

Environmental drivers of the distribution and density of the European badger (*Meles meles*): a review

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Abstract: Knowing the environmental factors affecting species' distribution is an important basic step in ecological research. Here, we present a literature review on the environmental factors influencing European badger (*Meles meles*) distribution and density. According to the published literature, the badger is a highly adaptive species, capable of using different environmental services and adapting to different conditions. However, when studying badger populations across their distribution, a general pattern of preferred environmental characteristics and influencing factors arises. These environmental characteristics may indicate the badger's realised niche and may potentially give an approximation of its fundamental niche. A combination of environmental factors favouring both sett (burrow) location and food availability appears to drive local badger success: terrain characteristics (both suitable soil type for sett excavation and terrain heterogeneity for visual hiding), wood coverage and earthworm-rich grassland. The presence and density of badgers vary depending on the geographic study area and the relative importance of these specific environmental drivers. We discuss how these insights can assist spatial modelling studies, conservation and management, and future research on habitat suitability and badger density. We stress that more research is needed to understand how each component of the life cycle of badgers is affected by environmental drivers, and what the cumulative effect is on their spatial population dynamics.

Key words: environmental factors, European badger, fundamental niche, *Meles meles*, occurrence, review, sett.

Introduction

The European badger (*Meles meles*) is present in almost all European countries, from the British Islands eastwards to the west bank of the River Volga (figure 1). The species belongs to the family of Mustelidae, in the order of Carnivora. Recent studies showed that the genus *Meles* includes several distinct species, while this was considered only one species in the past, the Eurasian badger. Accordingly,

the European badger is now described as a distinct species from the Asian badger (*Meles leucurus*) and the Japanese badger (*Meles anakuma*) (Abramov 2001, 2003, Wozencraft 2005, Abramov & Puzachenko 2005, 2006). The Asian badger occurs from the east of the Volga River to China and Korea, till the border of the distribution of the European badger throughout the Lower and Middle Volga and the interfluves of the Volga and Kama (Abramov & Puzachenko 2006). A clear geographic border in the northern Caucasus between *Meles leucurus* and *Meles meles* has not yet been clearly defined, as they

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Figure 1. Distribution range of the European badger (*Meles meles*), based on the distribution maps of Del Cerro et al. (2010) and Abramov & Puzachenko (2013).

can occur sympatrically and may even reproduce, giving hybrids with mixed characters (Abramov & Puzachenko 2007). The Japanese badger occurs on the Japanese Islands (Baryshnikov et al. 2003). Finally, Del Cerro et al. (2010) provide evidence for a fourth species of badger named *Meles canescens*, distributed in South-West Asia, from south of the Caspian sea and the Northern Caucasus to Tajikistan. The taxonomic status of the badger nowadays admits therefore four distinct species (Abramov & Puzachenko 2013).

The European badger is a generalist, highly adaptive, species which is capable of exploiting a wide variety of habitats (Feore & Montgomery 1999, Kauhala & Auttila 2010). It is only absent from arctic zones, high altitude regions and some islands (Griffiths & Thomas 1993). Analyses of the dynamics of an English population have shown that badgers start

breeding at an age of two years, that annual juvenile survival (63%-77%) is lower than adult survival (76%-88%), giving a generation time of 5.8 years, and that by an age of 7.3 years an average female has contributed half of what she is going to contribute (through reproduction) to population growth in her life (Macdonald et al. 2009, van de Kerk et al. 2013). See figure 2 for a graphic representation of the badger's life cycle based on the study of Macdonald et al. (2009).

The European badger is relatively abundant in Europe, being only uncommon or present in lower densities in the Netherlands, Belgium, Estonia, Slovakia and Poland (Kranz et al. 2008). Nevertheless, there is a general concern about this species because it has showed strong fluctuations in numbers in many countries in the last century (Griffiths & Thomas 1993). In the 1970s and 1980s badgers obtained

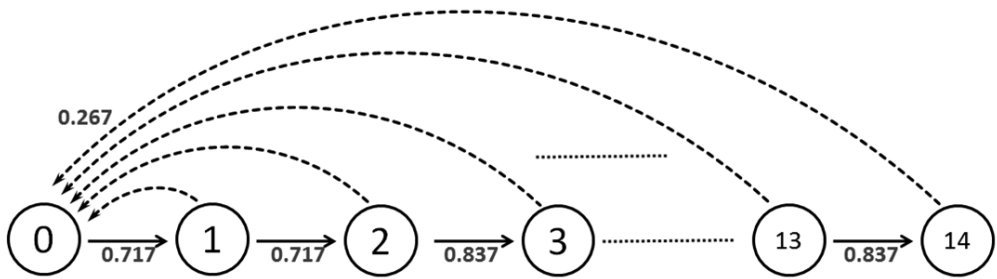


Figure 2. Matrix projection model for a European badger population near Oxford (Macdonald et al. 2009), based on post-breeding census data. The first stage therefore represents newborn cubs (zero-year olds). The population model consists of five parameters: age of first reproduction (2), age of last reproduction (15), juvenile survival (0.717), adult survival (0.837), and fertility (0.267).

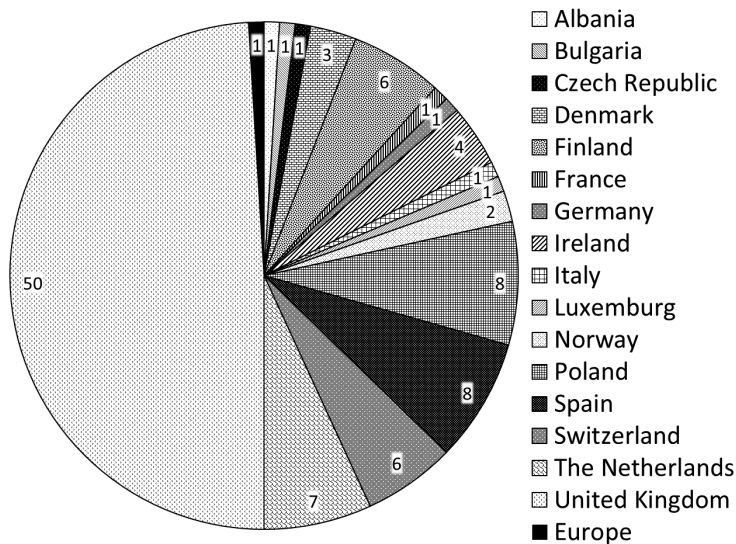


Figure 3. Countries where the studies containing data relevant to the search topic were performed, i.e. the factors influencing distribution and density of the European badger as presented in this review.

a protected status in Britain, Ireland, Spain, Portugal, Italy, Belgium, the Netherlands, Albania, Greece, Estonia, Luxemburg and Hungary (Griffiths 1991b). In 2008 the species was ranked as Lower Risk/Least Concern on the European Red List (Baillie & Groombridge 1996, Kranz et al. 2008), which means that protection had positive results. With its history as a threatened species it is an interesting object to formulate and study policy recommenda-

tions. Therefore, knowledge is required about the environmental factors driving the distribution and density of badger, which makes it possible to quantify habitat requirements, weighing management options, and assessing the impact of habitat change. In broader ecological studies, it is also of great importance to know the interaction of the species of interest with its environment in order to situate the species in the ecosystem, its used niche and so on.

Table 1. Main environmental drivers of badger spatial population dynamics.

Environmental driver	Components	Contribution	Potential effect on	Effect	Literature
Climate	Rainfall range	Higher seasonality	Badger presence, spatial organisation, population size and density and group size.	Negative	1–3
	Temperature range	Higher seasonality		Negative	
	Rain, temperature between 5–15°C and high air humidity	Favours earthworm availability.		Positive	
Terrain characteristics and sett site availability	Cold winters, dry summers and wind	Decreases earthworm availability.	Badger presence, size and shape of occupied territory and spatial organisation.	Negative	9
	Spring rainfall and high temperature	Increase cub parasitic susceptibility.		Negative	
	Suitable geology	Facilitates digging and drainage.		Limiting factor	
	Slope	Favours earth removal.			
Aspect	Selection of sites on south to west-facing slopes.				
Habitat type	Terrain heterogeneity	Visual hiding	Population density, group size and territory size.	Positive	1, 4–5, 10–15, 23–32
	Vegetation cover or small landscape elements	Visual hiding			
	Groundwater level	Sett building			
	Abandoned old setts	Possibility for recolonisation			
	Presence of habited setts	Induces construction of new setts.			
	Woodland	Offers cover, shelter, structural support for sett building and additional source of food items.			
	Hedgerows and scrub	Cover and shelter			
	Grassland and pasture	Foraging, source of earthworms. Short grass is more suitable.			
	Arable fields: e.g. maize, wheat, barley	Food source: cultivated food and earthworm content.			
	Food availability	Large variety of items: e.g. earthworms, other invertebrates, birds' eggs and chicks, rodents, carrion, fruits, cereals			

Built-up areas	Urban infrastructure	Decreases sett site availability. Habitat destruction. Fragmentation.	Badger presence, density and spatial organisation.	Negative	26–27, 44–48
	Human population density. Agricultural land	Disturbance on habitat. Habitat destruction. Fragmentation.	Population size and density. Badger presence and spatial organisation. Population size and density.	Negative Negative	
	Urban and industrial areas Roads	Provide anthropogenic food sources. Increase mortality. Habitat destruction. Fragmentation and disturbance.	Population size and density. Badger presence and spatial organisation. Population size and density.	Positive Negative	10, 14 14, 26, 45–55
Interspecific competition	Mainly <i>Vulpes vulpes</i> , <i>Nyctereutes procyonoides</i> but also other Carnivora.	Competition for sett sites and food.	Distribution, population size and density.	Potentially negative, but mostly neutral	4, 2, 6, 56–71
Purposeful killing	Allowed or regulated hunting and poaching.	Increases mortality.	Population size and density. In the most severe cases also distribution.	Negative	5, 72–75
Diseases and para-sites	Especially bovine tuberculosis (TB)	Increases mortality and triggers poaching.	Population size and density. In the most severe cases also distribution.	Negative	76–84
	Other diseases (e.g. rabies) and para-sites	Increases mortality.			85–88

Literature: 1. Virgós & Casanovas 1999a; 2. Kauhala 1995; 3. Johnson et al. 2002; 4. Kruuk 1989; 5. Kruuk 1978; 6. Griffiths & Thomas 1993; 7. Gerard 1967; 8. Bouché 1977; 9. Macdonald et al. 2010; 10. Huck et al. 2008; 11. van Apeldoorn et al. 2006; 12. da Silva et al. 1993; 13. Thornton 1988; 14. Skinner et al. 1991a; 15. Matyáščík & Bičák 1999; 16. Doncaster & Woodroffe 1993; 17. Neal 1972; 18. Neal 1986; 19. Broseth et al. 1997; 20. Macdonald et al. 1996; 21. van Moll 1999; 22. Roper 1992; 23. Feore & Montgomery 1999; 24. Hofer 1988; 25. Palphramand et al. 2007; 26. van der Zee et al. 1992; 27. Schley et al. 2004; 28. Jepsen et al. 2005; 29. Kowalczyk et al. 2000; 30. Palphramand et al. 2007; 31. Kruuk et al. 1979; 32. Kruuk & Parish 1977; 33. Kowalczyk et al. 2006; 34. Kruuk & Parish 1982; 35. Andersen 1954; 36. Neal & Cheeseman 1991; 37. Macdonald & Barrett 1993; 38. Kruuk & Parish 1981; 39. Kruuk & Parish 1985; 40. Henry 1984; 41. Lups et al. 1987; 42. Boyle & Whelan 1990; 43. Martin-Franquelo & Delibes 1985; 44. Wright et al. 2000; 45. Aaris-Sørensen 1987; 46. Skinner et al. 1991b; 47. Mader 1984; 48. van Apeldoorn et al. 1998; 49. Bennett 1991; 50. Clarke et al. 1998; 51. Vink et al. 2008; 52. Dekker & Bekker 2010; 53. Davies et al. 1987; 54. Harris et al. 1995; 55. Lankester et al. 1991; 56. Macdonald 1987; 57. Macdonald et al. 2004; 58. Neal and Cheeseman 1996; 59. Fedriani 1993; 60. Kowalczyk et al. 2008; 61. Drygala et al. 2010; 62. Oerlemans & Koene 2008; 63. Goszczynski 1999; 64. Kauhala & Auttila 2010; 65. Kauhala & Holmala 2006; 66. Jedrzejewska & Jedrzejewski 1998; 67. Martin et al. 1995; 68. Palomares & Delibes 1997; 69. Macdonald 2009; 70. Delibes & Calderón 1979; 71. Fedriani et al. 1999; 72. Grigorov 1987; 73. Cresswell et al. 1990; 74. Bego 1992; 75. Griffiths 1991a; 76. Gormley & Costello 2003; 77. Olea-Popelka et al. 2003; 78. Krebs et al. 1997; 79. Gallagher & Clifton-Hadley 2000; 80. Griffin et al. 2005; 81. Donnelly et al. 2003; 82. Woodroffe et al. 2006; 83. Dolan 1993; 84. WHO 1978-99; 85. Artois et al. 1991; 86. Schwierz & Wachendörfer 1981; 87. Harris & Yalden 2008; 88. Anwar et al. 2000.

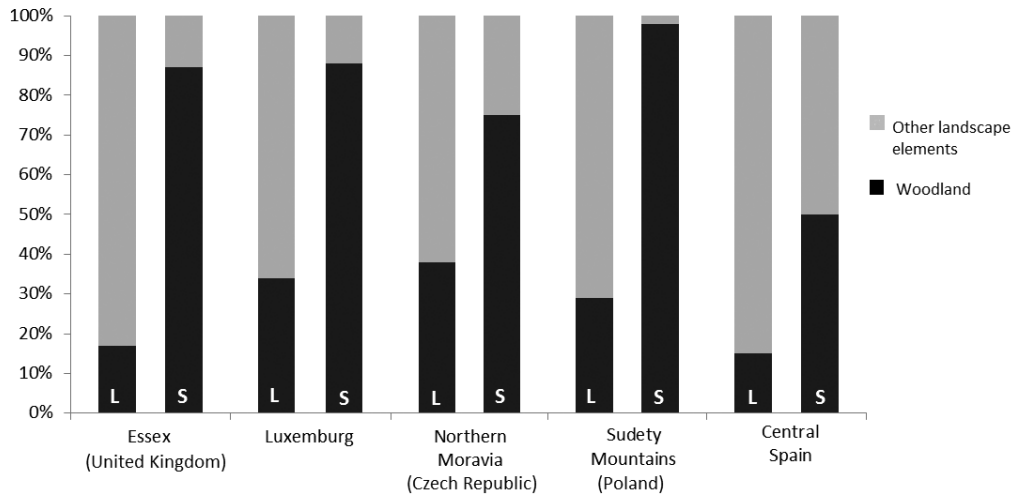


Figure 4. European badger sett site selection for either woodland or other landscape elements. Each pair of columns shows the results, respectively, from ecological studies in Essex (United Kingdom, Skinner et al. 1991a), Luxemburg (Schley et al. 2004), Northern Moravia (Czech Republic, Matyáščík & Bičík 1999), Sudety Mountains (Poland, Bartmańska & Nadolska 2003), and central Spain (Virgós & Casanovas 1999a). The first column shows the percentage of woodland present in the studied landscape (L). The second column shows the percentage of setts (S) located in woodland.

Methods

For this review we searched the ecological literature for information about the factors affecting badger distribution and density all around Europe, thus covering all different environments that this animal inhabits. We used the Web of Science and the search engine Google Scholar. The search terms were combinations of “European badger”, “*Meles meles*”, and “habitat”, “preferences”, “selection”, “environmental factors”, “drivers”, “distribution”, “occurrence”, “density”, “affect population”, “niche”, “sett”. Most of the search was focused on papers published in English and the search terms were always in English. However, some data were found in publications in other languages such as Spanish, French and Dutch. The time range of the collected findings is from 1970 until present. We use this time frame first because badger populations across Europe had started to fluctuate from around the early 1970s, mainly due to direct or indirect human pressure (Grif-

fiths & Thomas 1993), often becoming endangered, and of global concern and thus ecological studies on this species started to increase. Therefore, more data is available from then on. Moreover, due to the rapid landscape change all around Europe, studies performed before these dates may not be applicable nowadays. All factors that were reported to influence the spatial population dynamics of the badger, from habitat composition to resources availability and abiotic and biotic interactions, are subsequently presented and discussed. We organised the driving factors in several categories. First we present the abiotic factors in the landscape: climate factors (such as temperature and meteorology), terrain characteristics and factors determining badger sett (burrow) site availability (such as soil characteristics, slope and orientation and groundwater level), habitat composition (such as land use factors and landscape elements), and finally food and food availability. Subsequently we analysed anthropogenic factors: built-up areas and human density, roads and

hunting. Finally we present the biotic factors such as interspecific competition, diseases and parasites.

Results

We found 96 studies from 18 different European countries providing relevant information on the research topic. The UK had the most performed studies (50 containing data presented in this review), followed by Poland (8), Spain (8), the Netherlands (7), Finland (6) and Switzerland (6) (figure 3).

In the following sections we present an overview of the most important factors we found determining the distribution and density of badgers (see also table 1).

Climate

Climate is the best explanatory factor of badger occurrence in different countries, e.g. in Spain (Virgós & Casanovas 1999a) and in Finland (Kauhala 1995). Across Europe, Johnson et al. (2002) demonstrated that badger group size decreases with rainfall range and that badger density is negatively correlated with temperature range (difference between maximum and minimum temperature).

Hence, badgers are more abundant in rainy regions, as rain favours the presence of earthworms in the soil (Kruuk 1989, Griffiths & Thomas 1993). Climatic conditions are known to be important for earthworm availability especially during the night, when worms come to the surface and badgers can forage on them (Gerard 1967, Bouché 1977). Temperatures between 5-15 °C and high air humidity have a positive influence, while cold winters, dry summers and wind negatively influence the presence of earthworms (Kruuk 1978). Thus, climatic factors can affect badger populations indirectly by influencing earthworm availability.

In the United Kingdom, Macdonald et al. (2010) showed that seasonality, through a

variation of temperature and rainfall, has a complex influence on badger populations. Late-summer low temperatures and rainfall have a significant positive influence on badger survival, as cool and moist conditions favour earthworm availability on the soil surface. On the other hand, spring rainfall and temperature negatively influence badger populations as wet and warm conditions lead to higher parasite susceptibility of the cubs. Finally, colder winters generally result in badgers staying underground and this reduced activity has a positive effect on survival due to fewer badgers being hit by cars.

Terrain characteristics and availability of potential sett sites

Location suitability for sett building may determine the size and shape of badger occupied territory (Doncaster & Woodroffe 1993) and spatial organisation within a region (da Silva et al. 1993). A good sett site requires a suitable soil to facilitate digging and drainage, such as sandy soils, in combination with some gradient and vegetation cover (Neal 1972, Neal 1986, Thornton 1988, Skinner et al. 1991a, Good et al. 2001, Fischer & Weber 2003). Not only the presence of gradient but also orientation of the slope is an important factor influencing sett location. This was an important driver of sett site selection in Essex, Norway and Northern Moravia: south to west facing slopes were preferred most (Skinner et al. 1991a, Broseth et al. 1997, Matyáščík & Bičík 1999). On the other hand, it has also been shown that badgers prefer terrain heterogeneity independently of slope orientation (Thornton 1988, Macdonald et al. 1996). Groundwater level can also be relevant for sett excavation, as it is impossible to dig a sett when the groundwater level is too high (van Moll 1999). Therefore, in grounds with high groundwater levels, this will be a constraint.

Hence, the location of badger setts is selected according to the presence of favour-

able conditions, which results in an heterogeneous distribution of setts in an area (van Apeldoorn et al. 2006). Abandoned old setts can be suitable for badger recolonisation, and the presence of inhabited badger setts also positively influences the construction of new setts (Roper 1992).

Habitat composition

Besides terrain topography, the type of habitat (e.g. woodland, shrubs, pastures) also affects badgers. Feore & Montgomery (1999) showed a preference of badgers for sett sites at or near the interface of two habitat types, especially woodland or shrubs with pasture. Huck et al. (2008) found that habitat type was the most important factor explaining sett location in urban areas: the presence of wood and scrub mattered more than soil conditions and food availability.

In the Netherlands, Apeldoorn et al. (2006) found in a local study on habitat use and composition (between the towns of Utrecht and Hilversum) that pastures were the main drivers of badger distribution due to the provision of food, followed by broadleaf forest which was preferred for digging setts, mixed forest and maize fields. They also found badger setts specifically located near the edge of the forest, close to the grasslands and arable fields. The presence of water was also important for badger inhabitation. This suggests that this habitat mosaic was selected to enhance both sett building and food searching.

In England, the reproduction and weight of badgers were higher in deciduous woodland than in any habitat type, such as pasture (da Silva et al. 1993). This was a paradoxical finding as pasture contains a higher biomass of earthworms (Kruuk 1978, Hofer 1988), which are one of British badgers' main food item. The higher weight of badgers in woodlands may have been the result of providing an additional source of food items (e.g. carrion, blackberries and acorns), humidity

and protection from the wind (da Silva et al. 1993). Also in the United Kingdom, coniferous woodland appeared to be more important than previously thought. The positive effect of woodland on the badger population is likely due to the fact that woodland constitutes a refuge from human activity and provides structural support for the construction of setts within the root system (Palphramand et al. 2007).

Woodland is in fact strongly preferred by badgers for sett location and therefore strongly influencing badger density (figure 4). In England, wood density in the landscape was positively correlated with sett density (Thornton 1988), which is taken as representative of badger density in most studies. This effect was especially important in more open landscapes in the Netherlands (van der Zee et al. 1992). In Essex (United Kingdom), even when 73% of the country is covered by arable and pasture land, 87% of all setts were located in woodland, hedgerows and scrub (Skinner et al. 1991a). In Luxemburg 88% of setts were located in forest while only 34% of the land is covered by forest (Schley et al. 2004). The most preferred forests were conifer and deciduous forest (38% of total setts each), followed by mixed forest (12%). The other habitats with setts were shrub (5%), hedgerow (3%), grassland (2%) and arable soil (0.3%).

In Northern Moravia (Czech Republic), woodland was also the most preferred habitat for sett construction, as 75% of setts were located in this habitat type (Matyáščík & Bičík 1999). The most frequented habitat was mixed forest (33%), followed by coniferous and deciduous forests (26% and 16% respectively). Other setts were located in habitats with rocks (11%) and only 6% in fields. In the Polish Sudety Mountains badgers show a very strong preference for woodland when building their setts, as 98% of setts were found in woodland, and only 2% in the open areas, although forests cover only 29% of the mountains (Bartmańska & Nadolska 2003). Of the setts located in woodland, 57% were found

in deciduous and mixed forests, and 43% in coniferous forests. In a study in central Spain there was also a clear preference for wooded places, as 50% of setts were located at sites with >50% tree cover (Virgós & Casanovas 1999b). In Denmark forest cover, together with terrain heterogeneity, were the most important explanatory variables for sett presence using species distribution modelling (Jepsen et al. 2005). Variation in wood cover explained 22% of the total variation in badger sett densities in Białowieża Primeval Forest in Poland (Kowalczyk et al. 2000).

Small landscape elements like hedgerows, orchards and small patches of woodland offer coverage and favour badger sett location, especially in agricultural land (Neal 1972, Thornton 1988). These small landscape elements, however, have been removed to create larger fields for agriculture in many regions, which might negatively influence badger populations (Thornton 1988).

Food and food availability

Badger territory size and density of setts in the landscape are mainly shaped by food abundance and availability (Kruuk 1989, Kowalczyk et al. 2000). In areas with low or dispersed food sources badgers move longer distances, cover larger daily ranges and defend larger territories (Kowalczyk et al. 2006). Anyhow, badgers behave as contractors, which means that they keep a minimum territory where they can find just the sufficient resources (Kruuk & Macdonald 1985). The mean size of group territories strongly differs between European regions, from 0.14 km² in the open habitats of the British Isles (Cheeseman et al. 1981) to 25 km² in the continuous woodlands of Poland (Kowalczyk et al. 2003). The amount of food available in the territory also strongly influences the number of individuals and group size in badger populations (Kruuk & Parish 1982). Therefore it is important to know the common food sources of this species.

The European badger's diet is very variable. This species is the most omnivorous mustelid, an opportunistic forager that takes a large variety of animal and plant food sources, such as earthworms and other invertebrates, birds' eggs and young, rodents, carrion like road kills, fruits, bulbs, acorns, oats and wheat (Andersen 1954, Neal & Cheeseman 1991, Macdonald & Barrett 1993). In temperate areas in Europe, like the British Islands, earthworms are the main food source for badgers (Kruuk & Parish 1981, 1985, Henry 1984, Lüps et al. 1987, Boyle & Whelan 1990). But in drier regions, such as Spain, earthworms are not always available and badgers specialise more in lagomorphs, mainly rabbits (*Oryctolagus cuniculus*), and some fruits such as olives and also arthropods (Barea-Azcón et al. 2001).

In temperate regions, the main food items for badgers consist of earthworms, especially *Lumbricus terrestris*, the whole year and maize from arable fields during autumn and winter (van Apeldoorn et al. 2006). As a main food source, the abundance of earthworms can strongly influence badger populations. Indirectly, the presence of earthworms and the distribution of earthworm patches have also been shown to affect the number of badgers in a social group, the spatial organization (Kruuk & Parish 1982) and the configuration of badger territories (Hofer 1988). Earthworms are common in pasture and old forest. Acidity of grassy peatlands and forested sandy soils lead to low earthworm biomass densities, which results in poor conditions for badgers. In Oxfordshire (England), grasslands and broadleaf forests were proven to offer relatively good food conditions, while mixed and coniferous forest offered worse food conditions (Kruuk 1978, Hofer 1988, da Silva et al. 1993).

In England, barley, wheat and acorns were shown to be secondary food items. Other food sources eaten by badgers were insects, pig-nuts, small mammals, birds, amphibians, carrion, etc. (Kruuk & Parish 1982). When feed-

ing from cereals, badgers preferred wheat and oats to barley (Kruuk 1989).

In the United Kingdom, territory size was found to be negatively correlated with grassland proportion (Palphramand et al. 2007), but it was positively correlated with the number of grassland patches. This suggests that grassland is a key resource for badgers, likely because it constitutes a source of earthworms. However, grassland influence depends on the length of grass. Long grass was shown to be unsuitable for badgers (Kruuk et al. 1979). Badgers visit grasslands especially to forage for earthworms (Kruuk & Parish 1977), and catching them is much easier in short grass. A thick soil cover, such as dead litter and vegetation, might also be more difficult to forage on earthworms.

Type and amount of crops and grasslands might therefore be important for badger populations, as they directly provide various food sources. Changes in agricultural land strongly affect earthworm biomass (Edwards & Lofty 1977, Kruuk 1978, Eijsackers 1983, Lofs-Holmin 1983) and can hamper earthworm availability, having a negative impact on badger populations.

Built-up areas and human population density

Many studies have found a negative correlation between human population density and badger sett density (e.g. Schley et al. 2004) and also between urbanised area and sett density (Wright et al. 2000). Urban areas, roads and agriculture have been responsible for badger population decline and distribution contraction throughout most of their geographic range (e.g. Aaris-Sørensen 1987, Skinner et al. 1991b). These factors lead to habitat fragmentation, reducing the suitable habitat to small unfavourable isolated patches (Mader 1984, van Apeldoorn et al. 1998), which can no longer support sustainable badger (sub) populations.

However, the anthropogenic transformation of the landscape may not always have a negative impact on badger populations. As demonstrated in Switzerland (Do Linh San et al. 2011), an increase of agricultural landscape provides an additional food source and badgers profit from this human-made food rich habitat by adopting cereals and maize as a main food item.

In the United Kingdom, Huck et al. (2008) showed that badgers are capable of establishing relatively dense populations in urban environments. These provide some advantages in providing anthropogenic food sources. In Essex 15.9% of setts were indeed found in urban and industrial areas, likely due to badgers avoiding agricultural land and searching for human-generated food (Skinner et al. 1991a).

Roads

Roads may affect the distribution and population size of badgers in three different ways: 1. They constitute a barrier for badger movement and dispersion causing habitat fragmentation. 2. They increase badger mortality through traffic kills, and 3. They decrease badger colonisation by producing disturbance by higher human activity and traffic noise (Bennett 1991, Clarke et al. 1998).

The increase in number of roads and their use was the major factor causing the historic decline in the badger population in the Netherlands (van der Zee et al. 1992) and is the main cause of badger mortality nowadays in this country (Vink et al. 2008). In the Netherlands, every year 10–20% of the total badger population is killed on roads, mainly in March and less in the winter months. Per km of road most mortalities occur on provincial roads (Dekker & Bekker 2010). Mitigation measures have been shown to reduce mortality of badgers (Vink et al. 2008, Dekker & Bekker 2010). These include construction of passages and fences, reducing speed limits

and closing critical roads.

In England, traffic is also the major reason for badger mortality, causing 49% of all mortalities (Davies et al. 1987, Harris et al. 1995). In Surrey and Gloucestershire the impact of road kills was even more dramatic: 59% and 66% respectively (Clarke et al. 1998). Road kills in England show a strong seasonal variation, with peaks in mortality occurring in spring and late summer (Davies et al. 1987). The relationship between road mortality and traffic load was found to be parabolic (Clarke et al. 1998), possibly because badgers are discouraged to cross the busiest roads (van der Zee et al. 1992). Therefore, major roads may have mixed effects: a higher impact on badger movements increasing the fragmentation effect of roads (Lankester et al. 1991), but a lower number of road kills as fewer badgers attempt to cross such busy roads.

In Essex, sett density was significantly influenced by road type and distance to roads. The busiest roads were clearly avoided: significantly fewer setts than expected were found within 10 m of a road than at 100–999 m from a road (Skinner et al. 1991a). The size of the badger population was also negatively correlated with road and traffic densities (Skinner et al. 1991b).

Hunting

Hunting of badgers was a real threat for badger populations all around Europe before protection policies were established. Hunting of badgers was a cause of population decline for instance in Albania (Bego 1992), Bulgaria (Grigorov 1987) and the United Kingdom (Cresswell et al. 1990). Nowadays, hunting of badgers is either strictly regulated or forbidden in the European countries where this species is protected: the United Kingdom, Ireland, the Netherlands, Denmark, Belgium, Italy, Greece, Spain, Portugal, Luxemburg, Hungary, Estonia and Albania (Griffiths & Thomas 1997). Nonetheless, in other Euro-

pean countries such as Poland (Mysłajek et al. 2012), this animal is still seen as a small-game hunting target or as a pest. This shows that badgers are perceived very differently within Europe (Griffiths 1991a). In most of the countries where hunting is allowed, this is prohibited during the reproductive season (Griffiths & Thomas 1993), but some countries offer very poor protection from hunting, such as Finland and Austria, or no protection at all, such as Bulgaria and Macedonia (Griffiths 1991a). In France and Germany hunting is popular but appears not to be a major threat (Keuling et al. 2011, FDC 2014). Compared to other mammalian game species, only in Sweden, Switzerland and Norway the numbers of badgers legally hunted surpassed 4% of the most popular mammalian game species (Griffiths & Krystufek 1993).

Nonetheless, poaching seems to be a threat to badger populations all around Europe (Griffiths & Thomas 1993), especially in the United Kingdom and Ireland (Cresswell et al. 1989, Smal 1995). Illegal hunting prevents the badger population in Albania to recover (Bego 1992). In summary, hunting may endanger badger populations in countries where it is still allowed or seasonally allowed or where it is practised illegally. For this reason the Council of Europe (1987) has asked all countries that allow hunting of badgers to take measures to protect their stocks.

Interspecific competition

Red fox (*Vulpes vulpes*) is a potential competitor of badger for food and sett sites because it occupies a similar ecological niche (Macdonald 1987, Kruuk 1989). Nevertheless, both species can apparently cohabit the same area. Aggressive as well as peaceful encounters have been reported (Neal & Cheeseman 1996), but most encounters are not significantly violent and badgers take the dominant role (Macdonald et al. 2004). The two species have even been found sharing the same sett (Macdonald

1987, Fedriani 1993).

The raccoon dog (*Nyctereutes procyonoides*) is an invasive species from Russia which has already successfully colonised many north-eastern European countries, including Finland, Norway, Germany and Poland (Kauhala 1995, Kowalczyk et al. 2008, Drygala et al. 2010) and the species is likely going to inhabit and quickly increase in other countries such as the Netherlands in the near future (Oerlemans & Koene 2008, Mulder 2012, Mulder 2013). This species is also a potential competitor for badgers for food and sett sites. Both species are omnivorous and though raccoon dogs do not construct burrows themselves, they often inhabit badger setts for reproduction and wintering (Goszczyński 1999).

Still, despite this ecological overlap, the rapid invasion and growth of the raccoon dog population in Finland has not been found to have a negative effect on the native badger population (Kauhala 1995). They have been sympatric for more than 50 years and both species increased in number during this period (Kauhala & Auttila 2010). According to these authors, the raccoon dog specialises more on plants and small mammals and the badger more on invertebrates. The preferred habitats of these species also differ: raccoon dogs prefer meadows, gardens and open woodland with tall and abundant undergrowth, whereas badgers prefer pine, deciduous and mixed forests with thick canopy but sparse undergrowth. Kauhala & Auttila (2010) concluded that the two species have different habitat preferences and therefore can coexist in an area. In Poland, facilitative interactions between badgers and raccoon dog contributed positively to the invasion success of the second (Kowalczyk et al. 2008). Raccoon dogs used badger setts as shelter from cold weather and to avoid predation. These two species could even overwinter in the same sett, using different parts. Badger densities did not show any decline as a consequence of this interaction. On the other hand, sett sharing could be dangerous for badgers because of transmission of diseases and exchange of parasites

(Kauhala & Holmala 2006). Overall, badgers and raccoon dogs apparently have adapted to coexist and make use of the available resources with minimal competition, by using different resources in the same habitat (Jedrzejewska & Jedrzejewski 1998).

In Mediterranean ecosystems the Iberian lynx (*Lynx pardinus*) and the badger are sympatric (Martín-Franquelo et al. 1995). These species have a similar size, are active during twilight (Palomares & Delibes 1997, Macdonald 2009) and prey on rabbits as a major food source (Delibes & Calderón 1979, Martín-Franquelo et al. 1995). Therefore, the niches of these two species may overlap during the year. However, they seem to be able to peacefully cohabit the same area by selecting different prey size and adopting slightly different activity patterns: lynxes catch larger rabbits and are most active at sunrise and dusk whereas badgers prey on small rabbits and are mainly nocturnal (Fedriani et al. 1999). Although badgers are also reported to be crepuscular (Macdonald 1984, Kowalczyk et al. 2003, Do Linh San et al. 2010), they seem to adjust their habits in order to cohabit peacefully with the lynx.

Other Carnivora, such as the golden jackal (*Canis aureus*), stone marten (*Martes foina*) and even otters (*Lutra lutra*), have only been found to compete with badgers to some extent in unusual situations, i.e. in strongly reduced badger populations as in Bulgaria (Griffiths & Thomas 1993).

Diseases and parasites

Badgers are highly susceptible to *Mycobacterium bovis* infection, the cause of bovine tuberculosis (Gormley & Costello 2003). This is a major mortality factor of badgers in Ireland and the United Kingdom (Olea-Popelka et al. 2003). It is also present in Spain, France and Switzerland (Gortazar et al. 2011, Payne et al. 2013, Schoening et al. 2013). Some studies indicate that badgers are a reservoir of cattle infection in south-west England, Wales and

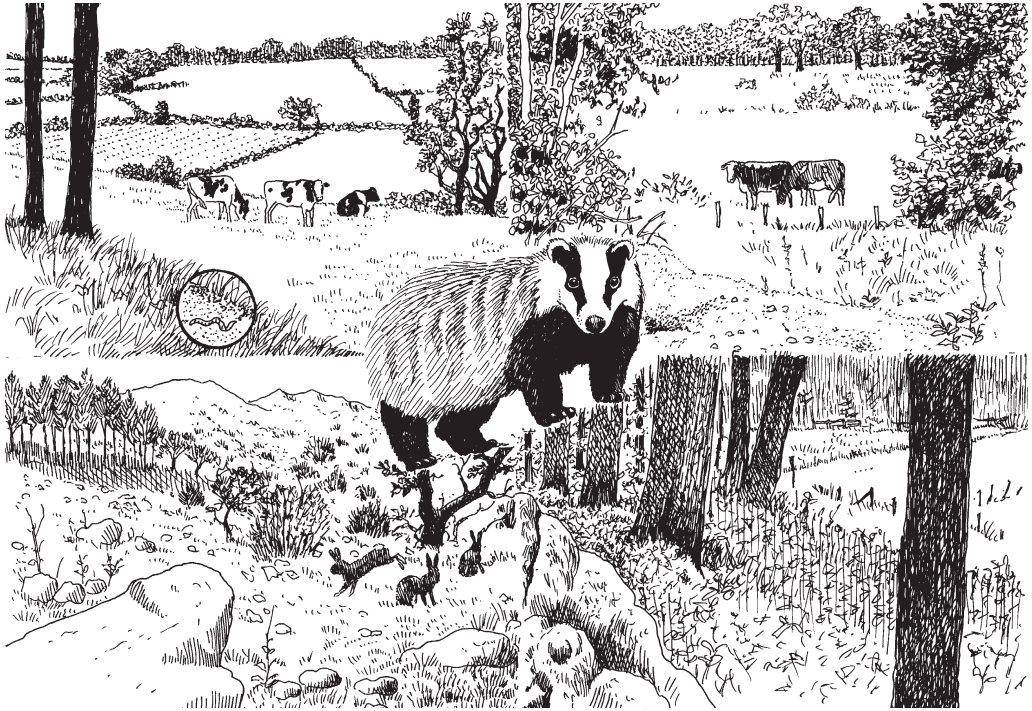


Figure 5. Illustration of four different landscapes that the European badger inhabits across its geographical range, each showing the elements that the badger preferably selects from. The very different landscape compositions illustrate the adaptability of the species. Upper-left, the landscape in the United Kingdom is represented, with a great proportion of grassland rich in earthworms, arable land, woodland, hedgerows and other small landscape elements providing cover, as well as some terrain heterogeneity. Upper-right, the landscape in the Netherlands where badgers occur is illustrated, with a big proportion of woodland, terrain heterogeneity and cover elements, sandy and dry soils and little presence of fields and grassland. On the lower right side a Polish landscape is represented, with a dominant presence of woodland, a minor presence of grassland and arable fields, and including some rocks and other small elements for cover. Finally, on the lower left side the landscape in Spain is illustrated, poor in woodland, with rocks and scrubs providing shelter and rabbits as an important food source. *Illustration: Ed Hazebroek.*

Ireland (e.g. Krebs et al. 1997). However, published results are contradictory about whether culling badgers is an effective measure to reduce or eliminate bovine tuberculosis in cattle or whether it is even counterproductive, as badger dispersal may increase as a result of it (Gallagher & Clifton-Hadley 2000, Donnelly et al. 2003, Griffin et al. 2005, Woodroffe et al. 2006). Still, culling of badgers has been performed as a measure against bovine tuberculosis all around Europe, severely threatening badger populations (Griffiths & Thomas 1993), especially in the United Kingdom (Dolan 1993).

The outbreak of rabies from the 1950s on, together with the subsequent attempts to control rabies, was a major reason for the decline of badger populations all around Europe in the 20th century (Griffiths & Thomas 1993, Smith 2002). Although the red fox is the main reservoir for rabies in Europe, badgers were also infected in many European countries (WHO 1978–2013). Rabies infection can potentially reduce badgers' population densities by 90% (Schwierz & Wachendörfer 1981). In the United Kingdom, badgers have contributed to rabies outbreak (Macdonald 1995, Morgan 1995) and it is not clear whether vaccination is an effective

tive measure (Smith 2002). However, the number of infected animals has decreased significantly during the last decade, constituting only 0.5% of rabies cases in Europe from 2000 on (WHO 1978–2013) and may thus have only a limited effect on badger populations.

Other diseases to which badgers have been reported to be vulnerable include mustelid herpesvirus-1, canine distemper, arteriosclerosis, pneumonia, pleurisy, nephritis, enteritis, polyarthritis and lymphosarcoma (Harris & Yalden 2008). However, these diseases are of much lower concern compared to bovine tuberculosis or rabies and are therefore much less studied. Although these diseases may affect mortality of badgers, the impact on badger populations is lower.

Internal parasites common in badgers are trematodes, nematodes and several species of tapeworms (Harris & Yalden 2008). Cubs are also very susceptible to a coccidian parasite (*Eimeria melis*) (Anwar et al. 2000). Potential ectoparasites include fleas (*Paraceras melis* - badger flea, *Chaetopsylla trichosa* and *Pulex irritans*), lice (*Trichodectes melis*) and ticks (*Ixodes ricinus*, *I. canisuga*, *I. hexagonus*, *I. reduvius* and *I. melicula*). Badgers also suffer from mange (Harris & Yalden 2008). To counteract this problem, badgers spend much time practising self and social grooming (Stewart & Macdonald 2003). Parasites are of general low concern, because they do not have an important economic impact and the power of spreading is lower, and they also have a much lower impact on badger populations than bovine tuberculosis and rabies.

Discussion and conclusions

Main habitat characteristics

The reviewed literature shows that a variety of factors affect the distribution and spatial population dynamics of the European badger around Europe (see also table 1): e.g. climate and terrain characteristics such as soil type,

slope, heterogeneity and cover. Habitat composition, the presence of woodland, grassland and crops - such as maize, wheat and barley - and food availability are also of great importance (Kruuk 1989, Feore & Montgomery 1999). Built-up areas and roads negatively influence badger distribution through habitat fragmentation, while roads are also an important cause of mortality. Hunting, although forbidden or strictly regulated nowadays in most countries, is still allowed in some countries and, together with poaching, contributes to badger mortality. Biotic interactions such as interspecific competition are also explaining badger territory expansion. Finally, diseases may affect badger occurrence and densities.

However, the degree of influence of different factors varies greatly. According to the collected findings, the main factors enhancing badger distribution and population densities are those that favour sett building and food availability. On the one hand, sett construction is mostly promoted by factors providing shelter and facilitating sett excavation, that is the presence of woodland and other cover features such as hedgerows and shrubs, terrain heterogeneity, soils that are not too wet or difficult to dig, and distance to urban areas and roads. On the other hand, food availability is enhanced mostly by the presence of grassland, crops and woodland. It seems that it is a balance between these two needs which finally determines the habitat preferences of the European badger. The optimal habitat composition is given when both are supported. Several studies confirm the combined importance of food and sett site availability (e.g. Woodroffe & Macdonald 1993, Rosalino et al. 2005). More specifically, Rosalino et al. (2005) studied the relationship between food patches availability and suitable sett site availability and concluded that the presence of both factors was required by badgers and that either one or the other could act as a limiting factor for badger colonisation and density.

The European badger is, according to all the

sources we studied, very adaptive and able to make use of different environmental factors (figure 5). Badgers can find shelter in forests, in human-made hedgerows, in a heterogeneous rocky area, etc. Their diet is also very flexible, although earthworms are preferably taken when it is available in the habitat. If earthworms are not abundant enough to cover their needs, this opportunistic omnivore can feed from other sources such as cereals, small animals and plants, wild nuts and fruits, or even anthropogenic food near urban areas. The home range of the badger is also adaptable to different environments. As contractors, badgers will always establish a territory that has a minimum land size to cover their needs. But if the environmental factors for protection, shelter and feeding such as woody areas and food patches are too far from each other, badgers will increase the size of their territory in order to include the necessary environmental features. On the other hand, if food availability is low, they will also increase their home range and travel long distances daily to find the needed food. In conclusion, the European badger is a very opportunistic and adaptive animal, a fact that is continuously being reaffirmed by ecological studies performed on this species (e.g. Remonti et al. 2006). However, all over their distribution range, badgers preferably use certain environmental items and terrain characteristics. Thus, all around Europe the badger shows a defined general pattern in niche characteristics, indicating a common realised niche.

Regional variation and differentiation

Although the realised niche might give an approximation of the fundamental niche of the species, these may not always overlap. The species' ecological fundamental niche involves all conditions allowing long-term survival of the species in an area, while the realised niche is the portion of the fundamental niche that the species actually occu-

pies (Hutchinson 1957). The realised niche is smaller than the potential ecological range due to various constraints, notably human pressure, biotic interactions and geographic barriers. Therefore, it is difficult to estimate the entire fundamental niche of the badger, as only some components of the full ecological potential or fundamental niche are expressed depending on the environmental conditions.

Apart from habitat composition, we have seen how many other factors can influence, to a larger or smaller extent, the population dynamics of the badger, namely climate, anthropogenic impact through urban infrastructure, agriculture, roads and hunting, as well as diseases such as bovine tuberculosis and rabies. The magnitude of these influences varies depending on the region, the environmental and landscape characteristics, abiotic and biotic composition, history, the degree of badger protection, etc. Therefore, the most important factors affecting the distribution and density of the badger will differ depending on the study area. Also, environmental drivers do not equally affect the different elements of spatial population dynamics. For example, hunting may affect population size and density, while roads may also affect colonisation and migration. Thus, depending on the region and the focus of the study, the appreciation of the importance of environmental factors on the distribution and density of badgers may vary.

Reflections on historical ecology and niche evolution

Given the great adaptability of the badger, it is not surprising that they can easily adapt to new human modified landscapes, and even benefit from anthropogenic transformation of the landscape (e.g. Huck et al. 2008, Do Linh San et al. 2011). Being such an adaptive species, badgers modify their realised niche according to the environmental circumstances of the moment. Consequently,

the actual niche of the badger may be better understood by looking at the historical ecology of the species, which explains habitat preferences by flexible opportunism and adaptation rather than by intrinsic fixed preferences. Having this in mind, some reflections can be made on the historical niche evolution of the species. Using the United Kingdom as a case example, the preference for woodland could be partly explained by the human prosecution of the badger in agricultural zones due to crop damage (Moore et al. 1999), rather than by actual preference for this habitat. Moreover, sometimes agricultural fields are surrounded by electrical fences to prevent badger access (Poole et al. 2002), crops are treated with repellent to inhibit badger feeding (Baker et al. 2005) and farmers even illegally cull badgers to avoid crop damage (Enticott 2011). The badgers would then select woodland not for its better conditions compared to agricultural land but for its less significant human negative intervention and the impediment to use the agricultural fields. Also, the preference for sloped areas could be partly explained by the distribution of habitats in relation to terrain characteristics. Agricultural activities are preferably performed in flat land, while the more sloped land is left out of deforestation. Therefore, the badgers' preference for slopes can be the consequence of an artefact, i.e. their apparently preference for woodland (or forced avoidance of agricultural land). Likewise, badger setts in urban areas are also reason for human conflict (Davison et al. 2011) and the exclusion of badger from these setts could explain the avoidance of urban areas in the badger's distribution. In conclusion, we must be careful when drawing conclusions about habitat requirements and preferences by looking only at the actual distribution and density of the species. We should also relate the niche evolution to the historical ecology and environmental transformation that the species has experienced to fully understand its habitat relationships. This may have implications for conservation and management,

as the most important management strategy might not be the availability of the environmental items selected by the European badger in recent times, but its actual feasibility of using the different habitat elements.

Recommendations

This review provides an overview of factors affecting the European badger's distribution and density. This knowledge can be highly useful for future ecological research on this species. The main factors influencing the badger's spatial dynamics are those favouring both sett location and food availability. Therefore, multiple environmental factors contributing to these two requirements interact to favour the badger's presence and numbers in a certain area. Sett location requirements are most often enhanced by coverage and protection of woodland and other small elements, such as shrubs and hedgerows, and food availability is most often higher in grassland. However, depending on the study area this might vary and other elements may gain importance, such as suitable soil for sett building, specific crops, human influence, diseases, etc. Consequently, prior to every ecological study in which factors affecting the distribution and density of the European badger play an important role, a choice of the, potentially, most relevant factors has to be made carefully according to the study area characteristics.

Second, this literature review might also have implications for management. The European badger's great ecological flexibility could mean that the potential success rate of rehabilitation and reintroduction programs should be relatively high. This may encourage policy makers to take action when needed. However, natural colonisation is a slow process in badgers (Reason et al. 1993) and therefore providing artificial setts and translocation of displaced badger social groups may facilitate and accelerate badger expansion when desired.

There is a clear bias for research on the badger

in the United Kingdom, as 50% of the relevant data on factors affecting the distribution and density of badgers were performed in this European region. However, the environmental conditions are different throughout European regions and therefore the findings in the United Kingdom may not be applicable to other European countries. We encourage research on badger ecology in the countries where this is scarce, such as Italy, France, Belgium or Sweden.

Although extensive knowledge on factors affecting the distribution and densities of the European badger is available, little research has been conducted on the specific effects of environmental factors on life-cycle components, such as age-specific survival and reproduction rates. Several studies focused on the influence of environmental factors, such as roads or climatic conditions on badger survival (e.g. Clarke et al. 1998, Macdonald et al. 2010), but these do not include the effects on other life-cycle components. In fact, very little is known about the influence of environmental factors on other life-cycle characteristics such as group dynamics, reproduction or dispersal. Future research on badger ecology should try to answer the question of how and how much all components of the life cycle are affected and what the integrated effect is on the spatial population dynamics of the badgers.

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Samenvatting

Verspreiding en dichtheid van de das (*Meles meles*): een literatuuronderzoek naar sturende omgevingsfactoren

Deze literatuurstudie gaat over de milieufactoren die het voorkomen en de dichtheid van dassen bepalen. De geraadpleegde literatuur, uit de periode 1970-heden, laat zien dat de das zich aan verschillende situaties kan aanpassen. Gezien over het hele Europese verspreidingsgebied van dassen wordt een algemeen patroon zichtbaar van geprefereerde omgevings- en milieufactoren. De meest bepalende factoren blijken factoren te zijn die het voedselaanbod beïnvloeden en de geschiktheid van de bodem voor het graven van een burcht. Meer specifiek gaat het om een geschikt bodemtype om gemakkelijk in te kunnen graven, kleinschalige heterogeniteit van het landschap voor dekking en de hoeveelheid bos en grasland met veel regenwormen. Hoe belangrijk specifieke factoren zijn voor de das is per gebied verschillend, waardoor de aanwezigheid en de dichtheid van dassen wordt bepaald door de unieke samenstelling van een gebied, land of regio. We geven aan hoe de kennis over omgevings- en milieufactoren gebruikt kan worden voor ruimtelijke modelstudies, natuurbeheer en toekomstig onderzoek naar habitatgeschiktheid en dichtheid van dassenpopulaties. Desondanks is meer onderzoek nodig om beter en in detail te kunnen begrijpen op welke wijze de fases van de levenscyclus van de das worden beïnvloed door de gevonden specifieke factoren en wat het (cumulatieve) effect daarvan is op de (ruimtelijke) populatiedynamiek van dassen.

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