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Dutch hedgehogs *Erinaceus europaeus* are nowadays mainly found in urban areas, possibly due to the negative effects of badgers *Meles meles*

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In several west European countries, the distribution of hedgehogs *Erinaceus europaeus* is declining. In the UK, predation by the European badger *Meles meles* is considered to be the main death cause of hedgehogs. In the Netherlands, badger density is rising, which suggests the same cause for the decline. As landscape and land use largely differ between the UK and the Netherlands, we investigated the relationship between the distribution of badgers and hedgehogs in the Netherlands. Therefore, we used the presence of badgers and hedgehogs recorded in the period 2007–2010 in grid cells of 1 km², together with environmental variables, i.e. land-use types and soil types, to describe the habitat of both species. Although the distribution of badgers in the Netherlands is still limited, we found indeed a negative effect of badger presence on hedgehog presence. We also found a positive effect of urban area, recreational land use and roads on hedgehog presence, whereas these types had a negative effect on badger presence. Our study suggests that hedgehogs in the Netherlands are nowadays found close to human occupation, possibly due to the negative effect of badgers. These results contribute to understanding of the declining distribution of hedgehogs in western Europe.

In several west European countries, the distribution of hedgehogs *Erinaceus europaeus* is declining (Huijser and Berger 2000, Hof et al. 2012). For example, the Mammals Trust UK reported local declines in hedgehogs of up to 50% (Battersby 2005). In the UK, predation is considered to be the main death cause of hedgehogs, with the European badger *Meles meles* as the main predator of hedgehogs (Doncaster 1992). Although a hedgehog's spine coat serves as defence against many predatory mammals, it is useless in an encounter with a badger (Ward et al. 1997), which has strong and dextrous paws, enabling it to force open a curled up hedgehog (Neal 1986). In the Netherlands, the hedgehog distribution has declined, while the badger distribution is increasing (Van Moll 2005), which suggests the same cause for the hedgehog decline as in the UK. The exact cause of the hedgehog's decline in the Netherlands is not yet fully understood. Traffic might be one of the main causes (Huijser and Berger 2000), but the role of badgers is unknown. For its conservation, it is important to gain more insight in the causes of hedgehog decline. In this paper, we investigate the potential role of badgers in explaining hedgehog distribution in the Netherlands.

Hedgehogs and badgers share the same habitats, and both hedgehogs and badgers have earthworms as a major constituent of their diet (Reeve 1994, Doncaster 1994). When the conditions are suitable for badgers, this means that the conditions are generally also profitable for

hedgehogs. When sharing the same habitat, odour plays an important, if not life-saving, role in the recognition of badgers by hedgehogs (Monclús et al. 2006, McEvoy et al. 2008). Ward et al. (1997) found that hedgehogs show an innate response to the odour of badger faeces, suggesting a long history of this predator–prey relationship. When smelling a badger while foraging, a hedgehog fringes down and takes refuge in nearby edge vegetation (Hof et al. 2012). If badger density becomes very high, the distribution of hedgehogs in the UK tends to change to urban areas, which are avoided by badgers (Doncaster 1992, Doncaster et al. 2001). Indeed, hedgehog survival is found to decrease with increasing distance from urban areas (Doncaster 1992, 1994, Micol et al. 1994). In the UK, urban areas are thought to be particularly important to hedgehog females and their young as they are predator-free (Doncaster 1992, Micol et al. 1994, Young et al. 2006).

Although several studies showed that the badgers were the primary factor determining hedgehog distribution in the UK, the question is whether the badgers have an equally important influence on Dutch hedgehogs, because the UK and the Netherlands differ in landscape and land use. In the UK, human land use is more diverse, with smaller parcels and rural landscapes have less human interference. In the Netherlands, road density is very high, 1.86 km per km² (Van Langevelde et al. 2009), and the human population density is about twice that of the UK. Moreover, the hedgehog and

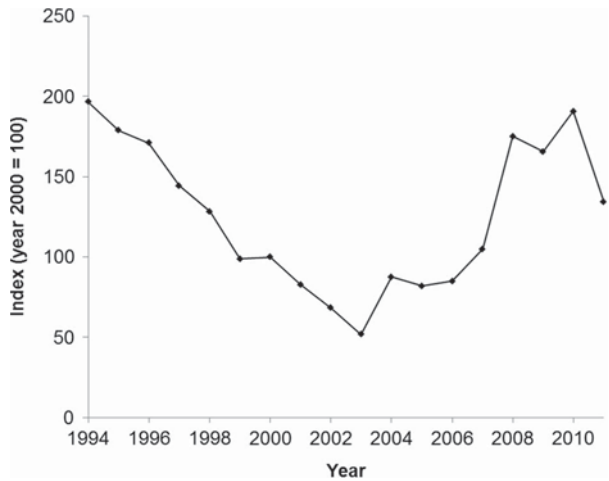


Figure 1. Population trends of the hedgehog in the Netherlands, based on systematic counts on fixed plots. Numbers are percentages relative to the number of hedgehogs counted in 2000 (Dijkstra and Van der Meij 2012).

badger habitat distribution in the Netherlands and the UK differs a lot. In UK the cover of forests is higher, resulting in more habitats that are suitable for badgers, while there are relatively more urban areas in the Netherlands, which are generally avoided by badgers. Badgers occur almost everywhere in the UK, while in the Netherlands badgers were on the brink of extinction (Fig. 1) and had a limited range. However, tides turned and they have been increasing in range and population size, most likely due to Dutch nature conservation (Van Moll 2005). Presently, the distribution of badgers and hedgehogs in the Netherlands differ (Fig. 2): there are areas with both badgers and hedgehogs and areas where hedgehogs are present and badgers absent. Besides the presence of badgers, environmental variables as proxy for habitat and food availability might also determine the distribution of hedgehogs. The aim of this study is to explain the distribution of both hedgehogs and badgers

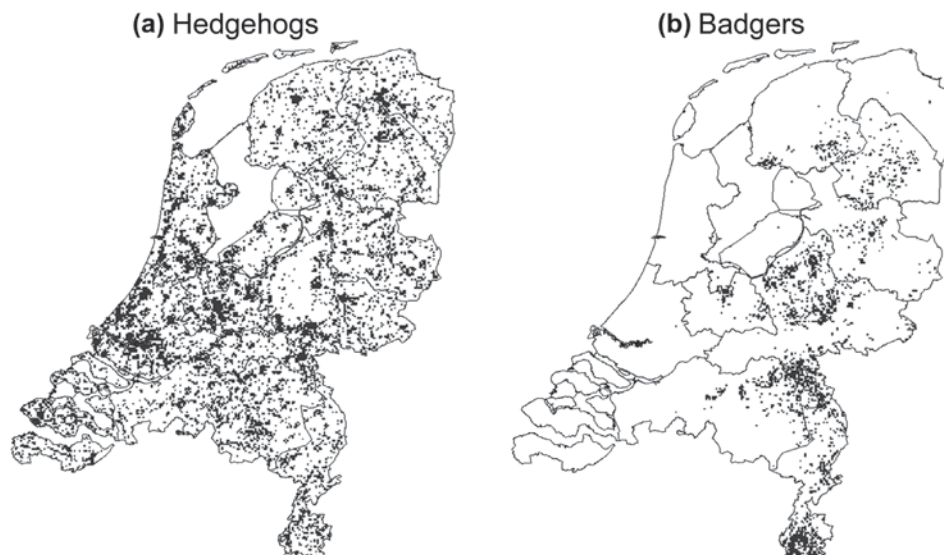


Figure 2. Distribution of (a) hedgehogs for the period 2007–2010 and (b) badgers for the period 2007–2009 (Dutch Mammal Society: <www.zoogdiervereniging.nl>, Thissen et al. 2010).

Table 1. Environmental variables (land-use types, soil types and other variables) used to explain the distribution of the hedgehog and badger in the Netherlands. Data are obtained from the Top10NL (Kadaster <www.kadaster.nl>).

Land-use types	Soil types
Arable (area with crops)	Heavy clay (consisting for over 50% clay)
Recreation (parks)	Heavy sab. clay (heavy clay, rich in sand)
Swamp (swampy areas)	Light clay (consisting for 25–35% clay)
Urban (urban areas)	Light sab. clay (light clay, rich in sand)
Wood (forested areas)	Loam (40% sand, 40% silt and 20% clay)
Heath (heathlands)	Peat (turf, partly decayed vegetation)
	Sand (sandy soil)
Other variables	
Roads total (summed surfaces of all types of roads, in %)	
AGLS (average groundwater level in spring, in cm)	

in the Netherlands using several environmental variables (Table 1) and, for the hedgehogs, the occurrence of badgers. Based on previous studies in the UK, we expect the Dutch hedgehogs to respond negatively to the presence of badgers. To support the possible negative effect of badgers on hedgehogs, we also included the resource selection of badgers in our study to show that the distribution of badgers includes the conditions where hedgehogs can also be found.

Methods

We used the presence of badgers and hedgehogs recorded by volunteers of the Dutch Mammal Society in the period 2007–2010 in grid cells of 1 km². Over this period, hedgehogs were found in 9032 grid cells and badgers in 2678 grid cells (Fig. 2). The badger distribution is collected by experienced civil scientists who checked suitable habitats for

inhabited setts. This is a continuation from the systematic censuses of 1990, 1995, 2005 and 2007, where all suitable habitats were checked for setts in grid cells of 1 km² (Wiertz 1992, Van Moll 2005, Witte et al. 2008). The civil scientists also reported badger signs such as tracks, dung pits or hair snagged in barbed wire. The hedgehog data was gathered more ad hoc: animals were sighted and reported by the public in both rural and urban areas. The Dutch Mammal Society organised the Year of the Hedgehog in 2009 with an outreach programme for hedgehog conservation and study, with a special data entry page (<www.zoogdiergezien.nl/>). This resulted in many observations from the general public. This made the data collected on hedgehog presence more variable between the years of our study period, but the combined data on hedgehog presence is reliable as the hedgehog is a very characteristic animal with no similar species occurring in the Netherlands. All data are entered into the National Database of Flora and Fauna and is validated by a team of experts from the Dutch Mammal Society.

We added environmental variables, i.e. land-use types and soil types, in the analysis that could describe the habitat and food availability of both hedgehogs and badgers (Table 1, Neal 1986, Reeve 1994, Doncaster 1992, 1994, Huijser and Berger 2000, Hof et al. 2012). All environmental variables were converted into percentages per grid cell of 1 km²: the relative cover of the grid cell's surface of a type of land use or soil type, except in the case of roads, where the average width of a road type (Van Langevelde et al. 2009) × road length was used to calculate the relative cover of roads in a grid cell. For groundwater level, we used the average groundwater level in spring (in cm) in a grid cell.

We investigated whether the presence of badger and the environmental variables could explain the presence of hedgehogs by means of species distribution modelling (SDM), using the algorithm MaxEnt (Phillips et al. 2006). As both hedgehogs and badgers are secretive species and we have presence data at national scale, we are not sure that the grid cells without hedgehogs or badgers are true absences. Therefore, we applied presence-only analyses. A presumed biotic interaction, such as the negative effect of badgers on hedgehogs, might in fact merely be caused by abiotic factors (Guisan and Thuiller 2005). We investigated the appropriateness of the inclusion of the effect of badgers on hedgehogs by means of SDMs, including also the interactions between the presence of badgers and the environmental variables to test whether the presence of badgers could increase the effect of the environmental variable. Besides, we also investigated whether the same environmental variables could explain the presence of badgers in the Netherlands. In MaxEnt, we used the default convergence threshold (10⁶) and maximum number of iterations (500) values. The whole area of the Netherlands was used as a background from which pseudo-absences were drawn. The area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Phillips et al. 2006) was used to assess the accuracy of the model. Furthermore, by means of a randomized partition, 30% of the occurrence data were set aside as 'test' data, comparing the AUC of these models with the AUC from

'training' models. We first tested the correlation between the independent variables as their effect in the presence-only analysis might be less visible when they are correlated.

Results

Testing for possible correlations between the environmental variables showed positive correlations between 'Recreation' and 'Urban' (Pearson correlation $r = 0.319$), 'Recreation' and 'Roads total' (Pearson correlation $r = 0.248$), 'Urban' and 'Roads total' (Pearson correlation $r = 0.470$) and 'Sand' and 'Wood' (Pearson correlation $r = 0.397$; all highly significant $p < 0.001$ due to the large sample size $n = 18\,064$), and no correlations between the other variables. The correlation coefficients were not large (all $r < 0.5$) that allowed us to do the presence-only analyses with these variables.

In the presence-only analyses, the variables 'Urban' (53.5% contribution), 'Road total' (26.0%) and 'Recreation' (11.4%) highly positively determined the current potential distribution range of the hedgehog, whereas the presence of badgers (4.2%) and 'Arable' (2.8%) also had an effect, although much smaller effect sizes (Fig. 3). The presence of badgers had a negative effect, and the percentage of arable land had a positive effect at low values and a negative effect at very high values. The AUC was 0.706. The other variables, including the interactions between the environmental variables and the presence of badgers, had a smaller contribution to the model (< 2.0%). In contrast, the variables 'Wood' (52.1%), 'Light clay' (19.4%) and 'Loam' (11.7%) positively determined the distribution range of the badgers. Here, the variables 'Sand' (4.7%) and 'Arable' (3.5%) had a smaller effect ('Sand' had a negative effect, whereas 'Arable' had a positive effect at low values and a negative effect at high values on badger presence). The other variables had a smaller contribution to the model (< 2.0%). For the badger model, the AUC was 0.710.

Discussion

In the Netherlands, hedgehog and badger distributions partly overlap (Fig. 2). Our study aimed to explain the distribution of both hedgehogs and badgers in the Netherlands using several environmental variables and to test whether badgers have a negative effect on the distribution of hedgehogs. Although the distribution of badgers in the Netherlands is still limited, our results show that the inclusion of badger presence enhanced the accuracy of SDMs to predict the hedgehog distribution in the Netherlands, although the additional negative effect of badgers on hedgehogs was small. This negative effect is in line with several other studies done in the UK (Doncaster 1992, 1994, Micol et al. 1994, Doncaster et al. 2001, Young et al. 2006, Hof and Bright 2010, Hof et al. 2012). When data permits, a better approach would be to look at changes in densities of both species and test whether there is a negative effect of badger density on hedgehog density, but we did not have these data.

It has already been shown that introducing species interactions, such as the assumed negative effect of badgers on hedgehogs in SDMs can considerably alter the output of

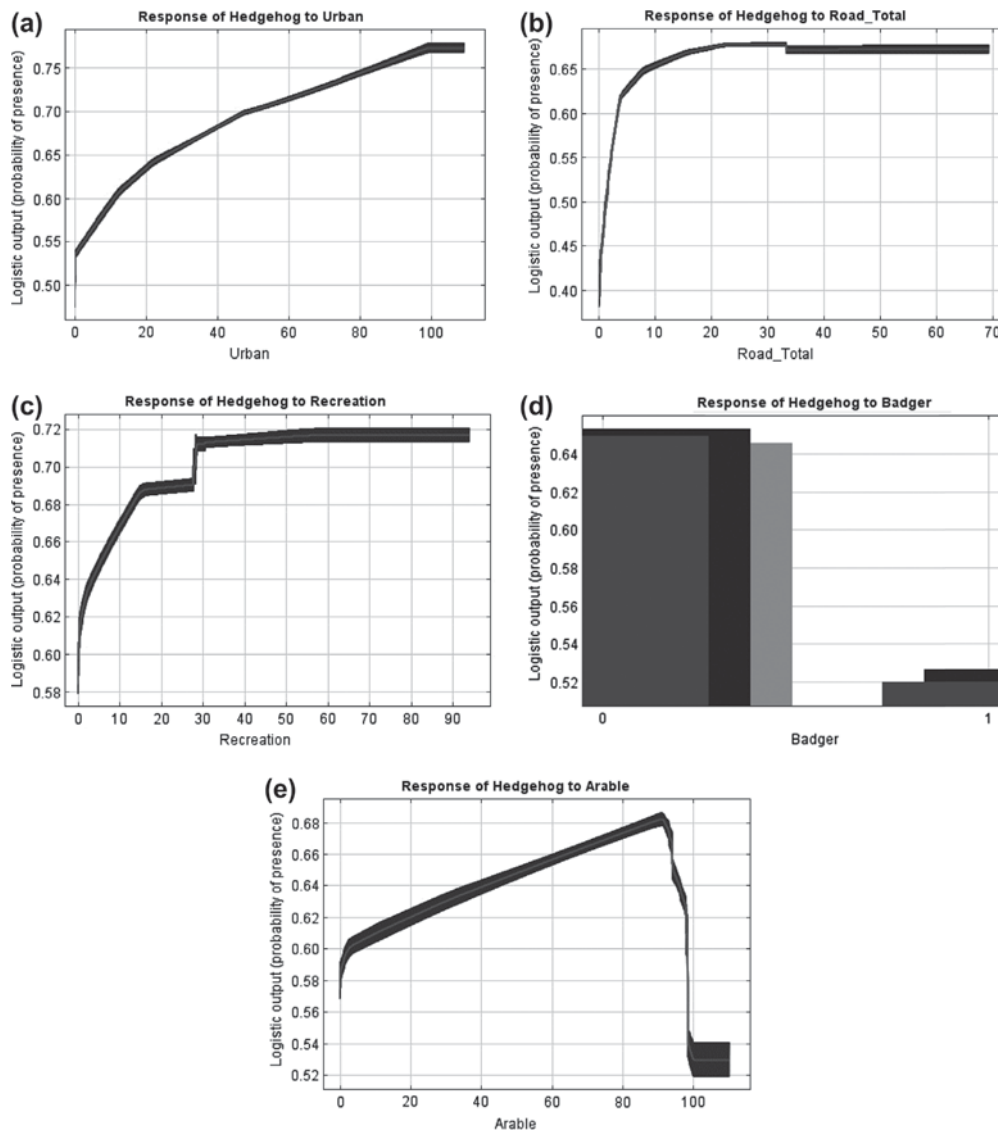


Figure 3. Response curves showing how each environmental variable affects the MaxEnt model for hedgehogs: (a) 'Urban', (b) 'Road total', (c) 'Recreation', (d) the presence of badgers, and (e) 'Arable'. The curves show how the logistic prediction for hedgehogs changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. The curves show the mean response of the 10 replicate MaxEnt runs (light grey) and the mean \pm one standard deviation (dark grey, two shades for the categorical variable badger presence). Note that the y-axes of the panels differ.

such models (Anderson et al. 2002, Meier et al. 2011). The distribution of hedgehogs was explained by several environmental variables (that could also explain the presence of badgers), and additionally we found a negative effect of badgers on hedgehog presence. Some variables had a negative effect on both hedgehog and badger occurrence (swampy areas, areas with high groundwater level, areas with light or heavy clay soils or with peat soils). These areas represent generally an open landscape without much cover, which are not preferred by hedgehogs (Huijser 2000) and badgers (Wiertz 1992). Environmental variables that had a positive effect on hedgehogs were urban areas, recreational areas and roads, whereas these types had a negative effect on badger occurrence. All these variables are related to human occupation, which usually means that there are urban areas with gardens and parks, and garbage production that might serve as habitat or food source for hedgehogs (Reeve 1994). Moreover,

linear wooded landscape elements can be found in urban and recreational areas and along roads to which hedgehogs might be attracted (Reeve 1994, Hof et al. 2012). As badgers tend to avoid urban areas (Doncaster 1992, Doncaster et al. 2001), these urban areas might provide a refuge for hedgehogs where they experience low predation risks (Hof et al. 2012) and probably high food availability.

The relative cover of sandy soils and woody cover showed a positive effect on badger occurrence, but these variables could not explain hedgehog presence. Woody cover might provide suitable habitat for badgers, possibly increasing predation risk for hedgehogs (Doncaster 1992). The relative cover of arable land had a positive effect on both hedgehog and badger occurrence. Presumably, if badgers can occur in areas with arable fields, the hedgehog will be able to survive here too, as they have similar habitats (Reeve 1994, Doncaster 1994, Ward et al. 1997). As the soil of arable land

has a high content in organic material, is moderately to well drained and pH is controlled, they are expected to contain high densities of earthworms, which make it plausible that both badgers and hedgehogs can be found here (Standen 1984).

Our analysis suggests that we can distinguish between three different areas: 1) areas where environmental conditions are unsuitable for both hedgehog and badger, such as very wet and open areas, 2) areas where environmental conditions are suitable for both hedgehogs and badgers, such as arable land, and 3) areas where environmental conditions are suitable for hedgehogs, but where hardly any badger is found, such as urban areas. In the Netherlands, hedgehogs are found close to human occupation, whereas badgers are less tolerant of human occupation. On the other hand, badgers might have a negative impact in areas where both species could potentially occur together. The latter suggests that urban areas might serve as refuge for hedgehogs. These findings contribute to our understanding of the declining distribution of hedgehogs in western Europe.

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