

REVIEW

ECOLOGY OF THE EUROPEAN BADGER (*MELES MELES*) IN THE WESTERN CARPATHIAN MOUNTAINS: A REVIEW

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Abstract

This article summarizes the results of studies on the ecology of the European badger (*Meles meles*) conducted in the Western Carpathians (S Poland) from 2002 to 2010. Badgers inhabiting the Carpathians use excavated setts (53%), caves and rock crevices (43%), and burrows under human-made constructions (4%) as permanent shelters. Excavated setts are located up to 640 m a.s.l., but shelters in caves and crevices can be found as high as 1,050 m a.s.l. Badger setts are mostly located on slopes with southern, eastern or western exposure. Within their territories, ranging from 3.35 to 8.45 km² (MCP100%), badgers may possess 1-12 setts. Family groups are small (mean = 2.3 badgers), population density is low (2.2 badgers/10 km²), as is reproduction (0.57 young/year/10 km²). Hunting by humans is the main mortality factor (0.37 badger/year/10 km²). Regardless of the altitude at which their main sett is located, badgers mostly forage in the foothills, as this climatic zone offers the richest food sources. Badgers mainly eat fruits (54% of biomass consumed) and earthworms (38%), but seasonal and altitudinal differences in diet are observed. Several factors may contribute to the differences between lowland and mountain badger populations, among which climatic zonation, shelter availability, distribution of food resources and human pressure seem to be the most important.

Introduction

Mountains, with their elevational gradients of abiotic and biotic conditions, have often been used as convenient study areas to investigate major issues of biogeography and ecology [1-2]. Numerous studies have revealed a link between altitudinal variation in environmental agents and diversity of species, and these have highlighted factors restricting the distribution of both plants and animals in mountains [3-5]. Organisms

inhabiting higher-elevated areas often morphologically and physiologically differ from their lowland relatives [6-7]. They also develop various ecological adaptations along environmental gradients [8-13], which may influence speciation [14].

The European badger (*Meles meles*), with its vast range stretching across Europe [15-16], occupies a variety of habitats: desert, steppe and forest, as well as agricultural and highly urbanized land [17-20]. Lowland badger populations have been well studied, but despite the presence of this species in all mountain ranges in Europe [21], research on its montane populations have mainly been conducted in the Swiss Jura Mts [22] and higher-elevated regions with a dry Mediterranean climate [23-25]. Until recently, the ecology of badgers in the Carpathian Mountains also remained poorly studied, and few papers, mostly grey literature published in local languages, have focused on their abundance, sett location and diet [26-33].

Here we summarize the results of the latest studies on the utilization of shelters, socio-spatial organization, demography and diet of the European badger in the Western Carpathians (S Poland) [34-37] and compare them with results obtained on the ecology of badgers inhabiting Polish lowland areas.

Study area

We studied the ecology of the European badger in the westernmost part of the Polish Carpathians (Fig. 1), situated near the national borders between Poland, Czech Republic and Slovakia (49°41' N, 19°01' E). The study area (1,039 km²) encompassed fragments of the Beskid Żywiecki Mts, the Silesian Beskid Mts, the Beskid Mały Mts, the Żywiecka Basin and the Silesian Foothills, where the elevation ranges from 245 m to 1,500 m a.s.l. The region is densely inhabited by people, on average 150 individuals/km², but with up to 300 individuals/km² in bigger towns. However, the majority of settlements are located below 600 m a.s.l. in foothills [38].

Local climate varies according to altitude, and may be divided into three major zones: (1) semi-warm (foothills; <670 m a.s.l.), (2) semi-cool (lower montane zone; 670-980 m a.s.l.) and (3) cool (upper montane zone; >980 m a.s.l.). The length of the vegetation season and mean annual temperature decrease with the altitude, while the annual precipitation and length of snow cover increase [39] (Table 1).

Table 1: Characteristics of the three main climatic zones in the Western Carpathians (data after [39]).

Parameter	Climatic zone		
	Semi-warm (foothills)	Semi-cool (lower montane)	Cool (upper montane)
Mean annual temperature (°C)	6-8	4	2
Length of the vegetation season (days)	200-220	170	140
Annual precipitation (mm)	800-1,000	1,400	1,600

Habitats occurring within climatic zones are very contrasting. Primarily, the foothills are overgrown with deciduous forests dominated by oak (*Quercus* sp.), lime (*Tilia* sp.) and hornbeam (*Carpinus betulus*), with alder (*Alnus* sp.) and ash (*Fraxinus excelsior*) being more abundant along watercourses. The forests of the lower montane zone consist mostly of European beech (*Fagus sylvatica*), fir (*Abies alba*) and Norway spruce (*Picea abies*), but Norway spruce gained an advantage over other tree species

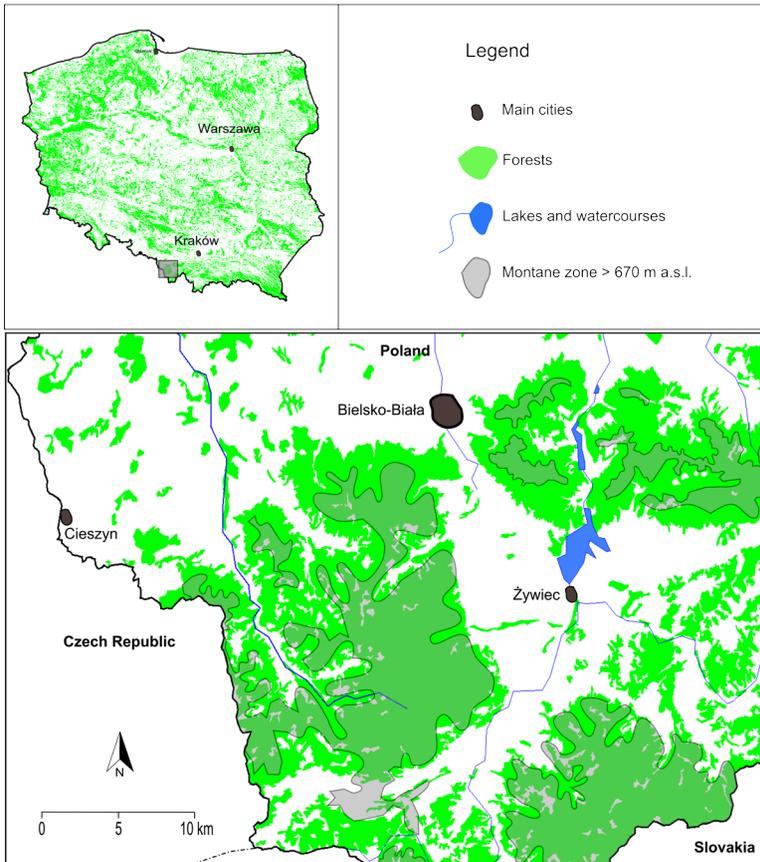


Figure 1: Study area - the Western Carpathians in southern Poland.

in the upper montane zone [40]. Over the last centuries, people have dramatically transformed natural plant formations. Nowadays, the landscape of the foothills mainly consists of agricultural lands and human settlements, while forests cover only 26% of the area. Small patches of deciduous and mixed woods largely occur along watercourses and on hills, where conditions are not favourable for agriculture. The natural forests of the mountain zones were converted into Norway spruce monocultures intensively managed for wood, with patches of artificial mountain meadows used as pastures for livestock. The remains of primeval forests are protected in small nature reserves, which cover less than 1% of the area [41]. At the turn of the 21st century, the majority of mountain meadows were abandoned and spontaneously overgrown with trees and bushes following the decline of sheep grazing [42]. Spruce monocultures, severely affected by droughts and strong winds, as well as fungal and insect parasites, collapsed across large areas [43] and are now being systematically replaced with tree stands of a species composition similar to the natural one [44].

In the Western Carpathians, the European badger coexists with numerous other carnivores: brown bear (*Ursus arctos*), grey wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), Eurasian otter (*Lutra lutra*), red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), stone marten (*Martes foina*), pine marten (*M. martes*), common

polecat (*Mustela putorius*), stoat (*M. erminea*) and least weasel (*M. nivalis*) [45-47]. The European badger is a game species in Poland. The hunting season for this species lasts from 1st September to 30th November, but in hunting grounds inhabited by either Capercaillie (*Tetrao urogallus*) or Black grouse (*Tetrao tetrix*), as is the case in the Western Carpathians, badgers may be killed throughout the year.

Methods overview

We conducted studies on the ecology of the European badger in the Western Carpathians from 2002 to 2010 using a wide array of methods (see [35-37] for further details). We discovered badger shelters during the snow-tracking and radio-telemetry of five individuals, but we also obtained and checked information from local foresters, hunters and naturalists. Setts were classified as main, secondary or temporary, based on signs of use, presence of offspring, and evidence of overwintering. We calculated the badgers' selection of elevation zone, slope aspect and habitat at the sett location using Ivlev's electivity index D , which ranges from -1 (the strongest negative selection) to +1 (the strongest positive selection), with 0 representing random utilisation. We assessed the number of individuals within family groups of badgers through direct observations conducted near setts. In territories in which badgers used more than one sett with a similar intensity, observations were conducted simultaneously near the main hole and one or two secondary burrows.

We calculated the mortality of badgers due to human hunting based on reports from the local hunting grounds. We also assessed wolf predation on badgers by examining wolf faeces collected within the study area. The number of wolf scats containing badger remains was considered equivalent to the number of individuals killed by those predators. We recalculated the data as the number of badgers killed annually per 10 km², taking into consideration the mean wolf territory in the Western Carpathians, which is 120 km² [47].

We radio-tracked five adult badgers (three males and two females) belonging to four family groups. These were captured either using box traps or with stopped chest snares equipped with alarm systems. Captured badgers were immobilized with an intramuscular injection of ketamine hydrochloride, sexed, aged, and fitted with radio-collars (Andreas Wagener Telemetrien-Anlagen, Germany). Marked animals were followed with an antenna (Telonics, USA) and receiver (Yaesu, Japan), and their locations were determined either by triangulation or by direct observation with binoculars (Olympus, Japan) or night-vision equipment (Yukon Advanced Optics Worldwide, Lithuania). Based on radio-telemetry, we calculated individual home ranges and assessed the activity of badgers within altitudinal zones and habitats. We calculated home range size using a minimum convex polygon (MCP100% [48]) and a local convex hull (fixed LoCoH [49-50]). The area of each home range was presented: (1) for the flat surface, without taking into account the terrain and (2) taking into account the factor-corrected mountainous terrain, adopted after Nowak *et al.* [47] from the same study area. We estimated the population density using the following calculation: number of main setts found within the study area * mean number of individuals within the family group, based on direct observations.

We estimated the availability of the potential food resources utilised by badgers

(small terrestrial mammals, amphibians, earthworms, fruits and large ground-nesting birds) using a variety of methods (see [37, 51] for details). Badger diet was assessed based on faecal analysis and results were expressed as the percentage of occurrence and the percentage of biomass consumed by badgers. Ingested food biomass was estimated by multiplying the weight of different food remains in scats by digestibility coefficients. To estimate the biomass of consumed earthworms, 0.1 g of each dried scat was taken for a microscope count of chaetae. The biomass of consumed earthworms was calculated assuming 1,000 chaetae per earthworm and a mean body mass of 2.5 g per earthworm [37].

Review of results

Setts and secondary shelters

In the Western Carpathians, the density of main badger setts was relatively low, namely 0.95 main setts/10 km² [35], which is comparable with lowland Poland where the density was 0.4-1.1 setts/10 km² [52-54]. In the mountains, this species utilized various shelters [35], but the majority of main and secondary setts ($n = 77$) were either excavated dens (53%; Fig. 2) or caves and crevices in rocks (43%; Fig. 3), although burrows under buildings were also recorded (4%). Badgers also used old military bunkers and the ruins of wooden huts as well as piles of planks as secondary shelters [35]. In contrast, in the lowlands of Poland badgers mainly used excavated setts [54]; however, in pristine forests they frequently sought shelter in hollow trees [55].



Figure 2 (left): Sett of European badgers (*Meles meles*) in the foothills of the Western Carpathians, Poland, with a hunting tower erected nearby (Photo by R.W. Mysłajek).

Figure 3 (right): Small cave utilized by European badgers as a main sett in the montane zone of the Western Carpathians, Poland (Photo by R.W. Mysłajek).

In the Carpathians, most setts (64%) were located in the foothills, and 35% in the lower montane zone; setts were recorded sporadically in the upper montane zone. Setts dug directly in soil were situated below 640 m a.s.l. Above this altitude, badgers used caves and rock crevices, due to the shallow soil layer which does not allow for digging. Despite the substantial availability of caves in both lower and upper montane zones, badgers used caves only up to 1,050 m a.s.l., as they were probably discouraged by the severe climatic conditions in higher-elevated areas. Using Ivlev's electivity index D , we determined that, when choosing locations for their setts, badgers slightly

avoided foothills ($D = -0.19$), preferred lower montane zones ($D = 0.32$), and avoided upper montane zones ($D = -0.73$) [35].

Carpathian badgers located their burrows in woods (83%; Ivlev's electivity index $D = 0.70$) or in dense brush (12%), and very rarely in open areas (5%) [35], which is also true for lowland populations [53-54]. Northern slopes were avoided in all altitudinal zones, but badgers readily set up setts on slopes with southern, eastern or western exposure. Permanent shelters were situated closer to main food sources (meadows rich in earthworms), but further away from human settlements and public roads compared with randomly selected points [35].

In the Carpathians and inside the territories of radio-tagged badgers ($n = 5$), we recorded from one to 12 active setts [35], while in lowland primeval forests of north-west Poland badgers possessed on average nine different shelters per territory (range: 4-20) [55]. Individuals that used territories stretched over foothills and lower montane zones possessed setts in both zones, but the overwintering burrows were in all cases located above 800 m a.s.l. The following other species visited or even used badger setts as well: red foxes, grey wolves, Eurasian lynx, martens (*Martes* sp.), domestic cats (*Felis silvestris catus*), domestic dogs (*Canis lupus familiaris*), bank voles (*Myodes glareolus*) and fire salamanders (*Salamandra salamandra*). Also, people visited the vicinity of setts, e.g. for hunting purposes - hunting towers were erected in the vicinity of 8% of setts located in the foothills [35].

Socio-spatial organisation

In the Western Carpathians, badgers lived in small family groups or solitarily. The mean number of individuals in a group was only 2.3 (SE = 0.34, range: 1-5, $n = 16$), including on average 1.7 adults (SE = 0.15, range: 1-3) and 0.16 juveniles (SE = 0.29, range: 0-3) [36]. Badgers utilised large territories (Table 2), the size of which - depending on the method used - averaged 5.42 km² (MCP100%) or 3.27 km² (Fixed LoCoH, $k = 10$) when calculated on the flat map surface. However, the actual territory size, obtained using the correction factor for mountainous terrain (*1.32, see [47] for details), averaged 7.15 km² (MCP100% [48]) or 4.2 km² (LoCoH [49-50]). The home ranges of individuals living in the same family group largely overlapped (87% for two males using one main sett), but also the territories of individuals from neighbouring families could overlap (26% for a male and female from two families). Due to the small number of individuals in family groups and the vast territories, the density of population was low (2.2 badgers/10 km²) [36]. In the lowland forests of NE Poland, badger density was similar (2.1 badgers/10 km²), but the socio-spatial organisation of the population differed in terms of the group size (3.9 badgers per sett, on average) and the extent of individual home ranges, the mean size of which was 9.3 km², with a range from 4.0 to 24.4 km² [17].

In the Carpathians, offspring (Fig. 4) were recorded in only one-fourth of all badger family groups annually, thus reproduction was on average 0.57 badger/year/10 km². Among mortality factors, hunting pressure seems to be the most important. Annually, hunters killed 0.37 badger/10 km², which equated to 65% of the mean reproduction rate. Surprisingly, the estimated impact of wolf predation was very low, namely 0.07 badger/year/10 km² [36]. In Białowieża Primeval forest, NE Poland, the mean annual productivity of the population was 64%, while the average annual mortality was 22-38%, with car accidents being an important mortality factor [17].

Table 2: Home-range size of radio-tracked badgers in the Western Carpathians (data after [34, 36]). Correction for the montane terrain following the procedure proposed by [47]. MCP100% - minimum convex polygon with 100% of locations [48]; LoCoH - fixed local convex hull, $k = 10$ [49-50].

Badger	No of radio-locations	Standard home range size (km ²)		Home range size corrected for mountain terrain (km ²)	
		MCP100%	LoCoH	MCP100%	LoCoH
F-1	35	5.93	4.41	7.83	5.82
F-2	30	3.35	2.98	4.42	3.93
M-1	108	5.25	2.74	6.93	3.62
M-2	93	8.45	3.20	11.15	4.22
M-3	214	4.11	3.03	5.43	3.40
Mean	96.00	5.42	3.27	7.15	4.20
(± SE)	(± 33.28)	(± 0.88)	(± 0.29)	(± 1.16)	(± 0.43)



Figure 4: Young European badger in a small cave in the montane zone of the Western Carpathians, Poland (Photo by M. Figura).

Food habits

Carpathian badgers are omnivores that eat a large variety of plants and animals, ranging from grains, fruits and invertebrates to fish, reptiles, small rodents, insectivores, large ungulate carcasses. Nevertheless, badgers focused on vegetable matter (mainly fruits) and earthworms, which respectively constituted 54% and 38% of the biomass consumed annually. Mammals only accounted for 6%, and insects for 1% of food biomass. Diet varied according to season and altitude. In spring, badgers foraged mostly on earthworms, while in summer and autumn, they essentially relied on fruits (Fig. 5). Consumption of mammals substantially increased with altitude - 3% and 14% of food biomass in foothills and mountain zones, respectively [37]. Studies conducted in three localities across various habitats of lowland Poland revealed that in spring earthworms constituted over 80% of the biomass consumed by badgers, while in summer and autumn their importance decreased to 56% in pristine forests and down to 24% in mosaics of forests and agricultural lands. Lowland badgers supplemented their diet with amphibians and fruits [56].

There were dramatic differences in the availability of the badger's most important food sources among the foothills and mountain zones [37, 51]. Both earthworms and fruits were much more abundant below 670 m a.s.l. So, despite the location of main setts at various altitudes, all individuals mainly foraged in the foothills. Badgers

readily searched for food in meadows, pastures and arable fields (34% of telemetry locations) and among bushes on the banks of watercourses and in field verges (34%). However, while in spring badgers mostly foraged in meadows and pastures, in autumn and spring switched to shrubs and orchards [36].

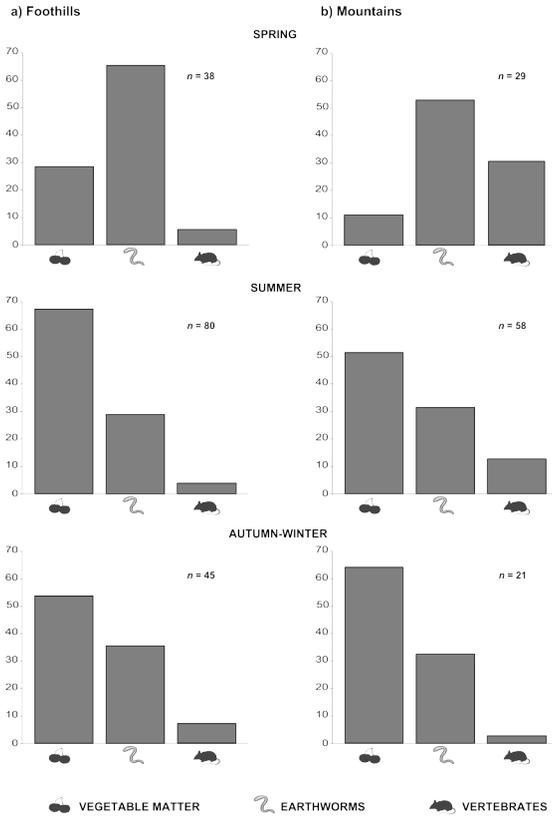


Figure 5: Seasonal and elevational differences in the consumption of main food sources (vegetable matter, earthworms and vertebrates) by the European badger in the Western Carpathians, Poland. Values are given as the percentage of biomass consumed. Data after [37].

Discussion

European badgers inhabiting mountains have to deal with numerous environmental constraints, e.g. a thin soil layer preventing excavation of setts or harsh climatic conditions shortening the vegetation season. However, recent studies have shown that badgers are able to develop various ecological and behavioural adaptations enabling them to inhabit less hospitable environments [57-59]. Instead of proper setts, usually dug in lowlands, mountain badgers occupy caves and rock crevices [29, 35, 60-62] and readily use various man-made structures, such as buildings or concrete constructions [32, 35, 63]. In locating shelters on southern, eastern and western mountainsides, they may benefit from a better sun exposure increasing the temperature and shortening the length of snow cover [27-29, 35, 63].

Badgers that use setts at higher elevations may overcome shortages of food in the mountains [37, 51, 64-66] by foraging in areas located at lower elevations, e.g. in the foothills [36]. As omnivores, they easily adapt to those food sources, which are locally abundant. In most European mountains, such as the Alps, Swiss Jura Mts, Subbetic Mts and Carpathians, badgers mostly eat plant food, although earthworms may also be an important food source, at least seasonally [22, 37, 65-69]. In higher parts of the mountains, mammals also become a key element of the badger diet [37, 65].

In mountainous conditions, European badgers live in small family groups and utilize vast territories, which results in low population densities [22, 30, 36, 60, 70]. Several factors may affect population parameters, e.g. availability of shelters, distribution and abundance of food resources, predation and hunting [36], and the importance of individual factors may vary spatially and temporally. Recent changes in the climate caused by global warming [71-72] raise questions about their significance for the mountainous populations of badgers. Climatic conditions may influence the badger physiological parameters [73-74], as well as the quality of their environment [75]. In semi-arid southern regions of Europe, badger abundance could be reduced due to a worsening of their habitat [76]. Conversely, in the Scandinavian Peninsula, badgers have extended their range, likely due to long-term improvement of the climate [77-78]. In the last decades, climatic conditions in the Western Carpathians have changed, causing a reduction of cold climatic zones and an extension of warmer ones [79], and these phenomena will become more pronounced in the coming decades [80]. In our opinion, mountains may serve as natural “laboratories” enabling scientists to understand the impact of climate change on animal ecology and behaviour. So, we urge the development of further research projects on populations of European badger and other species living in montane habitats.

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