially explained, the importance of fields as additional food for bears remains poorly understood. The objective of this study was to evaluate if human-derived foods are an important component of the bear diet and how maize fields influence the habitat selection of bears. We further evaluated seasonal variation in bear diet and quantified the energetic contribution of various food items. We expected changes in brown bear feeding habits to favour anthropogenic food, and a preference for fields over other habitats. The bear diet was investigated by the analysis of 243 scats. To explore habitat selection, we used the K-select analysis. Three prevalent food categories contributed to energy intake throughout the year: wild mammals, hard mast and cultivated plants. Contrary to expectations that cultivated plants add most to energy intake (estimated dietary energy content (EDEC)), natural foods were more important. It seems that the winter activity of bears was related to prolific crops of beechnuts and mild winters, rather than to supplementary feeding. Additionally, we revealed that maize fields affect the habitat selection of bears. Although the bear population in the study area has considerably increased over recent decades—probably due to profuse food resources and long-term conservation—no relevant changes in bear behaviour jeopardising human safety have been observed.

Keywords Anthropogenic foods · Brown bear · Diet · GPS telemetry · Maize · *Ursus arctos*

Introduction

Bears are opportunistic omnivores. They feed on a variety of plants, insects and vertebrates, often scavenge on carcasses of wild and domestic mammals, and sometimes feed on agricultural crops or garbage (Edwards et al. 2011; Bojarska and Selva 2012). The ratio between animal matter and plant material in bear diet varies depending on geographical regions and the bear species (Hilderbrand et al. 1999a, b; Swenson et al. 2007; Vulla et al. 2009; Bojarska and Selva 2012). Studies from central and southern Europe demonstrated that bears mostly eat plant and scavenge (Frąckowiak 1997; Rodríguez et al. 2007; Domenico et al. 2012). Other findings, especially from North America, Scandinavia and Russia, indicate a more predatory lifestyle (Pazetnov 1987; Zager and Beecham 2006; Dahle et al. 2013; Cristescu et al. 2014).

Humans have profound effects on wildlife diet (Mattson 1990; Putman and Staines 2002; Cristescu et al. 2015). Anthropogenic food and cultivated plants can represent important additional sources of energy and nutrients for wildlife (Boutin 1990; Beckmann and Berger 2003). These factors can considerably modify feeding habits, habitat selection, physiology, as well as the behaviour of bears (*Ursus arctos*) and wildlife in general (Boutin 1990; Robbins et al. 2004; Peirce

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and Van Daele 2006). In many parts of Europe, maize (*Zea mays*) and other cereals make up most of the human-derived food available for bears either from fields or the supplementary feeding of wild ungulates (Frąckowiak 1997; Paralikidis et al. 2009).

Studies on bear diet in Europe presume that agricultural crops found in scats come exclusively from feeding stations for ungulates or from diversionary bear feeding (Vulla et al. 2009; Bojarska and Selva 2012; Kavčič et al. 2015). Only a few studies emphasize the importance of fields of cultivated cereals for brown bears, especially those from the European part of Russia (Pazetnov 1991), Japan (Sato et al. 2004) and Greece (Paralikidis et al. 2009), and in the USA for black bears (*Ursus americanus*) (Mattson 1990; Shivik et al. 2011) as well as brown bears (Mattson 1990).

The original idea behind the supplementary feeding of ungulates in Europe was to improve survival in winter, to improve the quality of antlers and to mitigate damage to forests (Putman and Staines 2002). More recently, feeding places established for bears or ungulates also serve to enhance hunting success, ecotourism and the monitoring of wildlife populations (Kojola and Heikkinen 2012; Steyaert et al. 2014). In the past, the food used for supplementary feeding was composed mainly of hay, oats (*Avena sativa*), grass silage and potatoes (*Solanum tuberosum*). Recently, maize has been added to this original fodder in a larger extent. Because maize is an attractive and high-calorie food for bears, they frequently visit feeding stations established for ungulates, especially in spring and autumn (Große et al. 2003; Vulla et al. 2009; Skuban 2011). According to Slovak hunting law, maize can also be used to lure wild boars (*Sus scrofa*) throughout the year in order to enhance hunting success aimed at reducing the population size and preventing outbreaks of swine fever (*Pestis suum*). Supplementary feeding may also stimulate the winter activity of bears (Štofik et al. 2013; Kavčič et al. 2015). Other authors contend that the interruption of denning is presumably related to an abundant supply of hard mast in winter (Slobodyan 1974; Naves et al. 2006).

Occasionally, diversionary feeding of bears is used in order to reduce encounters with people as well as damage to human property and forests (Ziegltrum and Nolte 2001; Sato and Endo 2006; Shivik et al. 2011). This practice is especially prevalent in Slovenia, where bears are widely provided with livestock carcasses, maize and other cereals (Kavčič et al. 2015). This extensive feeding of bears in Slovenia can result in localised population densities of up to 40 individuals per 100 km^2 (Große et al. 2003). Diversionary feeding of bears is occasionally employed around camping grounds and fields in North America (Mattson et al. 1992; Shivik et al. 2011) and Japan (Sato et al. 2004). The key question of whether supplementary feeding enhances habituation of bears to people is poorly understood. So far, a direct connection between habituation to humans, food conditioning and supplementary feeding has not been confirmed (Rogers 2011; Steyaert et al. 2014). However, black bear females utilising diversionary feeding spots were significantly younger than non-fed females in North America during first reproduction (Rogers 2011).

In Slovakia, the availability of food resources for bears has significantly changed over the last decades. Until the end of the twentieth century, agriculture was mainly focused on growing wheat (*Triticum* spp.), oats, barley (*Hordeum vulgare*) and potatoes. Škultéty (1967) showed that maize fields were not a very important crop for the diet of bears in the 1960s. Since Slovakia joined the European Union in 2004, agricultural policy has switched to the extensive cultivation of maize (Kalamarová 2012). However, this recent change in policy may have had an indirect effect on bear behaviour and human-wildlife conflict. The area of maize fields has almost doubled during the last decade and more maize is now cultivated within bear range (Kalamarová 2012).

In this paper, we evaluate if (i) human-derived foods are an important component of the bear diet and (ii) how maize fields influence habitat selection by brown bears in Poľana. We further evaluate (iii) the seasonal variation in bear diet and (iiii) quantify the energetic contribution of various food items. Determining which habitats and foods are selected more often than others was of particular interest in this study because these constitute fundamental information about bear ecology and how bears meet their requirements for survival. To our knowledge, the importance of maize fields for bear habitat selection has not been investigated in Europe.

Study area

The study was conducted in the Poľana Mountains and adjacent areas of central Slovakia, latitude 48° 38′, longitude 19°29′. The study area encompasses the home ranges (MCP 100 %) of all bears ($N=7$) studied by GPS telemetry and spreads over 44,450 ha (Fig. 1). Poľana is a part of the Western Carpathian Mountains and was formed by volcanic activity around 13–15 million years ago. Erosion and denudation formed a caldera with a diameter of about 6 km, a circumference 20 km and a depth of approximately 800 m. Altitudes range between 400 and 1458 m above sea level. The average annual temperature is 5 °C. The mean monthly temperatures are lowest in January [−4.7 °C] and highest in July [15.2 °C]. The average annual rainfall is 888 mm. The average number of days with snow cover at the lower elevations is 40 and on the top of the mountains around 140. Maximum snow depth ranges from 40 to 180 cm. Seventy-five percent of the area is covered by vast and continuous forests predominantly composed of trees distinctive of the Carpathian Arc: beech (*Fagus sylvatica*), silver fir (*Abies alba*) and spruce (*Picea abies*). Almost annually, oak and beech produce mast during the autumn, which serves as an essential food for wildlife. Important fruit-carrying trees, such

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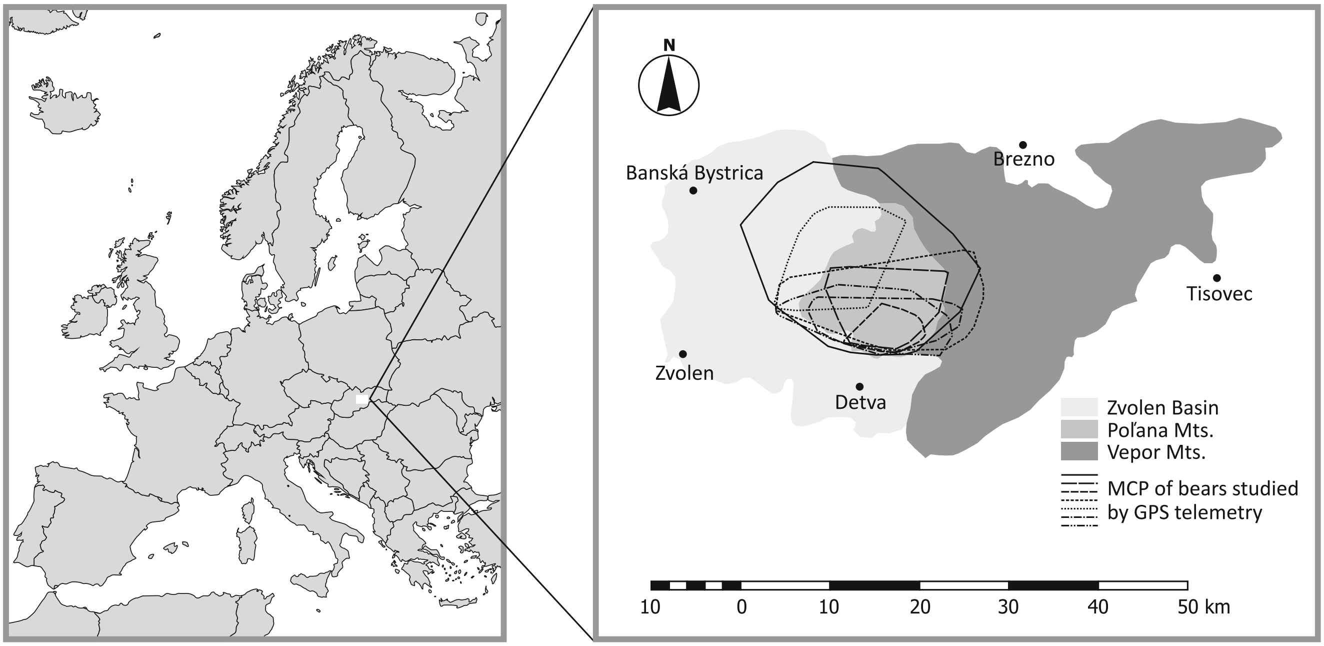

Fig. 1 Map of the study area in central Slovakia

as rowan (*Sorbus aucuparia*), wild and cultivated apple (*Malus sylvestris, Malus domestica*), common pear (*Pyrus communis)*, blackthorn (*Prunus spinosa*) and wild cherry (*Prunus avium*) are scattered across the area. Fruit-carrying shrubs important for wildlife are Cornelian cherry (*Cornus mas*), bilberry (*Vaccinium myrtillus*), raspberry (*Rubus idaeus*), blackberry *(Rubus fructicosus*) and gooseberry *(Ribes grossularia)*. Red deer (*Cervus elaphus)*, roe deer *(Capreolus capreolus*) and wild boar inhabit the area in very high numbers (Finďo and Skuban 2010). The brown bear (*Ursus arctos*) is the most common large predator, and its numbers are estimated at up to 50 individuals (Slovak Hunting Statistics 2012). The area is occupied by two wolf *(Canis lupus)* packs and about 11 Eurasian lynx (*Lynx lynx)* (Finďo and Skuban, unpublished data). The medium-sized carnivores include the red fox (*Vulpes vulpes*), European badger (*Meles meles*), European otter (*Lutra lutra*) and the European wild cat *(Felis sylvestris)*.

The area is sparsely inhabited by people. Nevertheless, various other human activities in the area include forestry, agriculture, hunting, outdoor recreation and nature conservation. The forests have been managed since the seventeenth century. Today, logging and hunting occur across the entire area with the exception of the National Nature Reserves and some other smaller protected areas. Supplementary winter feeding of ungulates is a common practise, whereas summer baiting of wild boars is only occasional. The main game species are the red deer, wild boar and, to a lesser extent, roe deer. Bears are protected from hunting but can be shot with exceptional permits. The foothills of Poľana are used for agriculture. The main crops are wheat, oats, barley, potato and maize. Besides this arable land, there are hay meadows and pastures grazed by cattle and sheep. The fields and pastures are interspersed by hedgerows, small clumps of trees and abandoned land encroached by shrubbery. The damage to livestock caused by large carnivores is negligible (Slovak Hunting Statistics 2012); however, bears and ungulates can cause serious damage to agricultural crops (Finďo and Skuban, unpublished data).

Materials and methods

Analysis of bear diet

In total, a sample of 243 bear scats were collected within the study area in 2006–2010. Repeatable survey routes designated for sample collection included bear trails, logging roads and hiking paths. These same routes were walked by two people, collecting scats for 1 or 2 days, every 2 weeks throughout the year. All scat samples were usually gathered within 14 days of deposition, being periodically collected on a biweekly basis. If several scats were found at the same location, only one sample was taken for analysis. Only rarely was more than one scat sampled from the same spot, when they appeared to contain different food items (Munro et al. 2006). Scats were bagged and stored at −18 °C until analysis. To investigate seasonal variation in diet composition, the year was divided into four seasons: spring (March–mid June), summer (mid June–mid September), autumn (mid September–November) and winter (December–February). These seasons were defined by shifts in the availability of major foods.

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The whole scat was analysed to determine individual food items. Scats were washed through a sieve with the mesh size of 0.8 mm until the water was clear. After drying out, all diet items were separated from each other and macroscopically identified to the finest taxonomic level possible by using a binocular loupe. Volumetric proportion (FV) of each food item in the scat was visually estimated as described by Mattson et al. (1991).

Frequency of occurrence (FO%) and faecal volume (FV%) of each food item in the scats were calculated for each season according to Dahle et al. (1998). Correction factors (CF1) given by Hewitt and Robbins (1996) were used to estimate the original composition (estimated dietary content, EDC, in percent) from FV. The FV of each food item in a season was multiplied by its respective CF1: field crop (wheat, corn, oats) 1.5, hard mast (mainly acorns and beechnuts) 1.5, grasses and herbs 0.25, insects 1.1, fruits 0.51–0.93 depending on the species, small mammals 4 and large mammals 3.

We used the following energy coefficients (CF2) to convert dry matter (EDC) to digestible energy (percent of estimated dietary energy content (EDEC)): grasses and herbs 7.4, fruits 11.7, small rodents 18.8, insect 17.7 (Dahle et al. 1998), wild mammals 19.3 (Persson et al. 2001), cultivated plants 13.2 (Widyaratne and Zijlstra 2007) and mast 22.7 (Ciesla 2002).

A Wilcoxon rank sum test in R (R Development Core Team 2011) was used to test for differences in distributions of FV of the major food categories between seasons of the year. The test is based on ranking observations of the combined sample. The test statistic (W) is calculated as sum of the ranks of the first sample with minimum value subtracted. Minimum value is calculated as $m(m+1)/2$ where m is the size of the first sample. The hypothesis that a location shift between sampling distributions is equal to zero was tested. All test were two-sided, and the differences were considered statistically significant when $p < 0.05$.

Bear habitat selection

Bears were tracked using GPS-GSM collars (Vectronic Aerospace GmbH, Germany) scheduled to take a fix every hour resulting in a maximum of 24 locations per day. Each collar was fitted with a timer-controlled drop-off to secure non-invasive removal of collar from the animal, and release time was set for 24 months. The Ministry of Environment of the Slovak Republic issued the permit for the capturing and handling of the bears (No. 10155/2010-2.2). Because there is no ethical clearance on wild animal research in Slovakia, we followed the recommendations of the Scandinavian biomedical protocols for capture, chemical immobilisation and radio tagging of free-ranging brown bears (Arnemo 2005). Bears were captured in a metal box and culvert traps in five different places within the study area. For every trap, a TT3 trap transmitter (Vectronic Aerospace GmbH, Germany) provided regular status messages, and also an instant alert message via satellite communication was received whenever the alarm had been triggered. Captured bears were darted using a remote drug delivery system (Dan-Inject, Denmark). Standard doses of medetomidine (Domitor® 1mg/mL) and tiletamine-zolazepam (Zoletil®) were used to immobilize the bears (Kreeger et al. 2002, Arnemo 2005). To reverse the immobilisation, 5 mg of atipamezole (Antisedan®) per milligram of medetomidine was intramuscularly administered (Arnemo 2005). During immobilisation, bears were equipped with a GPS-GSM collar, ear-tagged, aged, weighed and measured, and a blood sample for genetic analysis was taken.

In this part of the study, we evaluate how maize fields influence habitat selection by bears (hypothesis ii). GPS locations of seven bears were used, including two females, one of them accompanied by yearlings, one subadult male and four adult males (Table 1). Location errors are inherent with this kind of data, which can potentially induce bias in habitat selection analysis (Martin et al. 2010). Therefore, potentially large location errors were eliminated by data screening based on two-dimensional (2D) and three-dimensional (3D) fixes in relation to the dilution of precision (DOP). Following the recommendations on receiving and managing data from the producer of the GPS collar, only 3D-validated locations with the DOP less than 10 were retained in the analysis. In total, 11,610 locations were acquired between 20 June to 20 September 2012. This is the time when crops ripen and bears begin to

Table 1 Bear characteristics monitored by GPS telemetry and the number of locations used for habitat selection analysis

ID	Sex	Estimated age	Weight (kg)	No locations	No night locations	No day locations
3811	♂	4	110	1877	650	1227
8894	♂	3	85	1833	609	1224
3832	♂	8	170	1521	593	928
9736	♂	13	310	1870	650	1220
9738	♂	6	150	1695	583	1112
9735	♀	5	110	1011	413	598
9737	♀	4	90	1803	615	1188

Note: The bear 8894 was considered a subadult, as bears normally reach sexual maturity at the age of 4 years (Pazetnov 1991)

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visit the fields. This period was furthermore split in two stages: the ripening of wheat, oats and barley (20 June–31 July) and the ripening of maize (1 August–20 September). These seasons do not overlap because wheat, oats and barley are usually harvested by the end of July. Additionally, for each bear, daytime and night locations were differentiated. For the nocturnal activity of bears, the time between sunset and sunrise was calculated according to Duffet-Smith (1988). The number of daily coordinates was almost double that of night due to the longer daylight period in the summertime (Table 1).

We explored habitat selection within the home ranges of brown bears using the K-select analysis (Calenge et al. 2005). The data matched to the design III studies, where the animals are identified and both the use and availability are measured for each one (Thomas and Taylor 1990; Manly et al. 2002). For each animal, the strength of habitat selection was assessed using marginality, i.e. the difference between the mean environmental conditions encountered in the home range (estimated using the classical method of minimum convex polygon (Mohr 1947) with 5 % outermost relocations excluded) and the mean conditions used by each individual, based directly on the relocations. Availability was sampled by looking at the proportion of each habitat class within the home range of every individual bear. K-select is mainly an exploratory analysis similar to principal component analysis (PCA) on the marginality vectors and returns a linear combination of the environmental variables that maximizes the mean marginality, thus extracting the relevant part of the habitat selection. If animals have the same pattern of habitat requirements, all their marginality vectors will be orientated in the same direction and the mean marginality explained by the first axis will be high. The marginality explained by the first axis decreases as the variability in habitat use by individuals increases (Martin et al. 2010). This analysis is suitable when the objective is to define one or several groups of animals that select the same habitat characteristics (Calenge et al. 2005).

The main outputs of the K-select analysis used to interpret graph results were the eigenvalue, the variable loading and the individual animal (see Figs. 2 and 3). The animals show habitat selection if most of the mean marginality is explained either by the first factorial axis or by the first two factorial axes (indicated by a clear break after the bars in the graph of "eigenvalues"). The "variable loadings" graph shows the scores of the variables and provides a biological meaning to the axes. The "animals" graph shows the recentered marginality vectors (i.e. shifted so that they have a common origin). For details and the mathematical procedure of K-select, see Calenge et al. (2005).

For the K-select analysis, eight environmental variables were used: coniferous forests (CF), mostly coniferous forests (MCF), deciduous forests (DF), mostly deciduous forests (MDF), mixed forests (MF), pastures and meadows (PM), fields (F) and other land around human settlements (OT) (Table 2). The geo-database of the National Forest Centre (Slovakia) was used for the analysis. The whole analysis was carried out using the "adehabitat HS" package (Calenge 2011) for the R software (R Development Core Team 2011).

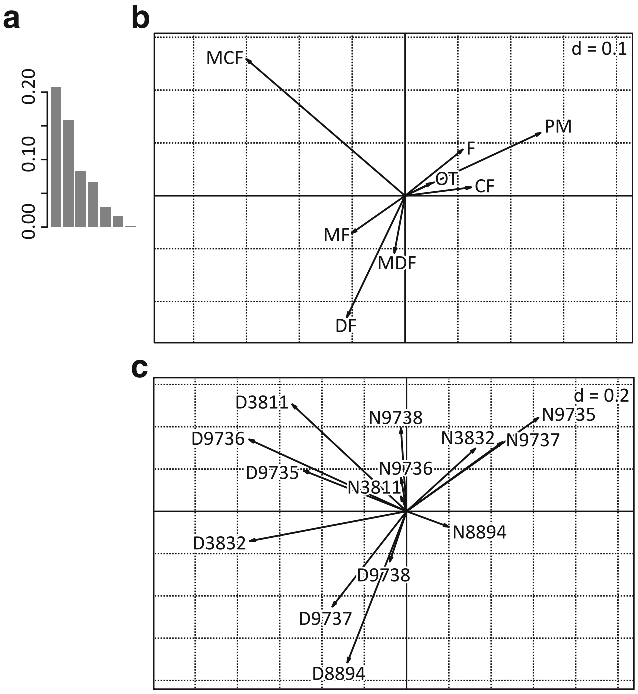

Fig. 2 Results of the K-select analysis carried out to measure habitat selection by brown bears (*Ursus arctos*) in the Poľana Mountains during the grain maturity season from 20 June to 31 July 2012. **a** *Bar chart* of the eigenvalues, measuring the mean marginality explained by each factorial axis. **b** Variable loadings on the first two factorial axes: *CF* coniferous forests, *MCF* mostly coniferous forests, *DF* deciduous forests, *MDF* mostly deciduous forests, *MF* mixed forests, *PM* pastures and meadows, *F* fields and *OT* other habitats. **c** Projection of the marginality vectors of all animals on the first factorial plane. All marginality vectors are recentered such that habitat availability is the same for all animals. To distinguish day and night locations, either D or N was placed in front of the ID of every studied bear

Results

Composition and energetic value of the bear diet

The main food categories that contributed to the total energy intake varied throughout the year. Wild mammals and cultivated plants were an important and regular source of energy from spring to winter. EDEC values of mast were especially high in autumn and winter. Insects and fruits contributed the most to the assimilated energy during summer time (Table 3).

Wild mammals

The intake of meat from wild mammals by Poľana bears was virtually the same from spring to autumn ($p > 0.05$). However,

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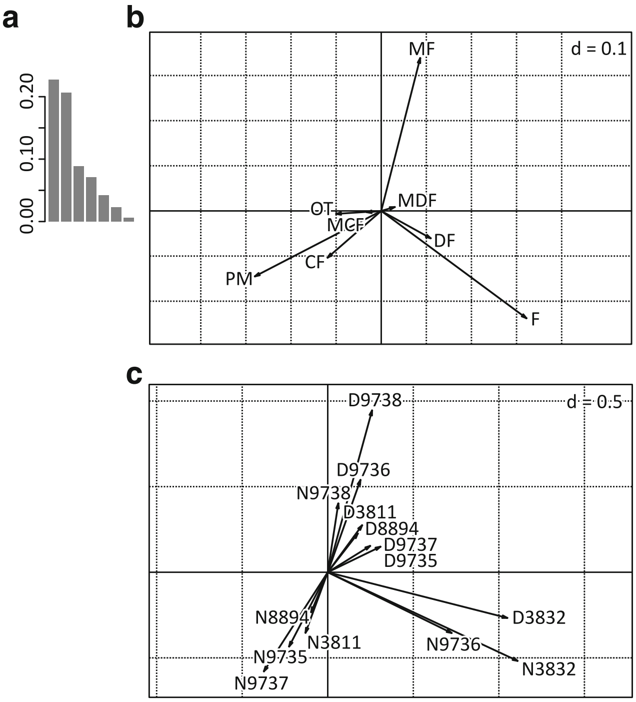

Fig. 3 Results of the K-select analysis carried out to measure habitat selection by brown bears (*Ursus arctos*) in the Poľana Mountains during the maize maturity season from 1 August to 20 September 2012. **a** *Bar chart* of the eigenvalues, measuring the mean marginality explained by each factorial axis. **b** Variable loadings on the first two factorial axes: *CF* coniferous forests, *MCF* mostly coniferous forests, *DF* deciduous forests, *MDF* mostly deciduous forests, *MF* mixed forests, *PM* pastures and meadows, *F* fields and *OT* other habitats. **c** Projection of the marginality vectors of all animals on the first factorial plane. All marginality vectors are recentered such that habitat availability is the same for all animals. To distinguish day and night locations, either D or N was placed in front of the ID of every studied bear

the Wilcoxon test showed a significant location shift between distribution of proportions of wild mammals in autumn and winter ($W=102$, $p=0.041$). The highest EDEC value was in spring (46.6 %) followed by lower values in winter, summer and autumn (29.1, 28.7, 27.5 %, respectively). The most energy was obtained from red deer (spring 23.2 %, summer 17.9 %, autumn 13.3 % and winter 27.4 %) and wild boar (spring 20.9 %, summer 8.3 % and autumn 14.3 %). Wild boar did not contribute to the energy intake in winter.

Cultivated plants

Testing of FV values did not show any significant seasonal differences in the consumption of cultivated plants by Poľana bears ($p>0.05$). Human-derived food from supplementary feeding, the baiting of wild boars in the summer or from the crop fields was eaten by bears throughout the year. The EDEC values were similar in spring, summer and autumn (20.8, 22.3 and 20.4 %, respectively). Energy intake from cultivated plants in winter originated exclusively from feeding stations established for ungulates (EDEC 12.1 %). From spring to autumn, maize was a more important source of energy than other cereals, including oats and wheat, but winter EDEC values for grain (oats 6.4 %, wheat 2.4 %) were slightly higher than for maize (3.3 %).

Mast

Bears consumed hard seeds significantly less in summer than in other seasons ($W_{\text{summer-spring}}=64$, $p=0{,}008$, $W_{\text{summer-autumn}}=56.5$, $p<001$ and $W_{\text{summer-winter}}=8$, $p=0.001$). The intake of mast in spring, autumn and winter was nearly the same ($p>0.05$). Mast composed mainly of beechnuts and acorns was the most important natural source of energy in autumn and winter (EDEC 46.7, 53.8 %, respectively). In winter, the relevant available

Table 2 Description and proportions of environmental variables and bear positions within the study area

Variable	Label	Description	ha	Percentage	Bear positions %		
					Day	Night	Total
Coniferous forests	CF	Percentage of leafy trees less than 10 %	4778	10.8	3.2	2.2	5.4
Mostly coniferous forests	MCF	Percentage of leafy trees from 11 to 25 %	3881	8.7	6.1	1.7	7.8
Deciduous forests	DF	Percentage of conifers is less than 10 %	3597	8.1	10.1	3.6	13.7
Mostly deciduous forests	MDF	Percentage of conifers from 11 to 25 %	7834	17.6	14.0	6.6	20.6
Mixed forests	MF	Percentage either coniferous or leafy trees ranges from 25 to 75 %	12,560	28.3	26.7	8.6	35.3
Pastures and meadows	PM	Hay meadows and old pastures encroached by shrubbery, clumps of trees with numerous ant hills	7708	17.3	3.1	8.7	11.8
Fields	F	Cultivated fields (oat, wheat, barley and maize)	3282	7.4	1.3	4.0	5.3
Built-up area		Villages and other human settlements	715	1.6	0.0	0.1	0.1
Other	OT	Orchards, gardens around human settlements and waterways	95	0.2	0.0	0.0	0.0
Total			44,450	100	64.5	35.5	100

Note: Built-up areas were excluded from the K-select analysis

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Table 3 Frequency of occurrence (FO), faecal volume (FV), estimated dietary content (EDC) and estimated dietary energetic content (EDEC) of food items found in 243 brown bear scats from the Poľana Mountains in 2006–2010. Correction factors CF1 and CF2 are reported in columns 2 and 3. Non-food items (wood, waste, debris) were excluded from the table

Food item	CF1	CF2	Spring (*n* = 62)				Summer (*n* = 78)				Autumn (*n* = 87)				Winter (n = 16)			
			FO%	FV%	EDC%	EDEC%	FO%	FV%	EDC%	EDEC%	FO%	FV%	EDC%	EDEC%	FO%	FV%	EDC%	EDEC%
Grasses and herbs	0.25	7.4	61.3	35.9	7.4	3.3	24.4	12.1	2.6	1.2	5.8	3.6	0.6	0.2	6.2	3.1	0.5	0.2
Fruit			11.3	2.6	1.3	0.9	66.7	29.6	20.1	15.2	31.0	9.7	3.9	2.5	31.2	10.3	4.1	2.5
Apple (*Malus* sp.)	0.51	11.7	6.5	2.0	0.8	0.6	14.1	5.4	2.3	1.8	18.3	6.4	2.1	1.3	18.7	6.9	2.2	1.3
Blackberry (*Rubus fruticosus*)	0.87	11.7					10.2	5.8	3.8	2.9	1.2	0.3	0.2	0.1				
Wild cherry (*Prunus cerasus*)	0.93	11.7					9.0	3.3	2.6	2.0	2.3	0.9	0.5	0.4				
Cornelian cherry (*Cornus mas*)	0.87	11.7					1.3	0.8	0.6	0.5								
Goosberry (*Ribes grossularia*)	0.87	11.7	3.2	0.4	0.3	0.2	6.4	3.6	2.7	2.0								
Hawthorn (*Crataegus* sp.)	0.87	11.7					1.3	0.1	0.1	0.0	1.2	0.4	0.1	0.1				
Pear (*Pirus communis*)	0.87	11.7																
Plum (*Prunus spinosa*)	0.93	11.7					1.3	0.1	0.1	0.1	3.4	0.7	0.4	0.3				
Raspberry (*Rubus ideus*)	0.87	11.7					20.5	8.8	6.6	4.9	2.3	0.6	0.3	0.2				
Rowan (*Sorbus aucuparia*)	0.93	11.7	1.6	0.2	0.2	0.1	2.6	1.7	1.3	1.0	2.3	0.4	0.3	0.1	12.5	3.4	1.9	1.2
Mast	1.5	22.7	12.9	8.0	10.0	13.4	11.5	2.3	2.9	4.3	55.2	39.4	37.5	46.7	75.0	50.0	46.0	53.8
Acorn (*Quercus* sp.)	1.5	22.7	1.6	0.3	0.4	0.5	6.4	0.8	1.0	1.5	13.8	8.6	8.2	10.2				
Beechnut (*Fagus sylvatica*)	1.5	22.7	9.7	6.1	7.6	10.2	3.8	1.4	1.8	2.6	41.4	30.8	29.3	36.5	75.0	50.0	46.0	53.8
Hazelnut (*Corylus avellana*)	1.5	22.7	1.6	1.6	2.0	2.7	1.3	0.1	0.1	0.2								
Cultivated plants	1.5	13.2	43.6	21.4	26.5	20.8	37.2	20.4	26.3	22.3	60.9	29.7	28.2	20.4	62.5	19.4	17.8	12.1
Oat (*Avena sativa*)	1.5	13.2	9.7	3.8	4.8	3.7	9.0	5.1	6.6	5.6	13.8	5.0	4.8	3.4	31.3	10.3	9.4	6.4
Wheat (*Triticum aestivum*)	1.5	13.2	6.5	2.2	2.7	2.1	3.8	0.5	0.7	0.5	9.2	5.5	5.2	3.8	6.2	3.8	3.5	2.4
Maize (*Zea mais*)	1.5	13.2	27.4	15.4	19.0	15.0	24.4	14.8	19.0	16.2	37.9	19.2	18.2	13.2	25.0	5.3	4.9	3.3
Wild mammals	3.0	19.3	30.6	16.4	40.6	46.6	14.1	8.7	22.7	28.2	21.8	14.4	27.6	29.1	43.8	17.2	31.6	31.4
Brown bear (*Ursus arctos*)	3.0	19.3									1.1	0.6	1.1	1.2				
Red deer (*Cervus elaphus*)	3.0	19.3	17.7	8.2	20.2	23.2	7.7	5.6	14.4	17.9	10.4	6.6	12.6	13.3	37.5	15.0	27.6	27.4
Roe deer (*Capreolus capreolus*)	3.0	19.3	3.2	0.9	2.2	2.5	1.2	0.1	0.2	0.3					6.3	2.2	4.0	4.0
Rodents (*Rodentia* sp.)	4.0	18.8					2.6	0.4	1.4	1.7	1.1	0.1	0.3	0.3				
Wild boar (*Sus scrofa*)	3.0	19.3	9.7	7.3	18.2	20.9	2.6	2.6	6.7	8.3	9.2	7.1	13.6	14.3				
Insect	1.1	17.7	30.6	15.7	14.2	15.0	55.1	26.9	25.4	28.8	13.8	3.2	2.2	1.1				
Ants (*Camponotus* sp., *Formica* sp., *Lasius* sp.)	1.1	17.7	29.0	15.2	13.8	14.5	42.3	23.9	22.5	25.7	5.8	1.7	1.2	0.4				
Wasps (*Vespula germanica, Vespula vulgaris*)	1.1	17.7	1.6	0.5	0.4	0.5	10.3	2.6	2.5	2.8	8.0	1.5	1.0	0.7				
Other (*mostly Coleoptera* sp.)	1.1	11.3					2.5	0.4	0.4	0.3								

Note: Numerals rounded to one decimal point and summed to 100 % for FV, EDC and EDEC. In the case of FO, summed values exceed 100 %

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food sources are mast, wild ungulates and cultivated plants from feeding stations set up for wild ungulates (EDEC 53.8, 31.4 and 12.1 %, respectively).

Insects

There was no difference in the consumption of insects by bears between spring and summer ($W=490$, $p=0.540$). Bears ate less insects in autumn than in spring and summer ($W_{\text{autumn-spring}}=172$, $p=0.019$, $W_{\text{autumn-summer}}=407$, $p=0.018$, respectively). *Hymenoptera sp*., especially ants, made a considerably contribution to the energy intake in spring and summer (EDEC 15.0 and 28.8 %). From the species of ants available within the study area, the bear diet was dominated by *Camponotus* sp., *Formica* sp. and *Lasius sp*.

Fruit

Bears consumed significantly more fleshy fruit in summer (FV 29.6 %) than in autumn (FV 9.7 %) ($W=922$, $p=0.023$). The EDEC for fruit contributed 15.2 % to the total energy in summer.

Habitat selection

Season of grain maturity

The first two axes of the K-select analysis were retained in the analysis because they accounted for most of the marginality, 65.2 %, for the seven bears (Fig. 2a). The first axis of the K-select analysis indicated a selection for pastures and meadows (PM) and less pronounced selection for fields (F) (Fig. 2b). Field crops consisted of wheat, barley and oats in the milk stage (Zadoks et al. 1974) or ripened until the harvest at the end of July or the beginning of August. However, the K-select analysis did not indicate a strong tendency for the selection of fields. The second axis corresponded to a selection of MCF with the proportion of deciduous trees from 11 to 25 % and a counter-selection of almost DF with less than 10 % of conifers (Fig. 2b).

The K-select analysis identified only one group of bears with a similar pattern of habitat selection (Fig. 2c). Two adult females (N9735 and N9737) and one adult male (N3832) clearly selected pastures and meadows (PM) and, to a lesser extent, fields (F) during the night. All the bears selected woodland habitats during the day, whereas only three of them (N9738, N9736 and N3811) did so at night.

Season of maize maturity

The first two axes of the K-select analysis explained 65.38 % of the marginality, so they were used for further interpretation (Fig. 3a). The maize season usually lasts from the beginning of August until the harvest in the second half of September or early October. During this season, well-distinguished habitat selection was observed (Fig. 3b). The first axis of the K-select analysis indicated a selection of maize fields (F). The second axis diverged with a selection of mixed forest stands (MF), in which the proportion of either deciduous or coniferous trees varied from 25 to 75 % and a less pronounced selection of pastures and meadows (PM).

The K-select analysis identified three groups of bears with similar patterns of habitat selection (Fig. 3c). Maize fields were strongly selected by the two adult males (N9736 and N3832) during the night. Interestingly, male 3832 selected fields not only at night but also during daytime. Six out of seven bears (D9738, D9736, D3811, D8894, D9737 and D9735) selected mixed forests (MF) during the day, while the male 9738 preferred all-day utilisation of this habitat. Two adult females (N9737 without cubs and N9735 accompanied by yearlings) as well as the two younger males (N3811 and N8894) selected pastures/meadows (PM) and to a lesser extent CF during the night.

Discussion

We found that human-derived foods comprised a significant part of bear diet (hypothesis i) and that maize fields were indeed an important component of habitat selection of the brown bears in our study area (hypothesis ii). However, natural foods and non-human-derived foods dominated the bear diet (Fig. 4).

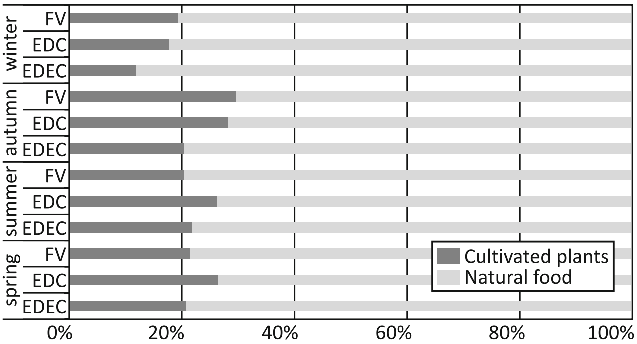

Fig. 4 Volumetric proportion (FV), estimated dietary content (EDC) and estimated dietary energy content (EDEC) of natural food items and cultivated plants found in different seasons in 243 brown bears scats collected in the Poľana Mountains, Slovakia in 2006–2010

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Diet analysis

Essentially, three major food categories—wild mammals, hard mast and cultivated plants—contributed to the energy intake of the bears throughout the year.

Wild mammals

Wild mammals, especially red deer and wild boar, added considerably to the energy budget of the bears during the entire year; however, no domestic livestock was found in the bear diet. The findings indicate that bears in Poľana show a more carnivorous lifestyle in comparison with bears living in other areas of central and southern Europe (Paralikidis et al. 2009; Domenico et al. 2012; Ciucci et al. 2014). The highest intake of energy from mammals was in spring and came near to the values reported from Estonia (Vulla et al. 2009). However, in Estonia animal matter was partly composed of domesticated animals. The importance of wild mammals in the spring diet has also been reported by Frąckowiak (1997) from the Bieszczady Mountains in southern Poland and Slobodyan (1974) from the Ukrainian Carpathians. Surprisingly, in other Slovak regions, bears ate only a very small amount of mammals (Rigg and Gorman 2005; Štofik et al. 2013). Poľana is a famous hunting area densely populated with wild ungulates, which might be the reason for the more carnivorous behaviour of bears here than in other parts of Slovakia (Slovak Hunting Statistics 1968–2014). With more available ungulates, the possibilities for scavenging and also predation are increased (Mattson 1997; Cristescu et al. 2015). We observed that besides starvation during severe winters, the main reason for natural mortality of ungulates is wolf predation. As wolves usually kill large prey in the bottom of valleys where human disturbance is common, only a small part of the carcass is eaten (Finďo and Chovancová 2004). Remains of wolf and lynx prey are quickly discovered by bears (Skuban 2011), which supports findings in other studies (Servheen and Knight 1993; Sidorovich 2006; Krofel et al. 2012). Additionally, after severe winters, ungulate carcasses are available in late winter and early spring. During the hunting season of ungulates, entrails left by hunters become available for bears. Based on the mean number of shot ungulates (195/year) (Slovak Hunting Statistics 1968–2014) and average weight of the entrails (12 kg), we estimated animal matter from this source of at least up to 0.13 kg/ha/year. The total amount of entrails is about 5.8 t per year for the entire study area. The importance of entrails for grizzly bears was stressed by Haroldson et al. (2004) together with Mowat and Heard (2006). But the use of this food item by bears is insufficiently understood in Europe. On several occasions, we observed the hunting of wild ungulates by bears. Predatory events included the raiding of wild boar nests and the killing of ungulate females at parturition. Besides old, sick and weakened animals, bears also killed inattentive individuals mainly at feeding stations, which is similar to other findings from Europe (Vulla et al. 2009; Blanco et al. 2010). Although in our study the energy intake of insects was high in summer and comparable to energy derived from wild mammals, bears in other European regions derived animal proteins almost exclusively from invertebrates (Swenson et al. 1999; Naves et al. 2006; Rodríguez et al. 2007).

Hard mast

As in several other studies (Cicnjak et al. 1987; Hashimoto et al. 2003; Ciucci et al. 2014), hard mast was an important food component during autumn and winter, as well as during spring, when bears consume hard mast from the previous year. Moreover, in autumn and winter, nuts added most to the total energy budget, despite the high availability of cultivated plants derived from feeding stations. Beechnuts were normally available every year with extraordinarily high amounts available during seed years. During the winter activity of Poľana bears, predominant food items were seeds, wild mammals and cultivated plants, whereas the highest energy contribution was derived from beechnuts. Most winter activity in 2006–2007 and 2013–2014 was related to mild weather and the high production of beechnuts (National Forest Centre database, Slovakia). We presume that the main driver for the winter activity of bears was the availability of hard mast in combination with mild winters, regardless of supplementary feeding from farm crops. There is still an ongoing discussion about the reasons for the winter activity of bears in Europe. Some authors explained this phenomenon by the availability of hard mast in winter (Slobodyan 1974; Cicnjak et al. 1987; Naves et al. 2006); others stressed the significance of supplementary feeding (Štofik et al. 2013; Kavčič et al. 2015). Only in Slovenia was the winter diet exclusively composed of cultivated plants and livestock carcasses (Kavčič et al. 2015). However, no study has considered the impacts of climate change on the winter feeding and habitat selection of bears, which would be interesting to explore in future research.

Cultivated plants

Humans create new and highly attractive feeding opportunities for bears through the cultivation of agricultural crops and the supplementary feeding of ungulates. The Poľana bears ate cultivated plants evenly during their active season. This was reflected by almost identical EDEC values in spring (20.8 %), summer (22.3 %) and autumn (20.4 %). After the bears emerged from their dens in spring, wheat, oat and especially

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maize were available at feeding stations established for ungulates. In Poľana, as in other parts of Slovakia, hunters occasionally lure wild boars with maize to enhance culling opportunities in the summertime (Finďo and Petráš 2011), but the amount and frequency of food provided in summer is much smaller than that of the supplementary feeding during winter. At the beginning of October, the supplementary feeding of wild ungulates starts again and continues until the following spring. Contrary to our findings, other studies of bear diet showed that the use of cultivated plants peaked either in spring (Frąckowiak 1997; Štofik et al. 2013) or in autumn (Rigg and Gorman 2005; Vulla et al. 2009; Kavčič et al. 2015). Bears in the Eastern Carpathians of Slovakia obtained more than 60 % of their dietary energy from cultivated plants in spring (Štofik et al. 2013). In Estonia, bears gained more than half of their energy in autumn by the consumption of cereals obtained from ungulate feeding stations (Vulla et al. 2009). Additionally in Poľana, fields with wheat, oats and maize are available from June till mid October. It is generally known that oat fields constitute an additional food resource for bears (Olejník 1965; Pazetnov 1987; Škultéty 1967; Slobodyan 1974; Elfström et al. 2014); however, there is a lack of information about the importance of wheat and maize fields for the nutrition of bears in Europe. The relevance of wheat fields was stressed in Greece (Paralikidis et al. 2009) and maize fields in Slovakia (Skuban 2011; Kalamarová 2012), but not investigated in depth. Although the Poľana bears had access to cultivated plants from various sources, natural foods such as wild mammals, hard mast and insects contributed more to the total energy intake (hypothesis i, Fig. 4).

EDEC from fleshy fruits was important for Poľana and Eastern Carpathian bears only in summer (Štofik et al. 2013). In other European areas without or with just a small occurrence of hard mast, fruits were the most energetic foods in autumn (Dahle et al. 1998; Persson et al. 2001; Vulla et al. 2009).

Habitat selection

Our data from the analysis of food in 2006–2010 cannot be directly compared with the results of habitat selection in 2012. However, we think that the short time difference between the two analyses has no essential impact on the evaluation of hypotheses i and ii. So we present the comparison here.

During the grain maturity season, bears preferred habitats with profuse natural food resources distinctive of early summer. Some bears selected pastures and meadows as well as fields at night. However, wheat and oat fields were not strongly favoured. These cereals are probably not such an attractive food in comparison with maize or natural foods rich in energy and protein. Other bears utilised woodland without showing any special preference for a particular forest type.

During the maize maturity season, however, studied bears showed a marked habitat selection. Maize fields were selected preferentially by large males in one case even during daytime (Koreň et al. 2011). In contrast, another large male selected woodland habitats, although we observed this bear sometimes also feeding in the maize fields. Smaller males and females with or without cubs selected habitats with natural food resources such as woodland or pastures and meadows, rather than maize fields where high intra-species competition could be expected. Nevertheless, smaller bears occasionally visited the maize fields. These findings corresponded to our hypothesis that highly attractive field crops can notably influence the habitat selection of bears (hypothesis ii).

Maize fields can be considered as a temporary human-made habitat suitable not only for bears but also for other wildlife. We revealed circadian utilisation of these fields by some GPS collared bears, even for several consecutive days. During the study, the daytime occurrence of non-collared bears in maize fields was confirmed. If maize stalks reach heights of around 2 m, they provide animals with shelter and concealment from people. Additionally, water puddles can be found in soil depressions. A high concentration of wild ungulates and bears in maize fields can enhance the hunting opportunities for bears (Skuban 2011). Wolves were also observed hunting these prey species in maize fields.

Our study showed that bears ate natural foods more than human-derived foods from feeding stations and fields. Supplementary feeding together with the extensive growing of maize may have profound effects on the physiology and behaviour of bears (Boutin 1990; Partridge et al. 2000). High-caloric food available for most of the year increases the reproductive success of bears (Robbins et al. 2007; McLellan 2011; Rogers 2011). In fact, the bear population in this study area has been increasing over the last few decades (Slovak Hunting Statistics 1968–2014).

Nevertheless, we have not observed relevant changes in bear behaviour jeopardising human safety. Fatal bear attacks have not been recorded from the beginning of the twentieth century until the present (Skuban 2011). During 2007 and 2014, the number of bear attacks to people ranged between 0 and 9 (Slovak Hunting Statistics 1968–2014). However, none of them took place in our study area. Moreover, we recorded only occasional damage by bears to livestock, apiaries and other human properties, except for fields. But under mild winter conditions coupled together with profuse crops of hard mast, denning can be interrupted, which should be taken into consideration during outdoor activities. The supposition is that supplementary feeding and maize fields create a dependency on particular feeding spots (Fersterer et al. 2001; Shivik 2014), but this is not necessarily producing either "habituated" or "food-conditioned" bears (Ziegltrum

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2008; Rogers 2011; Steyaert et al. 2014). With the absence of hard mast, berries and fleshy fruits during hyperphagia, Poľana bears can substitute this nutritional lack by consuming human-derived food from maize fields and feeding stations.

How anthropogenic food eaten by bears influences redistribution of nutrients and other ecological processes is a poorly understood issue that clearly warrants further attention.

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ARTICLE

Bears napping nearby: daybed selection by brown bears (*Ursus arctos*) in a human-dominated landscape

Michaela Skuban, Slavomír Find'o, and Matúš Kajba

Abstract: Daybeds are essential for the survival of brown bears (*Ursus arctos* L., 1758) and may represent a population-limiting resource in human-dominated landscapes. In this study, we demonstrate which land-cover types and bear characteristics affect daybed selection in north-central Slovakia. We used the positional and activity data of 21 bears acquired by GPS–GSM telemetry to identify 3864 daybeds. By use of *K*-select analysis and linear mixed-effects modelling, we explored how bears chose these places for their daytime resting. The most important drivers for daybed selection were the presence of dense regenerating forests and forest–shrubbery belts in farmland. Bears avoided resting in older forests without suitable undergrowth. Females selected daybeds differently depending on the presence of dependent cubs. During spring – early summer, females with cubs of the year avoided other bears by selecting more rugged terrain. These females also selected daybeds significantly closer to human settlements than adult males, possibly to avoid the risk of infanticide. In late summer – autumn, all bears selected daybeds closer to human settlements than in spring, probably because they were attracted by maize (*Zea mays*) fields and fruit trees. Many daybeds were located outside protected areas in farmland closer to people, which could increase bear–human conflicts.

Key words: brown bear, *Ursus arctos*, daybed selection, infanticide, human disturbance.

Résumé : Les couches sont essentielles à la survie des ours bruns (*Ursus arctos* L., 1758) et pourraient représenter une ressource qui limite les populations dans les paysages où dominent les humains. Nous examinons les types de couverture terrestre et caractéristiques des ours qui ont une incidence sur la sélection des couches dans le centre-nord de la Slovaquie. L'utilisation de données sur l'emplacement et l'activité de 21 ours acquises par télémétrie GPS–GSM nous a permis de cerner 3864 couches. En utilisant l'analyse *K*-select et la modélisation linéaire à effets mixtes, nous examinons comment les ours ont choisi ces endroits pour se reposer durant la journée. Les plus importants facteurs intervenant dans la sélection des couches sont la présence de forêts en régénération denses et de ceintures de forêt–fruticée en zone agricole. Les ours évitaient de se reposer dans les forêts plus vieilles sans sous-bois convenable. La sélection des couches par les femelles dépendait de la présence d'oursons dépendants. Au printemps et au début de l'été, les femelles avec des oursons de l'année évitaient les autres ours en sélectionnant des reliefs plus accidentés. Ces femelles choisissaient également des couches significativement plus proches d'établissements humains que les mâles adultes, possiblement pour éviter le risque d'infanticide. À la fin de l'été et à l'automne, tous les ours sélectionnaient des couches situées plus près d'établissements humains qu'au printemps, probablement parce qu'ils y étaient attirés par des champs de maïs (*Zea mays*) et des arbres fruitiers. De nombreuses couches étaient à l'extérieur de zones protégées, en zone agricole à proximité d'humains, ce qui pourrait accroître les conflits entre ours et humains. [Traduit par la Rédaction]

Mots-clés : ours brun, *Ursus arctos*, sélection de couches, infanticide, perturbation d'origine humaine.

Introduction

Due to a steady increase in the world's human population, many landscapes have been severely altered and are often characterized by simplified food webs, landscape homogenization, and high nutrient and energy inputs (Western 2001; Robertson et al. 2013). The impact of people's presence on the planet, the so-called "human footprint", harbours both benefits and danger for wildlife (Sanderson et al. 2002; Carter et al. 2012). Generalist species can profit from human presence by utilizing new feeding opportunities, such as supplementary feeding stations, clearcuts, and crop fields (Nielsen et al. 2004; Roever et al. 2008; Sorensen et al. 2014; Skuban et al. 2016). Some animals can use urban environments not only in search of food but also as a shelter against conspecifics or other predators (Bateman and Fleming 2012). On the other hand, human disturbance is disrupting wildlife habitat and can limit the existence of animals (Ripple et al. 2014; Robertson et al. 2013).

Bears are a "conflict-rich" species and show no clear response to people, but behavioural effects exists, for example, in relation to movement, habitat selection, or life-history traits (Carter et al. 2010; Can et al. 2014). Some consider the relationship between people and bears a predator–prey system, whereas the responses of bears towards human activities are defined as antipredatory behaviour (Ordíz et al. 2011; Huusko 2012). It is argued that from an evolutionary perspective, human disturbance could be analogous to predation risk (Frid and Dill 2002). However, other studies

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have shown that bears can, in fact, be attracted to urban environments (Elfström et al. 2012). Bears are able to exploit anthropogenic food resources around settlements, such as agricultural crops, orchards, or garbage (Beckmann and Berger 2003; Akhtar et al. 2007; Berland et al. 2008; Skuban et al. 2016). Additionally, young individuals or females with cubs can take advantage of human presence as a shield against dominant adult males (Elfström et al. 2014). However, the habituation to humans harbours a risk of human-induced mortality by either vehicle or train collisions (Lamb et al. 2017) or escalating human–wildlife conflicts that lead to the removal of individuals (Can et al. 2014). Areas with food resources provided by humans can function as ecological traps or attractive sink habitats (Nielsen et al. 2006; Nielsen 2011; Linke et al. 2013). This correlation has already been shown in the case of American black bears (*Ursus americanus* Pallas, 1780) (Beckmann and Lackey 2008) and grizzly bears (*Ursus arctos horribilis* Ord, 1815) (Lamb et al. 2017). These relationships between people and wildlife warrant further research and adjusted management tools to mitigate any such ecological traps (Robertson et al. 2013).

For the survival of bears, a suitable habitat needs two main resources: feeding possibilities and shelter areas (Garcia et al. 2007). Especially in densely settled environments and highly fragmented forests, bears need refuges where they can retreat for resting not only during hibernation (Pigeon et al. 2016*a*, 2016*b*), but also on a daily basis (Gibeau et al. 2002; Garcia et al. 2007; Koreň et al. 2011). Brown bears in many parts of Europe live in human-dominated landscapes. Most European forests are managed or used for hunting and other recreational purposes. Because human disturbance is typical during the daytime, some authors suggest that bears avoid confrontation with people by switching to a crepuscular and nocturnal lifestyle (Kaczensky et al. 2006; Moe et al. 2007), also defined as a spatiotemporal avoidance strategy (Martin et al. 2010; Sahlén et al. 2011).

The process of daybed selection in bears is still not fully understood. To our knowledge, only a few studies have exclusively dealt with daybed selection by brown bears (e.g., Mysterud 1983; Ordiz et al. 2011; Huusko 2012; Cristescu et al. 2013). Daybeds fulfil important behavioural needs and bears can spend up to 60% of a day at a daily resting site during summer (Mysterud 1983). In general, bears avoid resting in open landscapes (Zhiryakov and Grachev 1993) and need some kind of cover. Vertical cover provides protection against inclement weather such as rain, wind, and heat stress (Merrill 1991; Mysterud and Østbye 1995; Cristescu et al. 2013). Horizontal cover provided by dense vegetation supplies concealment options against human disturbance (Ordiz et al. 2011; Cristescu et al. 2013; Ciarniello et al. 2014). Many studies have shown that the main factor for bears in selecting daily resting sites is dense horizontal cover, especially important in human-dominated environments (Akhtar et al. 2007; Ordíz et al. 2011; Cristescu et al. 2013).

Food distribution and abundance can also influence the selection of habitat and, consequently, the choice of resting place (Lyons et al. 2003; Akhtar et al. 2007; Munro et al. 2006; Pineau 2014). If highly attractive food and dense cover are located near human settlements, then bears are able to rest in the vicinity of people (Akhtar et al. 2007; Cristescu et al. 2013; Takahata et al. 2014). Contrary to this, Ordíz et al. (2011) revealed that bears in Scandinavia retreated farther from human settlements during autumn when the hunting season starts. Therefore, in a human-dominated landscape, daily resting-site selection can be considered a complex decision involving both foraging possibilities and levels of human disturbance (Davis et al. 2006; Ciarniello et al. 2014).

Additionally, sex, age, the presence or absence of dependent cubs for females, and the physiological status of bears have a clear effect on the selection of habitat (Martin et al. 2010), den site (Pigeon et al. 2016*a*, 2016*b*), and daybed (Moe et al. 2007; Carter et al. 2010; Takahata et al. 2014). Females accompanied by cubs tend to separate themselves from adult males, mainly during mating season when the risk of infanticide is highest (Dahle and Swenson 2003; Steyaert et al. 2013). Sometimes, these females are trading off between avoiding other bears and accessing attractive food resources (Ben-David et al. 2004).

Daily resting sites are essential for the survival of many carnivore species and can even represent a population-limiting resource, especially in a human-dominated landscape (Ross et al. 2010; Bateman and Fleming 2012). This has been documented for species such as the red wolf (*Canis rufus* Audubon and Bachman, 1851) (Dellinger et al. 2013), the cougar (*Puma concolor* (L., 1771)) (Dickson et al. 2005), the Pallas cat (*Otocolobus manul* (Pallas, 1776)) (Ross et al. 2010), the wildcat (*Felis silvestris silvestris* Schreiber, 1777) (Jerosch et al. 2010), the Eurasian lynx (*Lynx lynx* (L., 1758)) (Sunde et al. 1998), and the tiger (*Panthera tigris* (L., 1758)) (Carter et al. 2012).

At present, the bear population in Slovakia is not endangered, but the steady loss of suitable habitat due to human perturbation is a major problem for bear and other wildlife conservation (Find'o et al. 2007; Koreň et al. 2011). Slovakia is quite densely populated (90 inhabitants/km² in our study area) and bears need to cope with people nearly continuously. The analysis of daily resting sites of bears in Slovakia can provide relevant information about suitable habitats essential for the long-term survival of the species in human-dominated areas (Garcia et al. 2007; Huusko 2012). These habitats will need further and better protection, because bear population decline is linked to a loss of safe natural environments (Nams et al. 2006; Nielsen et al. 2006). Our study can provide new information on how agricultural crops and sex–age factors for bears influence daybed selection.

In this study, we assess which habitat and bear characteristics affect the selection of a daily resting site in a densely human-populated area. We predict that bears can rest outside the contiguous woodland in agricultural landscape, if suitable concealment options are available (hypothesis 1). Furthermore, we hypothesize that females with cubs of the year will avoid resting in areas occupied by adult males (hypothesis 2). We also predict that crops, orchards, and scattered fruit trees in farmland can attract bears to select daybeds near human settlements (hypothesis 3).

Materials and methods

Study area

We delineated the study area by the home ranges (100% minimum convex polygon (MCP)) of studied bears (Fig. 1). The 1463 km² study area is situated in north and central Slovakia (48°52′N, 19°08′E) and encompasses seven mountains ranges and two basins. These geo-morphological units include the Kysucká vrchovina Mountains, Oravská magura Mountains, Malá Fatra Mountains, Vel'ká Fatra Mountains, Starohorské Mountains, Pol'ana Mountains, Veporské Mountains, and Zvolen and Turiec basins. Elevations range from 363 to 1710 m (the summit of Vel'ký Kriváň in the Malá Fatra Mountains). The majority of the area is covered by mountain forests (66%) and by grasslands and pastures (25%), spreading over agricultural land in lower altitudes or above the timber line in alpine habitats. Fields cover 5% of the area. Important crops relevant for bears are alfalfa (*Medicago sativa* L.), white clover (*Trifolium repens* L.), oat (*Avena sativa* L.), potatoes (*Solanum tuberosum*L.), and especially maize (*Zea mays* L.). The main tree species are Norway spruce (*Picea abies* (L.) Karst.), European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), and Scots pine (*Pinus sylvestris* L.). There are several other tree species represented in substantially lower proportions, including sycamore maple (*Acer pseudoplatanus* L.), European ash (*Fraxinus excelsior* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), English oak (*Quercus robur* L.), rowan (*Sorbus aucuparia* L.), and European larch (*Larix decidua* Mill.). Domesticated forms of fruit-bearing trees (apple, pear, plum, and cherry) can be found in hedgerows spread over agricultural land,

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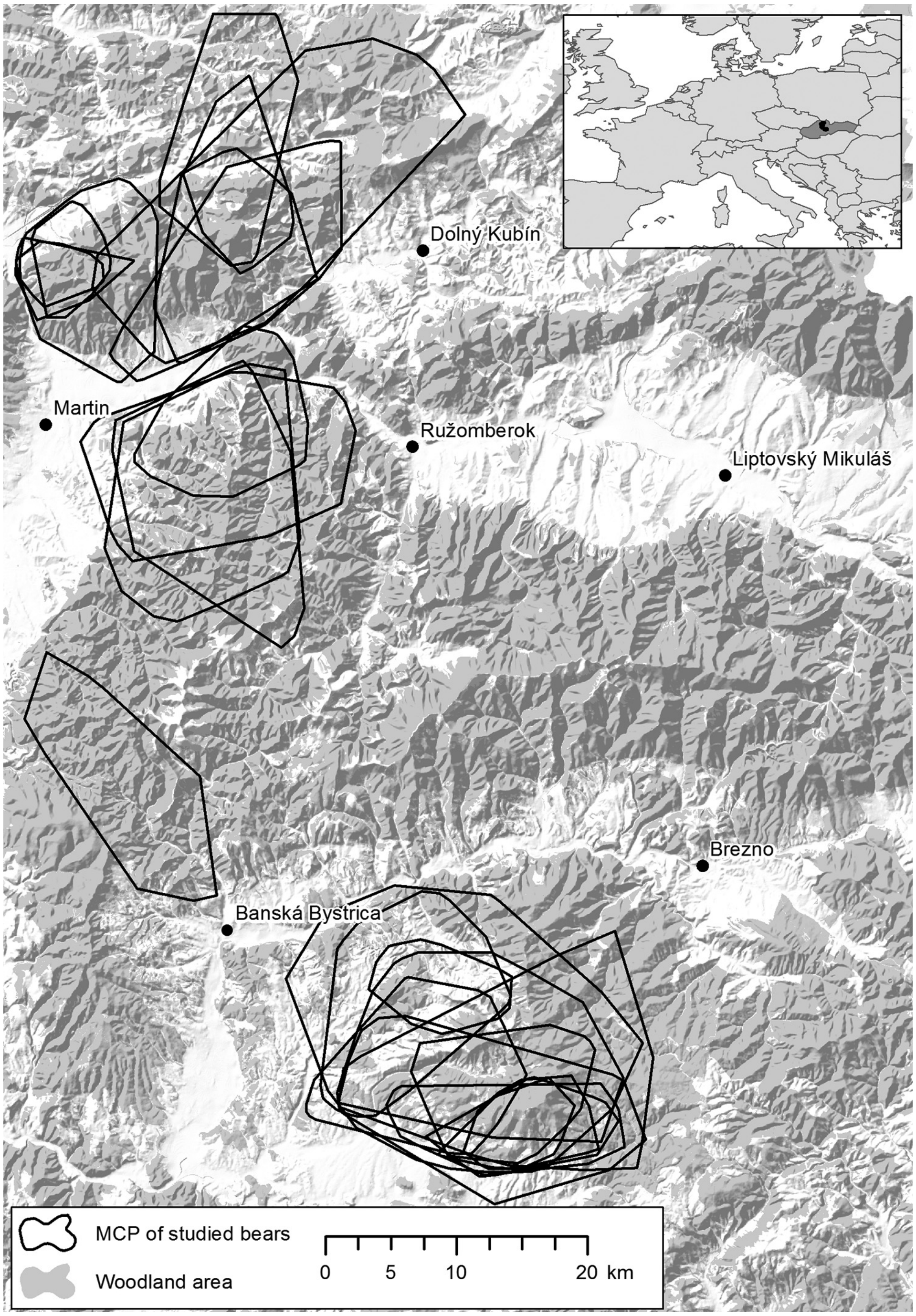
Fig. 1. Study area for daily resting-site selection by brown bears (*Ursus arctos*) in north-central Slovakia. The area was delineated by the home ranges (100% minimum convex polygon (MCP)) of the studied bears.



as well as near human settlements in gardens and abandoned orchards. Although fruit trees attract bears in late summer – autumn, the most relevant sources of natural food in autumn are beechnuts and acorns (Skuban et al. 2016).

The study area is densely inhabited by people below the lower timberline (90 inhabitants/km², on average; Statistical Office of the Slovak Republic). Human disturbance in woodland and alpine environments is mostly related to outdoor activities (hiking, berry and mushroom picking, mountain biking, and hunting), timber extraction, and livestock grazing on alpine meadows. Due to forestry and agricultural activities, the entire area is intersected by a network of paved and unpaved roads. There are several protected areas within the study area. In Slovakia, the brown bear has been protected since 1932 and is currently hunted only on a small scale. Nevertheless, nuisance individuals can be removed at any time.

Capture and monitoring

In total, we captured 21 bears in eight different locations within the study area using box or culvert traps (Table 1). Bears were monitored by GPS telemetry from 2008 to 2016. We installed a TT3 trap transmitter (Vectronic Aerospace GmbH, Berlin, Germany) at every trap, which provided regular status messages and an immediate alarm message in the case of a triggered trap. Every bear was equipped with a GPS–GSM collar (Vectronic Aerospace GmbH)

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Table 1. Coding of individual brown bears (*Ursus arctos*) for the *K*-select analysis and the number of identified daybeds.

		Number of daybeds		
Bear code	Estimated age	Spring–early summer	Late summer–autumn	Total
F1	Adult	59	54	113
F1COY	Adult	31	21	52
F2	Adult	62	81	143
F2COY	Adult	83	80	163
F3	Adult	78	54	132
F3COY	Adult	39	56	95
F4	Adult	103	122	225
F4COY	Adult	129	68	197
F5	Adult	57	84	141
F5COY	Adult	80	61	141
F6	Adult	52	57	109
M1S	Subadult	26	53	79
M2S	Subadult	55	36	91
M3S	Subadult	—	57	57
M4S	Subadult	153	121	274
M5A	Adult	48	68	116
M6A	Adult	119	69	188
M7A	Adult	74	42	116
M8A	Adult	—	63	63
M9A	Adult	137	153	290
M10A	Adult	92	90	182
M11A	Adult	41	—	41
M12A	Adult	180	173	353
M13A	Adult	87	90	177
M14A	Adult	82	88	170
M15A	Adult	67	89	156
All bears together		1934	1930	3864

scheduled to take a fix every hour, resulting in a maximum of 24 locations/day. A dual-axis activity logger was embedded in each collar. Additionally, collars were fitted with a timer-controlled drop-off with a release time of 24 months. The permit for capturing and handling the bears was issued by the Ministry of Environment of the Slovak Republic (No. 10155/2010-2.2). Because there is no ethical clearance on wild animal research in Slovakia, we followed the recommendations of the Scandinavian biomedical protocols for capture, chemical immobilization, and radio-tagging of free-ranging brown bears (Arnemo 2005). We darted captured bears by a remote drug delivery system (Dan-Inject ApS, Børkop, Denmark). To immobilize the bears, we used standard doses of medetomidine (Domitor®, 1 mg/mL) and tiletamine–zolazepam (Zoletil®) (Kreeger et al. 2002; Arnemo 2005). We reversed the immobilization by the intramuscular application of 5 mg of atipamezole (Antisedan®) per mg of medetomidine (Arnemo 2005). During immobilization, bears were ear-tagged, aged, weighed, measured, and a blood sample for genetic analysis was taken (Skuban et al. 2016).

The identification of a daily resting site

For the identification of a daily resting site, we used 1 h locations acquired by GPS telemetry from 21 bears from April to October. We only considered three-dimension-validated locations with a dilution of precision (DOP) less than 10 (Stache et al. 2012). Every GPS collar was equipped with an activity logger, which registered an activity index between 0 and 250 every 5 min. The activity logger recorded the movement of the bear's head in the "up–down" (vertical *y* axis) and "side-to-side" (horizontal *x* axis) direction. For each 1 h location of a bear, the activity index was a mean of the 12 recordings during the 60 min interval. We only included fixes for which the corresponding mean activity in horizontal (*x* axis) and vertical (*y* axis) directions was smaller than five and the distance between locations was less than 10 m. Under this condition, we identified those locations where bears stayed almost motionless at one spot during daytime hours. The main daily resting time was between0900 and 1500, which is in line with the findings of other authors (Mollohan 1986; Huusko 2012). This allowed us to distinguish daily resting sites from other activities that may result in a cluster of locations concentrated on a very small space, such as protection of a carcass or other food resources. Ebinger et al. (2016) demonstrated that the use of carcasses is connected with considerably higher activity than bedding. Based on this condition, we used 72% of locations for further analysis. For two bears, we had no activity data due to technical failure. Thus, we considered locations between0900 and 1500, which were at a distance of less than 10 m from each other. From locations selected in this way, we finally derived a centroid for each bear and each single day, which represented a daily resting site. In total, we identified 3864 daybeds (Table 1). ArcGIS version 10.3 (ESRI 2011) was used to identify daybed locations and to prepare environmental data.

Description of variables

We used eight land-cover types and five other variables for the analysis (Table 2). All environmental data were converted to raster layers with a spatial resolution of 30 m × 30 m. Forest growth stages were available from the Geo-database of the National Forest Centre (Zvolen, Slovakia), which is primarily used for the preparation of Forest Management Plans (LHP). Grasslands, pastures, fields, and nonforest woody vegetation were defined by the Land Parcel Identification System (LPIS), which was provided by the Soil Science and Conservation Research Institute (Bratislava, Slovakia). Because the structure and ecological function of nonforest woody vegetation interspersed across agricultural land is similar to that of regenerating forests, we joined both habitat types under the variable of "young forest" (YF). Remaining habitat variables, water bodies, and urban vegetation were extracted from the Land Register of the Slovak Republic (Geodesy, Cartography, and Cadastre Authority of Slovak Republic). We created the final habitat map by joining these three databases together (LHP, LPIS, and Land Register). The Topographic Ruggedness Index (TRI) was calculated according to Riley et al. (1999). TRI values are computed for each grid cell of a digital elevation model (10 m elevation contour interval) by using a "DOCELL" command in the ARC/INFO geographical information system that calculates the sum change in elevation between a grid cell and its eight neighbouring grid cells (Riley et al. 1999). To assess the influence of man-made habitats and structures upon daybed selection of bears, we included in the analysis straight-line distances to the edge of the nearest field (D_Field), permanently inhabited human settlement (D_Settl), paved roads (D_Rpaved), and unpaved roads (D_RUnpaved) (Table 2).

Analysis of daybed selection by bears

We applied the *K*-select analysis to reveal which variables are decisive for the selection of a daily resting site for bears. This method is commonly used for exploring habitat selection within home ranges of individual animals (Calenge et al. 2005; Calenge 2006). The use and availability were calculated for each bear, matching the data to the design III studies (Manly et al. 2002). The strength of daybed selection for each animal was assessed by using the marginality. For each animal, the difference between the vector of mean available habitat conditions and the vector of mean used conditions defines the marginality vector (Calenge et al. 2005). We sampled the availability by assessing the proportion of each environmental variable within the home range of the individual bears. Each habitat variable defines one dimension in the ecological space. *K*-select is similar to a principal component analysis (PCA) on the marginality vectors and returns a linear combination of the environmental variables that maximizes the mean marginality, thus, extracting the relevant part of the daybed

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Table 2. Description and acronyms of habitat and nonhabitat variables used in the analysis of resting-site selection by the brown bear (*Ursus arctos*) in north-central Slovakia.

				Area	
Variable	Acronym	Type of variable	Description	km²	%
Clearcut	CT	Categorical	Bare land or grasses and mixed herbaceous plants	2	0.1
Young dense forest, thicket	YF	Categorical	Trees naturally or artificially regenerated. Canopy is too dense to allow new saplings to grow into the canopy. Diameter at breast height (DBH) <12 cm. In agricultural landscape, woody vegetation is interspersed by domesticated forms of fruit trees	201	14.1
Older uneven-aged forest stand	OUAS	Categorical	Two or more distinct canopy layers. Density of undergrowth varies greatly. DBH >13 cm	275	19.3
Older even-aged forest stand	OEAS	Categorical	Single canopy stands consists of trees that are of equal height. DBH >13 cm	490	34.3
Grasslands and pastures	GP	Categorical	Hay meadows, pastures, and pastures encroached with low shrubbery	363	25.4
Field	F	Categorical	Fields with maize and other cereals (wheat, oat, barley)	73	5.1
Water body	W	Categorical	Rivers, streams, and dams	15	1.1
Urban	UV	Categorical	Gardens, orchards, and lawns around human settlements	9	0.6
Topography ruggedness index	TRI	Continuous	Quantitative measure of topographic heterogeneity		
Distance to field	D_Field	Continuous	Edge distance to the nearest field (m)		
Distance to settlement	D_Settl	Continuous	Linear distance to human settlements (m)		
Distance to paved road	D_RPaved	Continuous	Linear distance to the nearest paved road (m), medium and high traffic volume		
Distance to unpaved road	D_RUnpaved	Continuous	Linear distance to the nearest unpaved road (m), low traffic volume		

Note: Built-up areas were excluded from the analysis. Nonbear habitat removed from availability because we did not have any bear resting sites in built-up areas.

selection (Martin et al. 2010). The direction of the marginality vector indicates which habitat conditions are selected. The length of the marginality vectors shows the strength of the selection. If the bears show a similar selection pattern of daily resting sites, then their marginality vectors will have an orientation in an almost identical direction. The mean marginality explained by the first axis increases when animals show a comparable selection of variables. Conversely, the mean marginality (Calenge et al. 2005) decreases as the variability in daybed selection increases. If individual animals select variables in a similar way, then the *K*-select groups them together (Calenge et al. 2005). The outputs of the *K*-select are shown by the graphs eigenvalue, variable loading, and individual animals. If the mean marginality is explained by the first or the first two factorial axes in the eigenvalue graph (visible by a clear plummet after the first or the first two bars in the graph), then the bears show a specific pattern of daybed selection. The variable loading graph gives a biological meaning to the axes and shows the importance of environment variables for the selection of daily resting sites by all bears. In the individual animals graph, the marginality vectors of each individual are re-centered and can be interpreted in relation to the variable loading graph. This graph demonstrates which environmental variables are relevant for daily resting by individual animals. For more details and the mathematical procedure of *K*-select see Calenge et al. (2005).

Behaviour, movement patterns, and habitat use change seasonally during the entire period of bear activity (Mueller et al. 2004; Moe et al. 2007; Ordiz et al. 2011). Therefore, we split the identified daybeds into two seasons. The first season covered spring – early summer (April–July) and included the mating season of bears (Pazhetnov et al. 1999). The second season corresponded to late summer – autumn (August–October), which overlaps with the period of hyperphagia when bears gain fat resources for winter-denning (Farley and Robbins 1995). We performed the *K*-select analysis for each season separately. For each individual bear, the availability was defined by the home range (100% MCP), which was created from all validated GPS locations in every particular season. Positional data and derived daybed locations of individual bears were pooled across the years. Behaviour of bears is influenced by sex–age category and presence or absence of dependent cubs in females (Pineau 2014). Therefore, we pooled data of individual bears into the following groups: adult males (M), subadult males (MS), and females with and without cubs of the year (FCOY and F, respectively).

To have a closer view on how bears can co-exist with people in a densely populated area, we independently evaluated from the *K*-select analysis the distances of daybeds from permanently inhabited human settlements. We assessed the Euclidian distances of every single daybed from the edge of the nearest settlement. However, repeated measurements of distances to settlements for each daybed of an individual bear and categorizing bears into groups resulted in pseudoreplication in the data set. To account for this, we used linear mixed-effect models for the statistical analysis, implemented in the lme4 package (Bates et al. 2015) in the R programming environment (R Core Team 2014). We examined the influence of bear groups and seasons on the distance of daybeds from settlements. Visual inspection of residual plots and QQ plots showed deviations from homoscedasticity and normality. Therefore, we transformed the response variable with logarithmic functions and a Box–Cox power transformation (package car; Fox and Weisberg 2011). For further analysis, we chose a Box–Cox transformation with an estimated lambda parameter of 0.27 as being the most appropriate. We constructed two models with distance to settlements as the response variable, bear group and season as fixed effect (explanatory) variables, and bear ID as a random effect variable. The first model reflected the fixed effects of season and bear group on distance to settlements, in R notation:

$$\text{distToSettlement} \sim \text{bearGroup} + \text{season} + (1|\text{bearID})$$

The second model reflected the fixed effect of interaction of bear group and season on distance to settlements, in R notation:

$$\text{distToSettlement} \sim \text{bearGroup} \times \text{season} + (1|\text{bearID})$$

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For examining the significance of fixed effects in question, we used the standard procedure for backward elimination of nonsignificant effects of linear mixed effects, implemented in R package lmerTest (Kuznetsova et al. 2016).

Results

Selection of daily resting sites during the spring and early summer

The first two axes of the *K*-select accounted for 87% of the marginality. Therefore, we retained them for further analysis. However, the first axis explained most of the marginality (75%) (Fig. 2*a*). The first axis showed a common pattern of habitat selection by all bears; they selected for young dense forests (YF) and places farther away from paved roads (D_RPaved). In turn, they avoided grasslands and pastures (GP), as well as older even-aged forest stands without suitable hiding possibilities in the undergrowth (OEAS). The second axis was mostly explained by terrain ruggedness, longer distances away from unpaved roads (D_RUnpaved), and avoidance of older uneven-aged forest stands (OUAS) (Fig. 2*b*). In relation to the second axis, we identified one group of animals showing a distinctive selection pattern: females with cubs of the year including one female without young (F1COY, F2COY, F3COY, F4COY, F5COY, F4) (Fig. 2*c*). This group selected for more rugged terrain and farther away from unpaved roads (D_RUnpaved), as well as paved roads (D_RPaved). The female F4 selection of daily resting sites was similar, regardless of the presence or absence of cubs of the year.

Selection of daily resting sites during the late summer and autumn

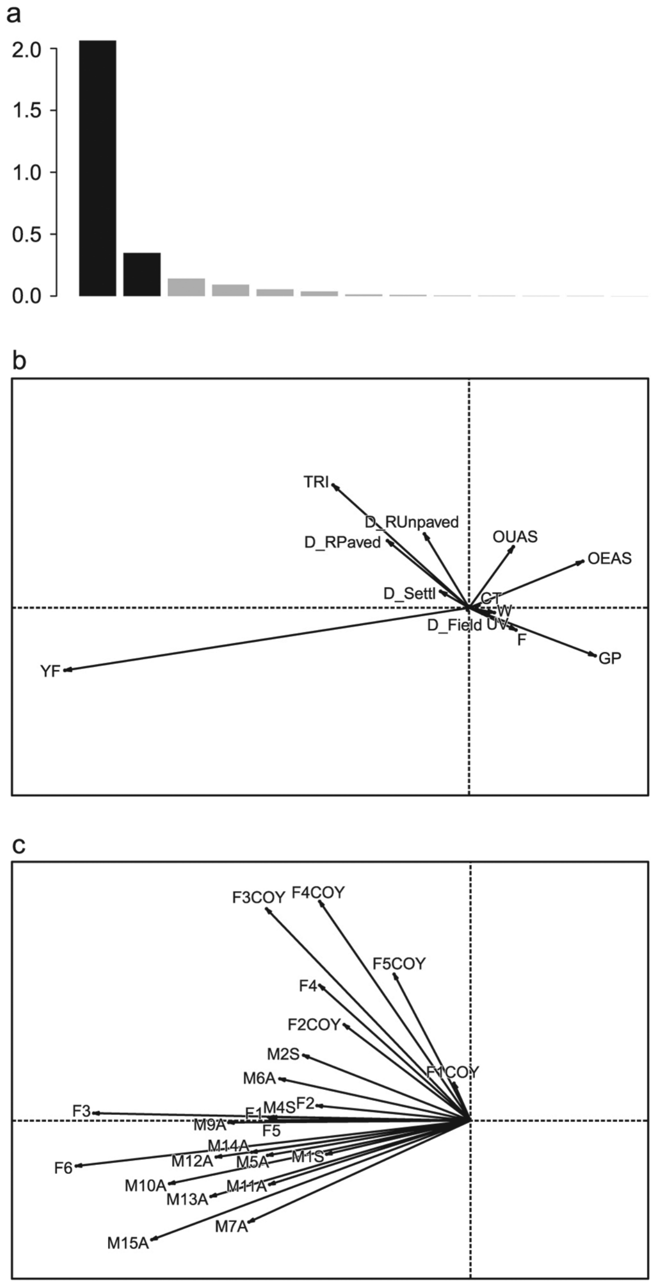
The first two axes explained 88% of the marginality (axis I = 76% and axis II = 12%) and were kept for further analysis (Fig. 3*a*). According to the first axis, all animals strongly selected daybeds in young forests and farther away from paved roads (D_RPaved). However, they avoided older forest stands without suitable concealment options in the undergrowth (OEAS, OUAS) and grasslands and pastures (GP). The marginality on the second axis was mostly explained by terrain ruggedness (TRI), distance to fields (D_Field), and distance to settlements (D_Settl) (Fig. 3*b*). However, these three variables played only a small role in the daybed selection of bears, so it was not possible to clearly identify groupings of bears, as all of them showed a similar pattern of daybed selection (Fig. 3*c*).

Distances of daybeds in relation to human settlements

In this part of the study, we were interested in the relationship between the distance of daybeds to human settlements and bear groups during both seasons. The first model assumed an influence of season and bear group on distance to settlement. The selection procedure eliminated the fixed effect "bear group" because it was insignificant ($p = 0.177$) (Table 3). The original model was reduced to a final model keeping the fixed effect "season". In the second model, the selection procedure kept both fixed effects (season and bear group) and showed that their interaction was highly significant ($p < 0.001$). Therefore, the original model was kept as the best alternative. The random factor of bear ID was kept in both models (Table 3). A summary of the selected models is included in Table 4. From this we can infer that season and, particularly an interaction with, bear group plays a significant role in the location of daybeds with respect to distance to human settlements.

Bears in our study area can rest within a range of 30 m to 9 km away from human settlements during the daytime. We found that

Fig. 2. Results of the *K*-select analysis carried out to measure daybed selection by 21 brown bears (*Ursus arctos*) in north-central Slovakia during spring – early summer from April to July. (*a*) Bar chart of the eigenvalues, measuring the mean marginality explained by each factorial axis; (*b*) variable loadings on the first two factorial axes (axis 1 is *x* axis and axis 2 is *y* axis): young dense forests (YF), topography ruggedness index (TRI), distance to paved roads (D_RPaved), distance to unpaved roads (D_RUnpaved), older uneven-aged forest stands (OUAS), older even-aged forest stands (OEAS), grasslands and pastures (GP), distance to fields (D_Field), distance to human settlements (D_Settl), clearcut (CT), water body (W), urban (UV), and field (F); (*c*) projection of the marginality vectors of all animals on the first factorial plane: females with cubs of the year (FCOY), females without cubs of the year (F), subadult males (MS), and adult males (MA). All marginality vectors have been re-centered to make habitat availability the same for all animals.



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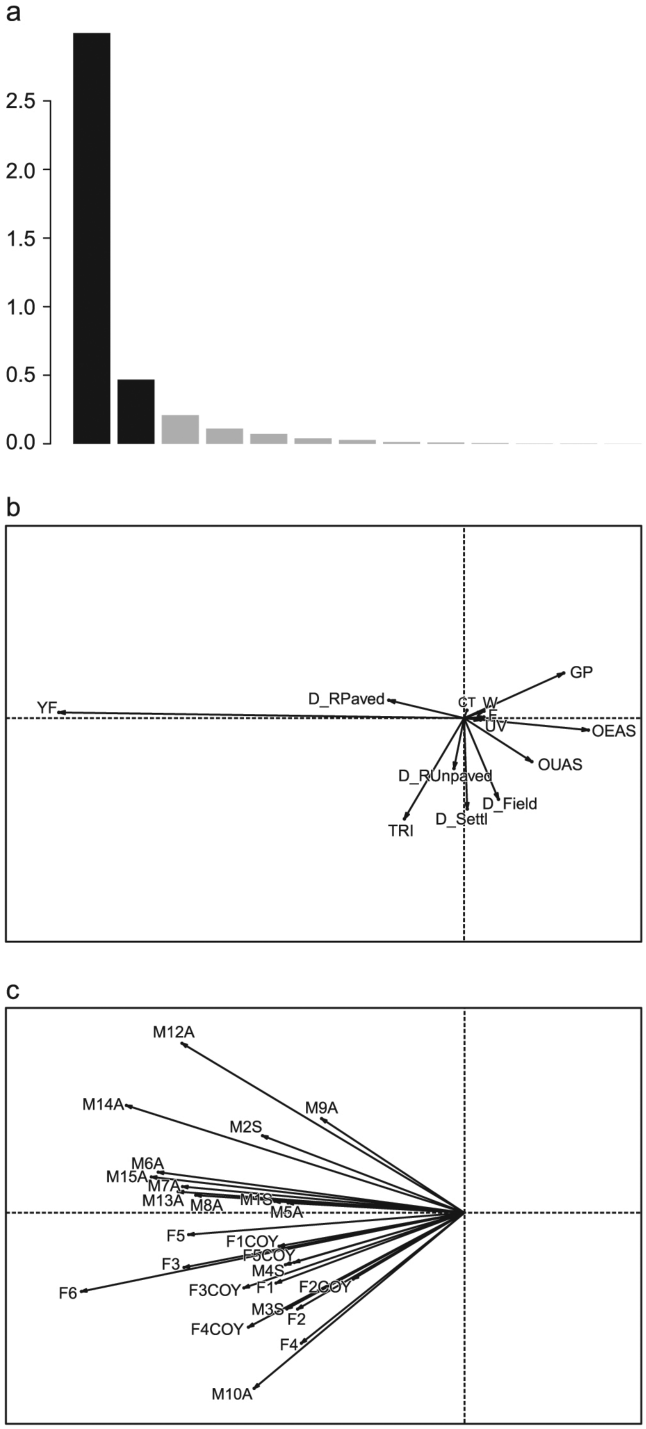

Fig. 3. Results of the *K*-select analysis carried out to measure daybed selection by 21 brown bears (*Ursus arctos*) in north-central Slovakia during late summer – autumn from August to October. (*a*) Bar chart of the eigenvalues, measuring the mean marginality explained by each factorial axis; (*b*) variable loadings on the first two factorial axes (axis 1 is *x* axis and axis 2 is *y* axis): young dense forests (YF), distance to paved roads (D_RPaved), grasslands and pastures (GF), older even-aged forest stands (OEAS), older uneven-aged forest stands (OUAS), distance to fields (D_Field), distance to human settlements (D_Settl), topography ruggedness index (TRI), distance to unpaved roads (D_RUnpaved), clearcut (CT), water body (W), field (F), and urban (UV); (*c*) projection of the marginality vectors of all animals on the first factorial plane: females with cubs of the year (FCOY), females without cubs of the year (F), subadult males (MS), and adult males (MA). All marginality vectors have been re-centered to make habitat availability the same for all animals.

bears can rest in close proximity to built-up areas and their surroundings, such as gardens and parklands, during the daytime. Some of the daybeds of females without dependent cubs and subadult males were situated at a distance of less than a hundred metres from villages during the second season. In contrast to the other bear categories, some adult males rested during the daytime in the most remote areas from human settlements (maximum distances 9013 m in spring – early summer and 7688 m in late summer – autumn).

Discussion

We found that the most important driver for daybed selection by bears is dense woody vegetation, such as young regenerating forests and shrubbery. Furthermore, we discovered that bears can rest during the daytime outside contiguous woodland if suitable cover is available (hypothesis 1). The daybeds of females with dependent cubs were spatially segregated from the daily resting sites of single bears during the mating season. These females selected for rugged terrain and shorter distances to settlements than adult males (hypothesis 2). The analysis of the distances of daybeds to settlements showed that bears shifted closer to villages during late summer – autumn, mainly due to the higher availability of crops and fruit trees (hypothesis 3).

However, daybed selection by bears has not been sufficiently understood. A number of factors influence how bears decide where to rest during the daytime, in particular: cover, distribution of food resources, topography, human disturbance, and intraspecific relations (Mollohan 1986; Ordíz et al. 2011; Cristescu et al. 2013; Ciarniello et al. 2015). Our results show the main predictor for choosing a daily resting site was the density of woody vegetation, which is consistent with findings from Spain (Garcia et al. 2007), Sweden (Ordiz et al. 2011), Finland (Huusko 2012), and North America (Ciarniello et al. 2014; Pineau 2014). In our study, young forest and forest shrub belts in agricultural areas provided cover for brown bears. A typical characteristic of such shelter is a very high density of trees and shrubs. Our anecdotal observations suggest that the vegetation around a daybed is nearly impenetrable for human beings, whereas animals such as wild boars and bears can make a network of tunnels to reach their lairs. The cover around a daybed can be composed of coniferous, deciduous, or mixed tree species. This is in line with the results of other studies, where the forest type and tree-species composition did not affect daybed selection (Cristescu et al. 2013; Ciarniello et al. 2014). In agricultural landscapes, a belt of woody vegetation creates a corridor for wildlife of various widths linking contiguous forest with open farmland. The density of vegetation in these corridors is similar to that of a young regenerating forest. Additionally, in farmland, fruit-bearing trees and shrubs intermix with other woody vegetation, which attracts bears during hyperphagia in autumn (Beckmann and Berger 2003). We observed that during the ripening of crops, especially maize, bears use these corridors not only for movement but also for daily resting. Moreover, we documented that six bears (five males and one female) rested 34 times in the maize fields during daytime hours. It can be concluded that both young forests and corridors composed of woody vegetation in farmland provide suitable concealment options for bears and protection against human disturbance (Fig. 4).

We also found that older even-aged and uneven-aged forests without dense undergrowth do not provide a suitable, safe habitat for bears, which is especially important in a human-dominated landscape. The horizontal structure of a forest is decisive for choosing a daybed, which was also emphasized by others, e.g., Mollohan (1986) and Cristescu et al. (2013). We presume that frag-

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Table 3. Results of the automated elimination process of fixed effects for constructed models.

Fixed effect	Denominator df	*F*	Elimination number	Pr (>*F*)
transDistToSettlement ~ bearGroup + season + (1|bearID)				
bearGroup	25.67	1.50	1	0.177
season	3856.37	38.06	Kept	<0.001
transDistToSettlement ~ bearGroup × season + (1|bearID)				
bearGroup	25.78	1.93	Kept	0.171
season	3860.30	7.12	Kept	0.008
bearGroup:season	3853.87	17.55	Kept	<0.001

Table 4. Parameter estimates and fit statistics of the best models (linear mixed model, random plus fixed effects) to demonstrate the influence of fixed effects "season" and "bear group" on distance of brown bear (*Ursus arctos*) daybeds to human settlements.

transDistToSettlement ~ season + (1|bearID)						
	AIC	BIC	Deviance			
Goodness of fit	23 440.5	23 465.6	23 432.5			
	Name	Variance	SD			
Random effect	bearID (Intercept)	7.182	2.680			
	Residual	24.575	4.957			
	Name	Estimate	SE	df	*t*	Pr (>|*t*|)
Fixed effects	season 1 (Intercept)	24.210	0.540	27	44.98	<0.001
	season 2	–1.016	0.165	3856	–6.17	<0.001
transDistToSettlement ~ bearGroup × season + (1|bearID)						
	AIC	BIC	Deviance			
Goodness of fit	23 395.4	23 458.0	23 375.4			
	Name	Variance	SD			
Random effect	bearID (Intercept)	5.688	2.385			
	Residual	24.249	4.924			
	Name	Estimate	SE	df	*t*	Pr (>|*t*|)
Fixed effects	bearGroupF (Intercept)	24.340	1.006	27	24.19	<0.001
	bearGroupFCOY	–2.582	1.260	27	–1.73	0.095
	bearGroupM	1.390	1.950	27	1.25	0.221
	bearGroupMS	–1.802	1.900	28	–1.12	0.272
	season2	–0.491	0.338	3839	–1.45	0.146
	bearGroupFCOY:season2	1.480	0.511	3842	2.70	0.007
	bearGroupM:season2	–1.677	0.413	3849	–4.06	<0.001
	bearGroupMS:season2	0.256	0.583	3863	0.44	0.661

Note: AIC, Akaike's information criterion; BIC, Bayesian information criterion.

mented forests without suitable concealment options additionally affected by human disturbance could be a limiting factor for bear existence. Similar conclusions have been made for the lynx in Scandinavia (Sunde et al. 1998), the sloth bear (*Melursus ursinus* (Shaw, 1791)) in India (Akhtar et al. 2007), and the brown bear in Greece (Garcia et al. 2007). These findings can possibly explain why bears are absent in many woodland areas of Slovakia (Koreň et al. 2011).

Bears selected daybeds differently during spring – early summer and late summer – autumn. Apparently, the same females behaved differently when they were with or without dependent offspring. When females were accompanied with cubs of the year, they displayed a different daybed selection pattern than all other bears during spring – early summer. These females selected habitats in rugged terrain and places farther away from roads. We believe the spatial segregation of females with dependent cubs from single bears is a way of reducing the risk of infanticide (Ben-David et al. 2004; Steyaert et al. 2016) and unpredictable human disturbance. However, the older female F4 (approximately 13 years) selected daybeds similarly, regardless of the presence or absence of dependent cubs. Behaviour of this female indicates that there might be some other reasons relevant for daybed selection besides infanticide.

Sharafutdinov and Korotkov (1976) and Darling (1986) described that females accompanied by dependent cubs occupied areas separated from single bears and stayed in rugged terrain mainly in spring. These authors defined such places as secure "nursery habitats". The avoidance of areas used by people and other bears can increase the likelihood of offspring survival (Suring et al. 2006).

A distinctive pattern of habitat selection (Suring et al. 2006; Pineau 2014; Takahata et al. 2014) and denning behaviour (Libal et al. 2011) in females with or without cubs was also documented by studies from Scandinavia, Japan, and North America, where it was suggested that they were avoiding adult males. We observed that during the second season, when the risk of infanticide was less profound than during mating season (Bellemain et al. 2006), the females with cubs of the year selected daybeds similarly to the other bears. At the age of 6 months, the cubs become more independent and can build their own daybeds (Mollohan 1986). They can survive without their mother from 7 months onwards

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Fig. 4. Study area illustrating interconnection between contiguous forests and farmland by belts of nonforest woody vegetation. White circles indicate brown bear (*Ursus arctos*) daily resting sites. Some bears were resting in maize (*Zea mays*) fields during daytime.

(Pazhetnov et al. 1999; Skuban 2011). This can explain the less wary behaviour of our female bears with dependent cubs during the second season.

If females were not accompanied by dependent cubs, then they displayed a similar daybed selection pattern as adult and subadult males throughout the entire period of activity. During the first season, this behaviour can also be related to mating season, when both sexes temporarily associate (Elfström et al. 2012). Additionally, we discovered that bears can use the same site for daily resting even after weeks or months, but we have not investigated this phenomenon in detail. This contradicts observations that bears usually do not revisit the same resting site (Ordíz et al. 2011; Huusko 2012; Cristescu et al. 2013), although revisiting of the same daybed was commonly observed in various parts of Russia (Danilov et al. 1993; Yudin 1993; Zhiryakov and Grachev 1993).

Separately from the *K*-select analysis, we performed distance analysis of daybeds to human settlements. Bears in our study area can rest within a range of 30 m to 9 km from human settlements during the daytime. In general, bears in Slovakia select daily bedding sites closer to areas inhabited by people than in Sweden (Nellemann et al. 2007; Ordíz et al. 2011). Slovakia is more densely inhabited than Scandinavia; therefore, bears cannot retreat far away from people on a daily basis.

In comparison with the first season, all bear groups shifted closer to human settlements during hyperphagia. It is likely that bears approached human settlements due to the availability of attractive food resources in farmland, for instance, agricultural crops, especially maize and fruit-bearing trees, which can enhance individual fitness (Libal et al. 2011). We suggest that the bears in our study shifted to the vicinity of people either to avoid intraspecific conflicts or in search of attractive food (Elfström et al. 2012). However, none of our bears entered villages (Skuban et al. 2016; M. Skuban and S. Find'o, unpublished data). Utilizing the proximity of people by bears has also been documented in North America and Scandinavia (Gibeau et al. 2002; Mueller et al. 2004; Elfström et al. 2014). These findings contradict the assumption that bears perceive people exclusively as predators and try to avoid them at all times (Ordiz et al. 2011; Huusko 2012). However, these studies were carried out in sparsely inhabited areas of Scan-

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dinavia, where bears are more able to retreat from people on a daily basis than in Slovakia.

From the conservation perspective, it is important to know whether protected areas can fulfil the necessary living conditions for bears. In our study, a considerable proportion of daybeds was situated outside protected areas in buffer zones and agricultural landscapes, especially in late summer – autumn. During hyperphagia, bears shifted closer to attractive food resources, especially maize fields, abandoned orchards, and scattered fruit trees in agricultural landscapes, where they could also find suitable concealment options (Skuban et al. 2016). Similar behaviour is described for grizzly bears, black bears, and sloth bears (Lyons et al. 2003; Akhtar et al. 2007; Cristescu et al. 2013). Interestingly, the bears in our study area were not always compelled to move from farmland into continuous forests by human activities for daily resting. This fact led us to the conclusion that nonforest woody vegetation in agricultural landscapes, such as hedgerows, tree–shrubbery belts (corridors), and stands of fully grown maize stalks, are suitable man-made habitats for bear daybeds.

Management implications

Woody vegetation scattered across farmlands in Slovakia is currently removed to reclaim abandoned pastures and expand areas with hay meadows. Nonforest woody vegetation is an important habitat not only for bears but also for other taxa and will need more protection in landscape planning.

During the mating season, females with cubs of the year selected daily resting sites separately from other bears and stayed closer to human settlements to avoid the risk of infanticide. Elfström et al. (2014) stated the presence of bear-family groups near human settlements could be temporarily restricted and is not necessarily a threat to human safety. However, this would mean bears are more visible for people, which can create a sense of threat. Management authorities should take this fact into consideration when dealing with potential nuisance bears near villages. During late summer – autumn, bears rested in closer vicinity to villages and exploited highly attractive food resources, such as maize fields and fruit-bearing trees. Several times we observed bears resting in fully grown maize fields during the day. These findings should be spread among the public to lower the risk of bear–human encounters.

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ORIGINAL ARTICLE

Effects of roads on brown bear movements and mortality in Slovakia

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Abstract The increasing development of road infrastructure considerably contributes to bear habitat fragmentation. The aim of this study was to examine the relationship between brown bear movements and secondary roads. The 1463-km^2 study area in the north-central Slovakia was defined by the composite home ranges (minimum convex polygon (MCP) 100%) of 21 bears studied by GPS telemetry from 2008 to 2016. Additionally, we used the data of 35 bears struck by cars and trucks across all of Slovakia during 2007–2015. We found that a traffic volume exceeding 5000 vehicles per 24 h completely restricted the movement of bears. Bears were more likely to cross during periods of low- rather than high-traffic volumes, and crossings occurred primarily at night. Males were able to cross roads with annual average daily traffic up to 5000 vehicles per 24 h, whereas females were only able to cross roads with less than 4000 vehicles per 24 h. Bears, regardless of age and gender, crossed roads more frequently during hyperphagia (August to November) than during the mating season (April to July). This was additionally confirmed by the comparison of annual patterns of crossings and road kills, which both peaked in August. The movement of these bears across roads was particularly motivated by the search for attractive crops in fields. Road crossings and road kills mainly occurred around midnight. Understanding the temporal and spatial use of roads by brown bears should provide valuable information for land use planners to effectively minimise the negative impacts of roads on bears.

Keywords Animal movement · Crossing index · GPS telemetry · Roads · Traffic volume · *Ursus arctos*

Introduction

People alter landscapes through urbanisation, agricultural and recreational activities (Western 2001). One of the negative consequences for wildlife is the fragmentation and loss of suitable habitat (Bennett and Saunders 2010). The continuous increase in road infrastructure also involves threats to wildlife (Coffin 2007), because many animal species need to cross roads either for migration, dispersal or as a part of their daily activities (Forman et al. 2003).

Road-crossing behaviour in bears is still not fully understood (e.g. Chruszcz et al. 2003; Waller and Servheen 2005). Road-crossing likelihood is determined by diel periods, sex and season (Beringer et al. 1990; Northtrup et al. 2012b). In terms of the periods of day when crossings occurs, many brown bears (*Ursus arctos*) prefer to cross roads during times of minor human activity, especially during night time and in early morning (Graves et al. 2006; Graham et al. 2010). The majority of crossings take place between 11 p.m. and 4 a.m. due to significantly lower traffic intensity (Waller and Servheen 2005). Because males and females do not cross roads equally, they can act as a sexual filter (Sawaya et al. 2014). Sometimes, males are more likely to cross roads

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(Gibeau et al. 2002; Procter et al. 2008), yet other studies emphasised that females stayed closer to the roads and crossed them more frequently than other bears (Graham et al. 2010; Lewis et al. 2011). Occasionally, the crossing intensity of males and females changes due to seasons. Gurthrie (2012) observed that males crossed roads more during the mating season in spring, probably while searching for mates. In contrast, females crossed roads intensively during the fall, as they prepared for the denning period (Gurthrie 2012). The presence or absence of dependent cubs with females can also significantly influence their willingness to cross roads. Bear females with cubs of the year were found to be more wary and to cross roads less frequently (Graves et al. 2006). Finally, seasons are defined by major changes in food distribution and availability, which can substantially influence the road-crossing behaviour of bears (Chruszcz et al. 2003; Berland et al. 2008). However, many roads can act as a home-range boundary and not all bears of a population are willing to cross them (Kaczensky et al. 2003; McCown et al. 2009; Lewis et al. 2011).

In addition to when, many factors influence where bears choose to cross roads. Wildlife crossings can cluster in so-called migration corridors (Graves et al. 2006). Site fidelity for road-crossing events has also been observed in bears (Lewis et al. 2011; Gurthrie 2012). Crossings are often motivated by reaching a higher-quality habitat on the other side of the road that offers better foraging possibilities (Chruszcz et al. 2003; Graves et al. 2007; Graham et al. 2010; Sawaya et al. 2014). However, movements of bears to these attractive feeding spots are often connected with increased mortality due to vehicle collisions. Waller and Servheen (2005) suggested that there might be a trade-off between the risk of undertaking crossings at high-traffic roads and reaching tempting bear foods. Therefore, attractive feeding spots near roads can act as ecological traps (Nielsen et al. 2006; Beckmann and Lackey 2008; Robertson et al. 2013; Lamb et al. 2016). Other life history traits, like potential mates and social interactions, are additionally suggested to influence a bear's readiness to cross roads (Gibeau et al. 2002; Lewis et al. 2011). Obviously, some bears can become used to predictable traffic disturbances (McLellan and Shakleton 1988). This habituation allows bears to exploit habitats close to roads, especially if human use follows predictable spatial and temporal rhythms (McLellan and Shakleton 1988; Hellgren et al. 1991; Chruszcz et al. 2003).

Higher traffic volumes are connected with increased barrier effects. Northtrup et al. (2012b) stated that volumes as low as 10 vehicles/24 h can act as a barrier for grizzly bears (*U. arctos horribilis*). Other studies indicate that bears are unable to cross roads with traffic volumes from volumes of 2400 vehicles/24 h (Waller and Servheen 2005) or 4800 vehicles/24 h onward (Graves et al. 2006). Black bears (*Ursus americanus*) seem to be more tolerant of higher traffic volumes (Kasworm and Manley 1990) and are able to cross roads with up to 6100 cars/day (Gurthrie 2012). However, in many densely populated areas in Europe, the traffic volume is much higher and poses a risk for dispersing bears (Kaczensky et al. 2003). Further evidence of barrier effect caused by high traffic volume is that bears avoid unfenced highways (Waller and Servheen 2005) and other high-use roads (Northtrup et al. 2012b). In Europe, little is still known about which traffic volumes impede movements of brown bears when crossing highways and secondary roads. However, it was found that the structures for wildlife crossings (e.g. green bridges, tunnels, culverts and viaducts) considerably facilitate bear movement across high-traffic-volume roads (Kusak et al. 2009).

Since Slovakia joined the EU in 2004, road infrastructure has expanded in combination with a dramatic increase in the amount of traffic. The results of a road traffic census showed that the number of cars increased by 28% during the period from 2005 to 2010 (E-Road Traffic Census 2010; Slovak Road Administration). Several highways and express roads pass through the range of the brown bear (Find'o et al. 2007). The international highway D1 divides the bear range into northern and southern parts. A recent study showed that this highway is likely to have a negative effect on the gene flow of bears in Slovakia (Straka et al. 2012). As a result, an increasing number of bears are killed due to vehicle collisions. A substantial part of traffic-related bear mortalities has happened on secondary roads and railways (State Nature Conservancy of the Slovak Republic).

In this article, we investigate the impact of various levels of traffic volume on secondary roads on the behaviour and movement of brown bears. Specifically, we examine brown bears' road-crossing behaviour, temporal pattern of cross-road movements and road mortality.

Study area

The 1463-km^2 study area was defined by the home ranges (minimum convex polygon (MCP) 100%) of the studied bears (Fig. 1). The area is situated in north and central Slovakia (latitude 48° 52′ and longitude 19° 08′) and includes seven mountains ranges as well as two basins. Elevations range from 363 to 1710 m. In total, 66% of the area is covered by mountain forests mainly composed of Norway spruce (*Picea abies*), beech (*Fagus sylvatica*), silver fir (*Abies alba*), and Scotch pine (*Pinus sylvestris*). Twenty-five per cent of the study area consists of grasslands and pastures in farmland or alpine meadows above the timber line. Fields cover 5% of the study area, where maize (*Zea mays*) fields provide the most important crop for bears. Bears can also feed on domesticated forms of fruit-bearing trees (apple, pear, plum and cherry) scattered in agricultural land or near human settlements in gardens and abandoned orchards (Skuban et al. 2016). The human population is quite dense, reaching up to 90 inhabitants/km^2 in average

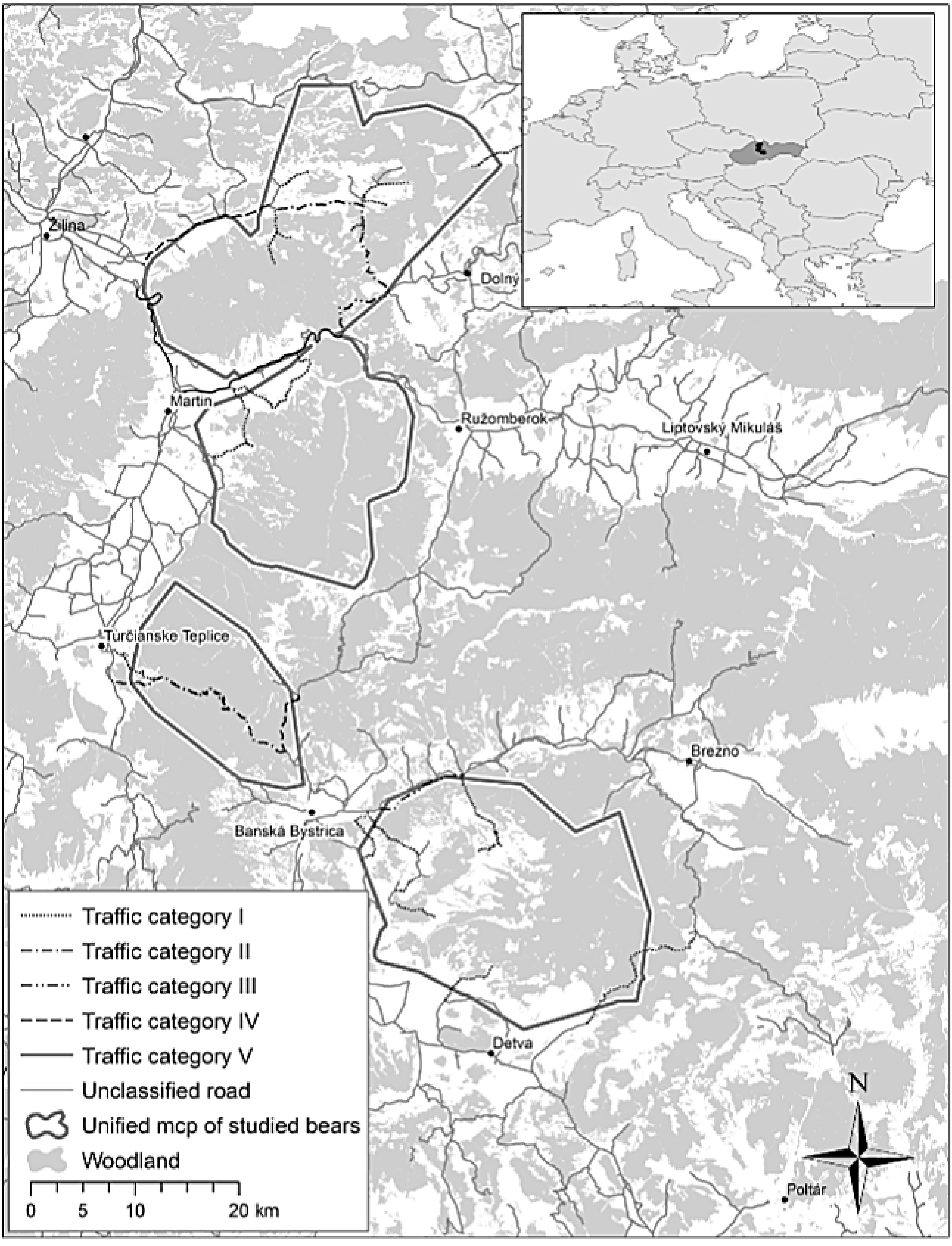

Fig. 1 Study area in north-central Slovakia delineated by the composite home ranges (MCP 100%) of brown bears (*Ursus arctos*) monitored by GPS telemetry. Secondary roads were reclassified according to traffic volume into five categories: < 2000 vehicles/24 h (TC-I); 2000–4000 vehicles/24 h (TC-II); 4001–5000 vehicles/24 h (TC-III); 5001–10,000 vehicles/24 h (TC-IV) and > 10,000 vehicles/24 h (TC-V)

(Statistical Office of the Slovak Republic; Counting inhabitants 2011). Due to forestry and agricultural activities, a network of paved and unpaved roads divides the entire area. Moreover, the area is intersected with a dense network of first-, second- and third-class roads for national and international transport and travel. However, no highway passes through the study area. Since 1932, the brown bear has been protected in Slovakia. At present, bear hunting is restricted and regulated by law.

Material and methods

GPS telemetry of bears

In total, 21 bears (6 females and 15 males) were captured in 8 different locations within the study area, either in box or culvert traps, between 2008 and 2016. Every bear was equipped with a GPS-GSM collar (Vectronic Aerospace GmbH, Germany) scheduled to take a position every hour, resulting in a maximum of 24 fixes per day. Only 3D-validated locations with a dilution of precision (DOP) less than 10 were considered. The Ministry of Environment of the Slovak Republic issued the permit for the capturing and handling of bears (No. 10155/2010-2.2). So far, there is no ethical clearance on wild animal research in Slovakia. Thus, the recommendations from the Scandinavian biomedical protocols for capture, chemical immobilisation and radio tagging of free-ranging brown bears were followed (Arnemo 2005). For more details about the capturing, handling and immobilisation of bears, see Skuban et al. (2016).

Assignment of roads to traffic volume categories

The responses of bears to first-class roads (international and national transport), second-class roads (connecting districts and counties within the country) and third-class roads (local paved roads) were investigated. In this article, we use for these three classes of roads the term “secondary roads”. Secondary roads were classified into five categories according to traffic volume (herein TC): < 2000 vehicles/24 h (I); 2000–4000 vehicles/24 h (II); 4001–5000 vehicles/24 h (III); 5001–10,000 vehicles/24 h (IV) and > 10,000 vehicles/24 h (V). On some sections of the roads included in the category V, the average traffic volume reached up to 26,000 vehicles/24 h and at peak times up to 40,000 vehicles/24 h. Traffic volume data was freely available from the 2010 e-road traffic census carried out by the Slovak Road Administration.

Index of road crossing

In order to examine the permeability of roads in regards to brown bear movement, a crossing index analysis was performed (Beringer et al. 1990; Chruszcz et al. 2003; Graham et al. 2010). Crossing locations were generated by intersecting a straight-line path connecting two consecutive GPS fixes on opposite sides of the road with the road layer. Furthermore, we determined the traffic volume category at the point of intersection. If a straight-line crossed the same road multiple times, it was eliminated from the analysis. Because animals do not move straight between the two consecutive GPS fixes, it is likely that the crossing point determined from GPS telemetry is different from that of the true crossing location of a bear. The longer the time span between the two GPS fixes, the greater the probability that the crossing point will be incorrectly determined. To minimise such errors, we excluded the movement path of a bear from further analysis, if the time span between two consecutive GPS fixes on opposite sides of the road was greater than 1 hour. The number of crossings is shown in Table 1.

The index of road crossing (herein RCI) was calculated for each bear according to the formula used by Serrouya (1999) and Chruszcz et al. (2003):

$$I_{ijk} = C_{ijk}/M_{ij}/L_{ijk}$$

where

I = crossing index for bear i in season j for TC k,

C = number of crossings made by bear i in season j for TC k,

M = total number of straight-line paths connecting two consecutive GPS locations made by bear i during season j and

L = length of roads of TC k within the seasonal home range (in m).

Behaviour, physiology, movement patterns and habitat use in bears change seasonally during the entire period of bear activity (Gibeau et al. 2002; Mueller et al. 2004). Therefore,

Table 1 Mean traffic indices (RCI) by traffic volume category (TC), gender and season for brown bears in north-central Slovakia, 2008–2016

Variable		No. of bears	No. of crossings	Mean RCI (× 1000)	SE (× 1000)	Wilcoxon test, p value
TC	TC-I	14	320	0.67	0.17	0.031
	TC-II	5	49	0.23	0.08	
Gender	Male	15	290	0.55	0.15	0.508
	Female	5	79	0.74	0.26	
Season	April–July	16	152	0.30	0.10	0.010
	August–October	18	217	0.84	0.22	
TC-I by seasons	April–July	14	129	0.31	0.14	0.069
	August–October	15	159	0.92	0.28	
TC-II by seasons	April–July	5	23	0.12	0.03	0.191
	August–October	5	26	0.31	0.13	

data was split into two seasons. The first season covered spring/early summer (April–July) and covered the mating season of bears (Dahle and Swenson 2003). The second season matched to late summer/autumn (August–November) which corresponds with hyperphagia in bears and the preparation for hibernation (Hilderbrand et al. 1999). By using R (R Development Core Team 2015), two-sample Wilcoxon rank sum tests were conducted to determine whether mean crossing indices differed across TC, season and gender.

Temporal pattern of crossing events and bear-vehicle collisions

We examined at which time of the day and in which month of the year the bears cross roads. None of the bears studied by GPS telemetry was killed by a vehicle. The time of crossing was estimated based on the times of two consecutive fixes on opposite sides of the road. We considered the half-time between these two fixes. The data on bears killed by traffic from 2007 to 2015 was obtained from the State Nature Conservancy of the Slovak Republic. For further analysis, we used only the road mortality cases. We assigned all mortality locations with a corresponding traffic volume. The date and the time of the collision for every bear killed were available, making it possible to analyse the temporal pattern of road mortality throughout the year and during a 24-h period. Data were pooled on all killed bears across the years. The daytime of successful crossings and the daytime of bears being killed by vehicles were compared to see if there was a difference. Similarly, we compared the temporal pattern of successful crossings and road mortality throughout the year. To assess the differences in means, we used an asymptotic two-sample Fisher-Pitman permutation test. This test eliminates the large differences in *N* between samples and does not require the assumption of normal distributions. To test the shift between medians, we used the asymptotic Wilcoxon-Mann-Whitney permutation test. For calculation of permutation tests, we used the coin package (R Development Core Team 2015). The significance level was set at 0.05.

Results

Road crossing index

Various levels of traffic volume differentially influenced the movement and the crossing behaviour of bears. Of the 21 bears tracked by GPS telemetry, 15 (12 males and 3 females) crossed one or more TCs. Both genders crossed TC-I (12 males and 2 females) and TC-II (4 males and 1 female), but only 3 males were able to get through TC-III. However, bears did not cross roads with a traffic volume higher than 5000 vehicles per 24 h (TC-IV and TC-V) (Fig. 2). Because of the small number of bears crossing TC-III, for further statistical analysis, we considered only mean RCIs calculated for TC-I and TC-II (Table 1). Bears crossed TC-1 more frequently than TC-II ($p = 0.031$) and more during August–November than in April–July ($p = 0.010$). Furthermore, we found that crossing TC-I and TC-II was not influenced by gender and season ($p > 0.05$) (Table 1).

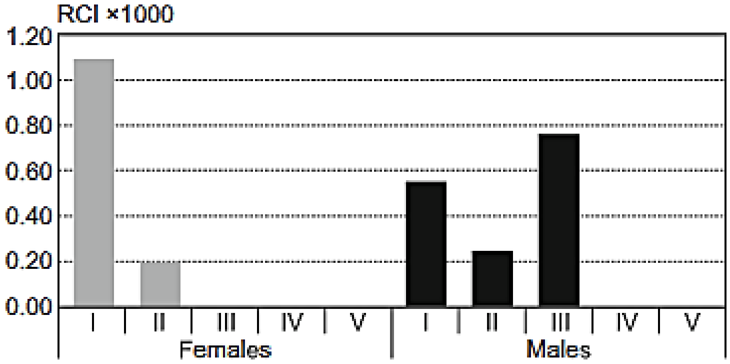

Fig. 2 Mean road crossing indices × 1000 for bears by gender and traffic volume categories (TC-I–TC-V)

Temporal pattern of crossing events and bear-vehicle collisions

In the period 2007–2015, 60 bears were killed either by motor vehicle ($N = 35$) or by train ($N = 25$) in Slovakia. Most of the bears killed (77%) were sub-adults ($N = 29$) and cubs of the year ($N = 18$). Sub-adults were defined as 4 years old and younger as per Pazhetnov et al. (1999). The sex ratio of these two pooled age classes was 28 males to 15 females, and the gender of the 4 remaining young bears was not identified. Additionally, five adult females, seven adult males and four bears with unknown gender died at traffic collisions. The majority of bear fatalities (66.7%) occurred on road categories TC-IV and TC-V, in which 50% was located on roads with more than 10,000 vehicles/24 h. The lowest rate of mortality was observed on roads of TC-III (5.6%). An equal proportion of bears (13.9%) was killed on roads of the two lowest categories TC-I and TC-II.

Diel pattern

Bears monitored by GPS telemetry successfully crossed roads mainly between 6.00 p.m. and 5.00 a.m. Most of the bear-vehicle collisions occurred between 6.00 p.m. and 7.00 a.m. The mean hour of successful crossing (10.51 p.m.) was significantly different from the mean hour (12.39 a.m.) of reported road mortality cases ($Z = 2.722$, $p < 0.01$). The corresponding median values were 11.00 p.m. for successful crossings and 1.00 a.m. for road kills, respectively. These results indicate that both crossings and road kills peaked around midnight. Road crossings and bear-vehicle collisions, however, were also found on a smaller scale during daytime hours (Fig. 3).

Monthly pattern

The road mortality of bears occurred from April to December, whereas crossings took place from February to December (Fig. 4). The month of the highest successful crossings and road kills was the same, i.e. August ($Z = -1.640$, $p = 0.095$). Both crossings and road kills peaked during the second season (Figs. 4 and 5).

Discussion

The majority of previous studies on the effects of roads on bears have investigated the influence of highways and express roads on bears (e.g. Chruszcz et al. 2003; Lewis et al. 2011; Sawaya et al. 2014). Highways are commonly considered as a potential home-range boundary due to their specific technical construction, fencing and high traffic volume (Kaczensky et al. 2003; Waller and Servheen 2005; Graves et al. 2006). On the other hand, some studies supported the notion that secondary roads do not affect the crossing behaviour of bears and other wildlife species (Beringer et al. 1990; Graham et al. 2010). In line with our expectations, high traffic volume on secondary roads considerably impacted the spatial behaviour of bears. Our study showed that roads of lower categories with high traffic volume can negatively affect the movement of bears. Roads with higher traffic volumes often pass through areas densely inhabited by people and with fragmented habitats. However, in our study, roads with high traffic volumes also intersected suitable bear habitats (Fig. 1).

We found that the traffic volumes exceeding 5000 vehicles per 24 h completely restricted the movement of bears, similar to the findings of Graves et al. (2006) for grizzly bears. Other authors showed that even lower traffic volumes can inhibit the movement of grizzly bears (Waller and Servheen 2005; Northtrup et al. 2012b). However, studies dealing with the influence of roads on bears in Europe did not provide thresholds of traffic volumes that limit bear movement (Kaczensky et al. 2003; Kusak et al. 2009). In our study, males tolerated a higher volume of traffic than females, considering their ability to cross the road. Indeed, males were able to cross roads with an annual average daily traffic up to 5000 vehicles per 24 h, whereas females only crossed roads with less than 4000 vehicles per 24 h. This result suggests that secondary roads with high traffic volume can also pose a sexual filter (Gibeau et al. 2002; McCown et al. 2009; Sawaya et al. 2014). However, improving the sampling effort is necessary to validate this difference in gender behaviour. So far, it has not been sufficiently understood why the frequency of road crossings is different for females and males. In contrast to our results, some authors have reported that females cross roads more frequently than males (Graham et al. 2010; Lewis et al. 2011). In compliance with our findings, however, the majority of studies have demonstrated that males are more likely than females to undertake the risk of crossing roads (Waller and Servheen 2005; Procter et al. 2008; McCown et al. 2009). This behaviour of males can possibly be explained by large home ranges on both sides of the roads, searching for mates in spring and exploring food resources in autumn (Chruszcz et al. 2003; Clevenger et al. 2009; Graham et al. 2010).

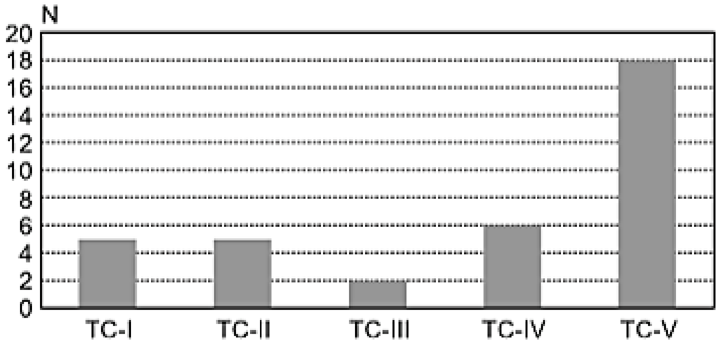

Fig. 3 Kernel density functions for road crossings of bears and bear-vehicle collisions during 24 h. Vertical lines specify the average time for crossings and road kills

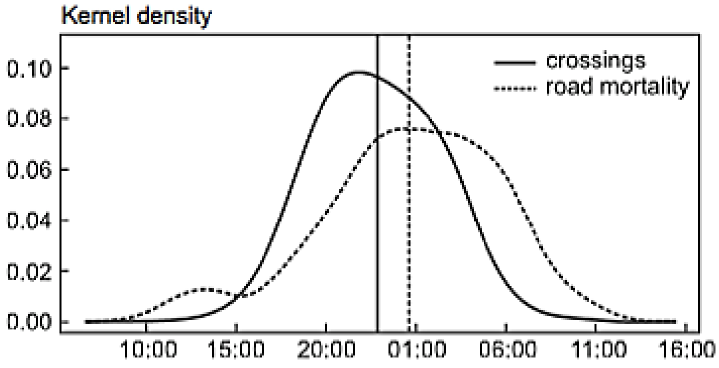

Fig. 4 Kernel density function for road crossings and road kills throughout the year. Vertical lines denote medians

Bears crossed roads more frequently in late summer–autumn that in spring–early summer. Higher crossing activity in autumn can be related to hyperphagia, when bears need to fatten up in order to survive the upcoming winter (Beckmann and Berger 2003; Gurthrie 2012). At this time,

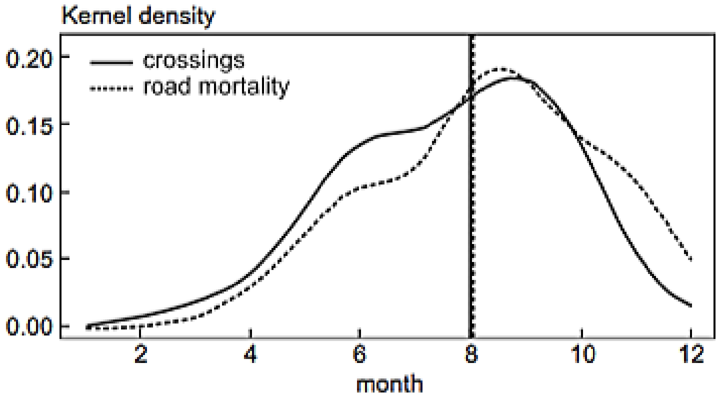

Fig. 5 Bears struck by cars and trucks attributed to traffic categories

bears in our study area shifted closer to human settlements where the density of roads is higher than in other parts of their home ranges (Skuban et al. 2017). We presume that in cultural landscapes, bears cross roads more frequently in search of attractive anthropogenic food, such as maize and fruits (Skuban et al. 2016). The results of stomach analysis of the bears killed by motor vehicles confirmed this (Database of the State Nature Conservancy of the Slovak Republic 2007–2015). More than two thirds of stomachs contained maize, apples, pears and plums. Maize fields and orchards alongside roads could, therefore, pose an ecological trap for hyperphagic bears in autumn (Nielsen et al. 2006; Beckmann and Lackey 2008; Lamb et al. 2016). The movement of bears searching for food is probably why the highest crossing activities are in August, which overlapped with the peak period of road mortality for bears. This is in line with findings from North America, where grizzly (Graves et al. 2007; Kite et al. 2016) and black bears (Beckmann and Lackey 2008; Lamb et al. 2016) were most frequently killed by motor vehicles in autumn. Similarly, Graham et al. (2010) stated that food importance value (presence of high-quality forage) can significantly increase the willingness of bears to undertake risky road crossings. In contrast, Kaczensky et al. (2003) revealed that in Slovenia, the road mortality of bears peaked during mating season in May and June. However, more recent data (2005–2014) from Slovenia and Croatia indicated that besides the spring peak of bear road mortality, there is even more pronounced autumn peak (Krofel et al. 2015).

The analysis of road mortality in Slovakia showed that 80% of killed bears were sub-adults and cubs of the year (57 and 23%, respectively). We suppose that the low level of experience with traffic is the main reason for high road mortality for these two age categories (see also Krofel et al. 2015). Moreover, sub-adults have an increased risk of being killed by a vehicle due to their extensive movements (Procter et al. 2008; Northtrup et al. 2012a). Sub-adult males roam especially widely within the home range or explore new areas (Kaczensky et al. 2003; Boulanger and Stenhouse 2014; Sawaya et al. 2014). This behaviour may explain the high road mortality of sub-adult males in our study and suggests that road-related mortality of bears can be explained by age rather than by gender (Boulanger and Stenhouse 2014). As regards traffic volumes, most bears were killed on roads with high traffic volumes, whereas most crossing events took place on roads with less traffic volume. We may state that bears crossing roads with higher traffic volumes are under increased risk of being killed. Obviously, traffic volume is one of the most important factors in making decisions about the installing of wildlife barriers (fences) along roads to reduce the risk for bear-vehicle collisions.

Bears in Slovakia live in a human-dominated landscape and are more or less permanently exposed to human disturbance (Koreň et al. 2011). They are typically active during crepuscular and night-time hours (Finďo and Skuban, unpublished data). Throughout the day, the bears studied by telemetry most frequently crossed roads shortly before midnight, whereas the traffic mortality of other bears peaked shortly after midnight. However, the traffic mortality continued to be high till early morning hours (Fig. 3). None of the bears studied by GPS telemetry was killed by a vehicle. In conclusion, we can say that road crossings and road kills peaked around midnight during minor human activity. Nevertheless, some bears in our study crossed roads or were killed by motor vehicles during daytime hours as well. Similar patterns of crossing behaviour for bears living in a human-dominated landscape have been described by other authors (Waller and Servheen 2005; Graves et al. 2006; Lewis et al. 2011).

Although road infrastructure seems to have profoundly negative effects on bears in some parts of Europe (Forman et al. 2003), this issue has been poorly studied. In this study, we showed that high traffic volumes on secondary roads can restrict bear movement and might influence the demography of this species through the removal of young animals from the population. Because even lower-class roads with high traffic volumes can significantly contribute to further fragmentation of the bear range in Slovakia, we recommend introducing mitigation measures on the most critical sections of these roads. Furthermore, we conclude that the riskiest period for a bear-vehicle collision is the time around midnight during late summer. In order to reduce bear-vehicle collisions, we recommend posting extra signage under warning signs when and where animals generally cross the road.

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CV MICHAELA SKUBAN, MSC., PHD CANDIDATE

PhD-candidate at the University of Munich under supervision of Dr. Matthias Starck: "Bears among people: Human influence on diet, habitat selection, and road crossing behaviour of the brown bear (Ursus arctos) in central Slovakia"
Co-supervised by Dr. Slavomír Finďo, NLC Zvolen, Slovakia and Dr. Walter Arnold, Leader of FIWI Research Unit, Vienna, Austria.

PROFESSIONAL INTERESTS

Wildlife ecology, wildlife management, protection of habitat and important wildlife passages, biology and ecology of wildlife species with special focus on brown bear, wolves and red deer

PROFESSIONAL EDUCATION

2000 – 2005	"Ludwig-Maximilian"-University of Munich, study of biology with main subject Zoology as well as Ecology, Neurobiology and Psychology,
Masterwork:	The diet of four different wolf (*Canis lupus*) packs in the Biesczcady Mountains, South-eastern of Poland". 12/2003 and 04/2004 – 08/004 fieldwork in Poland / Biesczcady-Mountains in the research group of Dr. Roman Gula: telemetry, snow-tracking, depredation analysis, scat analysis and autopsy of wolves, livestock and red deer.
1998 – 1999	Acting School: „Schauspiel München“
1996 – 1997	Technical University of Munich, study of biology
1987 – 1996	Gymnasium Geretsried, Germany; "Abitur"-certificate

PROFESSIONAL EXPERIENCES

Since 2006

Carpathian Wildlife Society
NGO Organisation in Slovakia with special focus on wildlife ecology behaviour and management as well as on habitat protection (www.**carpathianwildlife**.sk)
:

- Analysis of wildlife ecology and monitoring of the species brown bear, red deer and wolves.
- Analysis of VHF respectively GPS positional data by the help of Arc View as well as Adehabitate statistics (R-Statistics).
- Catching of brown bear into box-traps and narcotising red deer with narcotic gun what requires an intensive cooperation with local people, hunters as well as nature conservationists. I was leading several catching events and liked to communicate with locals from

my study area.
- Programming of GPS/GSM collars
- Intensive fundraising and preparation of project proposals in English, German and Slovak.
- Analysis of migration corridors of big mammal species alongside the planned highways and dual carriage ways by tracking literature research, statistical analysis and finally we addressed with our data responsible road building engineers for implementing the results. Final output was additionally a brochure in English. Financed by Frankfurt Zoological Society
- Translation of various documents from and to English, German and Slovak (ISO ELEKTRA Foundation)
- Intensive cooperation with local hunters, nature conservationists, foresters, and road building engineers to set up catching or promote and implement our results

Since 04/2017

State Nature Conservancy of the Slovak Republic
Participation in management of large carnivores

2016 – till now

Joachim und Hanna Schmidt Foundation, Hamburg, Germany
Analysis of brown bear behavior regarding roads, bear-vehicle mortality and modeling of habitat parameters at bear´s successful crossing routes

2016 – till now

EURONATUR Radolfszell, Germany
Start of a scientific monitoring of the wolf population, reducing of the hunting quota, contributing to a better protection via cooperation with Slovak State Nature Conservancy

2016

Gregor Luisoder Environmental Foundation Munich, Germany
Creation of a practical handbook for Bavarian farmers how to protect livestock against wolf attacks.

2015 – 2016

Slovak Ministry of Education, Science, Research and Sport
Scholarship for finalizing the last field work of the PhD thesis "Bears among people"

2014 - 2015

Ekopolis foundation, Banská Bystrica, Slovakia
Cooperation with the IMSA Knowledge Company Norway and the Friends of the Earth Norway "Protecting the wolves – lessons learned from Slovakia regarding Management and Livestock protection practises"
- Draft of the Action plan for Slovak wolves
- Rearing and testing the abilities of livestock guarding dog breeds and other techniques
- Seminars for important stakeholders in Norway and Slovakia
- Knowledge transfer of achieved results to Norway

2012 – 2013

NDS, Slovak Highway Association
- Several expertises for a planned highway in the Mala Fatra Mountains inclusive communication with local people, investors, politicians and press conferences.

2007 – 2009

Andrea – von – Braun Foundation
Fellowship for writing an interdisciplinary book about the brown bear. Thus, beside biology, behaviour and ecology of bears, I integrated economy, sociology, hunting, art, folk habits, mythology, fairy tales etc.The book was published in 2011 „Dem Braunbär auf der Spur. Lebensweisen, Geschichten, Mythen", and in 2013, I was awarded for

it from the “Yves-Rocher-Foundation”, supporting women in nature conservation.

2006 – 2010

Zoological Society Frankfurt (ZGF) Germany
- Working as a scientific researcher regarding wildlife migration corridors and brown bears.

08/2006 – 09/2006

Biosphere Travel Agency
Slovakia, free employment
- Ecotourism, leading groups of eco-tourists as well as organizing accommodation and food.
- Scientific analysis of the question: Influence of predators (bear, wolf, lynx and Golden eagle) on distribution of the “Tatra-chamois” in the Low Tatras. A current content article is in work.

PRICES

2013

Award winning, 2nd price, Yves-Rocher Foundation, Women in Nature Protection and environmental engagement. Stuttgart Germany

2006

Freies Theater Ruhr, 2nd price in the “short stage play competition”

PROFESSIONAL PRACTICAL TRAINING

08/2005

“**Mobile Herdenschutzeingreifgruppe” Switzerland**
- Work as a shepherd
- Integration of Livestock Guarding Dogs in existing sheep herds
- Monitoring of the efficacy of dogs

12/2003

Biesczcady Mountains, Poland (Akademia Nauk, Dr. Roman Gula/ LMU Munich, Dr. Matthias Starck)
- Practical training of telemetry, scat analysis and snow tracking required for the data collection for my master work

08/2001

Animal Organisation „Tierhilfe Süden“, Turkey
- Catching and castration of stray dogs
- Care for 160 dogs in the animal pond
- Behavioural analysis of stray dogs in comparison to pet dogs

1999

Animal Home Munich in Riem
- 6 month work on the department for dogs and cats
- Care and medical care, additionally work in the quarantine-station for ill cats and dogs but also confiscated monkeys
- Practical course regarding fighting dogs
- Coming in touch with CITES regulations regarding confiscated monkeys which had been housed in there

SEMINARS / WORKSHOPS

04/2008

Seminar of Dr. David Mech regarding wolf and wolf conservation in Czech Republic inclusive own presentation “Methods of protections and expected problems”

2008	Summer School in Bialowieza (Poland) Methods of fieldwork techniques and their analysis
2001	Workshop: “Ethological analysis of wolf behaviour”, Dr. Erik Zimen
1999	Seminar: The Wolf – ancestor of our dogs: Dr. Erik Zimen

FURTHER SKILLS

Languages:	German (native speaker) English (fluently), Slovak (fluently), Czech (good), Polish (basic), French (beginner), Latin (5 years, marks between 1 and 2)

	Understanding	*Speaking*	*Writing*
English	C2	C2	C1
Slovak	C2	C2	C1
Czech	B2	B1	A2
Polish	B1	A2	A2
French	A1	A1	A1

Computer skills	Windows, Arc GIS, Arc View, internal programs for telemetry equipment, insights in R-statistics
Other:	Education and practical courses in dog training and veterinary care
Personal Interests:	Swimming, Belly dance and Fusion, dogs and cats (especially my two own ladies), hiking, literature

Publications

Skuban M., Finďo S., Kajba M. Koreň M., Chalmers J., Antal V. (2017) Effects of roads on brown bear movement and mortality in Slovakia. European Journal of Wildlife Research 63:82

Skuban M., Finďo S., Kajba M (2017) Bears napping nearby: Daybed selection by brown bears (Ursus arctos) in a human dominated landscapes. Canadian Journal of Zoology.

García-Rodríguez A., Rigg R., Elguero-Claramunt I., Bojarska K., Zięba F., Zwijac-Kozica T., **Skuban** M., Pataky T. Selva N (send manuscript) Brown bear mating: linking local (North-eastern Carpathians) and global patterns. Folia Zoologica

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Skuban M, Morbach S (2016) Herdenschutz Der Wolf ist zurück in Bayern. Wie können wir unsere Herden schützen? Gregor Luisoder Stiftung München.

Finďo S., **Skuban M.** (2012): Ako chrániť hospodárske zvieratá proti veľkým šelmám. (How to protect livestock against attacks of large predators?) Carpathian Wildlife Society, in Slovak

Skuban M (2011). Dem Braunbär auf der Spur. Stocker, 330 p.

Keiser S., **Skuban M.** (2011). Den slowakischen Braunbären auf der Spur. ZGF/Gorilla 01/2011. (Tracking Slovak bears), in German

Finďo S., **Skuban M**. (2011): Ochrana hospodárskych zvierat proti veľkým šelmám (Protection of livestock regarding big predators) Chov oviec a kôz, čislo 1 / 2011, p. 30 – 31. In Slovak

Koreň M., Finďo S., **Skuban M**. (2011): Habitat suitability modelling from non-point data. The case study of brown bear habitat in Slovakia, Ecological Informatics

Finďo S., **Skuban M**. (2010): Ungulates and their management in Slovakia. In European Ungulates and their Management in the 21st Century. Apollonio, M., Andersen, R., Putman, R. (Editors), Cambridge University Press, S. 262 – 290.

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Findo S., **Skuban M.**, Fremuth W., Koreň M. (2009). Großsäugerkorridore in der Slowakei. Ein Beitrag zur Schaffung transeuropäischer Wildtiernetze (TEWN). (Corridors of big mammals in Slovakia. A contribution for the Transeuropean Wildlife network) Naturschutz und Landschaftsplanung 41, 9. In German

Finďo S., **Skuban M.**, Koreň M. (2007): Brown Bear Corridors in Slovakia, Identification of critical segments of the main road transportation corridors with wildlife habitats. Carpathian Wildlife Society, Zvolen.