

Mammals and a changing climate

We have just witnessed the warmest year on record, not only in the Netherlands, Belgium and Europe, but worldwide. Average global temperatures have now been increasing year on year for more than thirty years. But how should we react to this phenomenon? With concern or by enjoying it? Few people complain about spring temperatures in winter, or a walk on the beach in a t-shirt and shorts in early November. True, in the Netherlands, there were complaints about the month of August last year, the only month that was cooler, and wetter, than average; and about the absence of snow and ice in winter, frustrating (yet again) the dream of many an ice skater to participate in the *Elfstedentocht*. But generally, people seem to feel more than comfortable with the conditions they know from their holiday destinations further south and with lower gas bills.

Years with record high temperature averages, such as those in Europe (2014), Australia (2013) and North America (2012), are not solid proof of a changing climate. They may be coincidences, like all extremes. But the bigger picture has convinced most scientists and non-scientists that, worldwide, our climate is indeed shifting towards higher average temperatures and more extreme weather. In the Netherlands, climatologists expect a further temperature rise (i.e. milder winters and warmer summers) and the increased probability of extreme rainfall (KNMI 2014).

Climate change might affect animals and plants in a number of ways, but primarily through three mechanisms: (1) spatial changes: shifts in distribution area, including local extinctions near the edge of a species' distribution and changes in abundance, (2) temporal changes: timing of breeding, flowering, hibernation, etc. (phenology), and (3) erratic effects caused by extreme events such as hurricanes, flooding and wildfires.

The effects of climate change on birds and butterflies have been relatively well-studied. We are familiar with the studies of migrating birds arriving in their breeding territories too late to catch the insect peaks, leading to a decreased breeding success. Birds, butterflies and other insects have been shown to have become locally extinct in parts of their former areas of distribution, due to changing climate conditions that they can't cope with. But they also profit from warmer conditions, and expand their ranges into new areas where the climate is becoming more suitable (e.g. the swallowtail *Papilio Machaon* expanding into the Netherlands and Belgium).

So far, nearly half of the mammal species studied don't seem to have yet shown a response to climate change. Of the half that do, some are responding positively with increasing distribution ranges (usually in the direction of the poles or towards higher elevations), population sizes, or growth rates. Other mammal

species, however, are and will be negatively influenced by climate change. These include primate species in the tropics as well as marine mammals, including the polar bear, which rely on the presence of sea ice in the arctic.

Levinsky et al. (2007) used two different models to assess extinction risks of European mammals, based on different assumptions about species' ability to disperse. In the first model, which assumed that the species were able to disperse with no restrictions, they predicted that 1% of the 120 terrestrial, non-flying, mammal species in Europe are at risk of future extinction and 32–46% may be severely threatened (i.e. lose > 30% of their current distribution) through climate change. In the second model, which assumed that none of the species are able to expand their range the figures were 5–9% and 70–78% respectively. Obviously, in reality, most species will fall somewhere between these two extremes.

One of the most important constraints on mammals' movements is that, as opposed to birds and insects, the majority of mammal species can't fly. Their movements over land are slower, or may be constrained by barriers. As such, expansion towards new territory isn't that easy for most mammals, especially if the habitats are fragmented. In a study of 493 mammals currently present in the Western Hemisphere, Schloss et al. (2012) compared the velocities at which species will probably need to move in order to keep pace with expected changes in suitable climates with the speeds at which they are able to disperse. According to their analysis, up to 39% of mammal species will not be able to keep up with climate change; 87% of the species are predicted to have smaller distribution ranges, and 20% of these range reductions are likely to be caused by the mammals' limited dispersal abilities.

Therefore, dispersal limitation is an important factor for any species that has to cope with climate change. Flexibility may be another one.

Species that are able to enlarge the range of temperatures and humidity they experience by modification of habitat choices, timings of key activities, and temperature regulation may be less vulnerable to climate change than species which do not have those options. McCain & King (2014) reviewed 73 North-American mammal species and found that mammals that were active only during the day or only at night were more vulnerable to climate change than mammals having flexible activity times. Some small mammals may be able to escape from climate change by using a wider array of micro-climates available in the vegetation and soil. Such areas and conditions are not available to bigger mammals, which live above the vegetation and only experience ambient temperatures.

So, when it comes to mobility, large mammals seem to have the benefit, but flexibility seems to be in favour of the smaller mammals.

In the Netherlands and Belgium, last year's very mild winter, early spring and warm autumn have brought benefits and disadvantages to plants and animals. Some mammals may have benefited, for example by the high food availability in the colder months. This possibly explains the overabundance of voles (*Arvicolinae*) in 2014, especially in agricultural lands in the northern Netherlands. Others, such as bats, were able to store fat for a longer period in autumn, increasing their chances of surviving the winter. In the Oostvaardersplassen, one of the Netherlands' most treasured nature reserves, the populations of large herbivores (i.e. red deer, Heck cattle and koniks) started to increase again in 2014; after years of severe winter starvation, their winter survival rate was much higher. This is a fenced area, so the grazers cannot expand their territory when the population densities increase, making the Oostvaardersplassen less of a natural ecosystem than some want us to believe (see also Canters & Verboom's editorial in *Lutra* 56 (2)). The debate on this is one of the

subjects of the paper by van Vuure in this issue. He discusses the konik, a breed of horse that is commonly put out as a grazer in nature reserves in the Netherlands, and its supposed relation to the extinct wild horse.

In another paper in this issue, Piza Roca et al. review the current literature on the environmental factors that determine the distribution of European badgers. If we want to understand how climate change might influence badgers, it is necessary to know these factors and their relative importance. Earthworms, one of the badgers' main food items, play a key role here, and climatic features are one of the factors that determine earthworm abundance. A future climate with periods of drought alternated with periods of heavy rainfall might have a negative effect on the availability of earthworms to badgers.

One of the consequences of climate change is the future invasion of non-native species that can survive in areas which, formerly, had an unsuitable climate (see also Canters' editorial on 'moving mammals' in *Lutra* 56 (1)). Some of these new species compete with native species, with possible negative consequences. This seems to be the case with the American mink, although this mink invaded our countries after having escaped or been released from captivity. In their study on American mink in the Czech-Moravian Highlands, Hlaváčová & Hlaváč used different methods, including telemetry and camera trapping, to monitor several of these animals. Their findings on its spatial

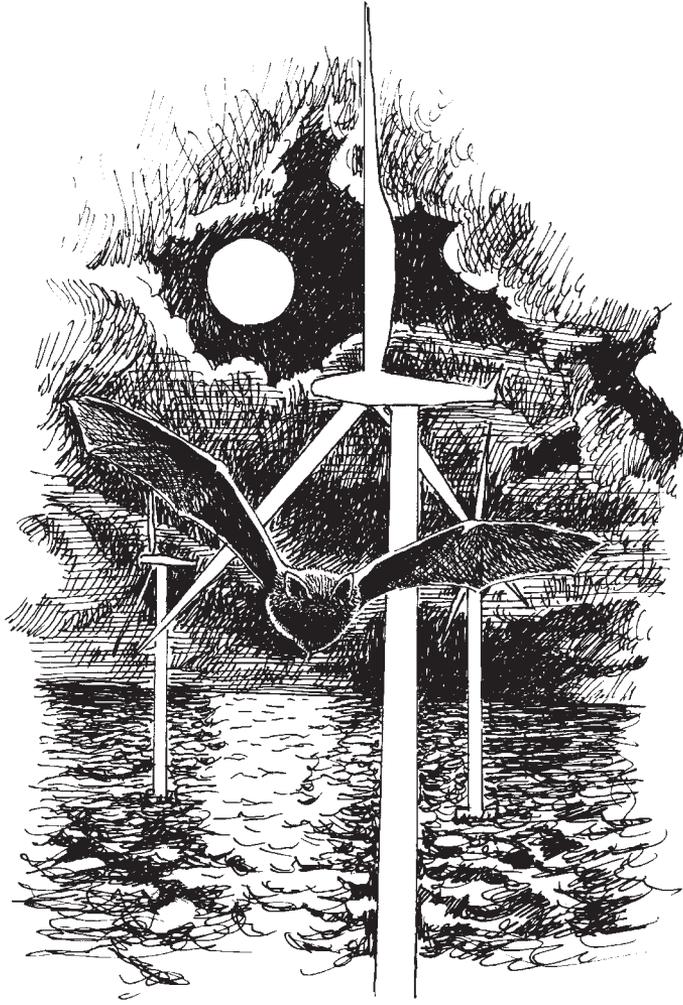
behaviour and reproductive biology help us to further understand this invasive species and its possible negative effects on the populations of native endangered animals.

Readers may be surprised by the findings of Lagerveld et al., who performed a pilot study of bats on offshore wind farms in the North Sea. Nathusius' pipistrelles was commonly recorded, albeit only in favourable weather conditions, by the ultrasonic detectors that were installed in two marine wind parks. These bats were probably migrating to suitable wintering areas.

We live in exciting times with many opportunities and threats ahead of us. Many of these are unknown and will be unexpected, but for scientists, they at least provide plenty of challenges.

Ben Verboom

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Bats in Dutch offshore wind farms in autumn 2012

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Abstract: In the autumn of 2012, we conducted a pilot study with ultrasonic recorders to assess the occurrence of bats over the North Sea. At Offshore Wind Farm Egmond aan Zee (OWEZ) a recorder was installed at the meteorological mast and at Princess Amalia Wind Farm (PAWP) a recorder was attached to the entrance platform of an offshore wind turbine. There were 189 recordings of bat echolocation calls at OWEZ and 25 at PAWP. Virtually all recordings concerned Nathusius' pipistrelle (*Pipistrellus nathusii*); noctule (*Nyctalus noctula*) was noted a few times. Bats were only recorded during nights with low or moderate wind speeds, no precipitation and a high ambient pressure. It seems unlikely that the observations referred to individuals which were blown off course by storms, and there are no indications that roosts were present in the vicinity of the recorders. The occurrence pattern of Nathusius' pipistrelle indicates that the observations were of migrating individuals. The observations of noctule possibly concerned migrants as well, but they could also be residents from the mainland which may use the wind parks as foraging area.

Keywords: bats, North Sea, sea, wind farm, migration, acoustic monitoring, wind speed, conservation, *Pipistrellus nathusii*, *Nyctalus noctula*.

Introduction

Several species of bat in northern Europe show seasonal migrations between their summer roosts and winter quarters. Most of them travel short or moderate distances, but some species like Nathusius' pipistrelle (*Pipistrellus nathusii*), soprano pipistrelle (*Pipistrellus pygmaeus*), noctule (*Nyctalus noctula*), Leisler's bat (*Nyctalus leisleri*) and parti-coloured bat (*Vespertilio murinus*) are long distance migrants, travelling from northern and eastern Europe to more temperate areas and vice versa (Hutterer et al. 2005, Krapp & Niethammer, 2011). Some bats migrate individually while others migrate in groups, sometimes even large groups (Dietz et al. 2009). Generally bat migration occurs at night, but some

species like noctule have been seen migrating in the morning or just before dusk (Randler 2001, Mostert 2012).

Not much is known about the migration routes of bats. At least some specific flyways are used, such as river valleys (Furmankiewicz & Kucharska 2009) and coasts (Dietz et al. 2009, Masing 2011, Šuba et al. 2012). At the North Sea coast, bat migration was studied on the German islands of Mellum, Neuwerk and Wanderooge (Bach et al 2009, Frey et al 2012) and on the Dutch island of Rottumeroog (Jonge Poerink & Haselager 2013). Bats do not migrate exclusively over land. A study of the Swedish coast of the Baltic Sea showed that migration commonly occurs over sea (Ahlén et al. 2007, 2009). Interestingly, this study also revealed that the local populations from the mainland used the coastal sea as foraging area. In particular offshore wind turbines were favoured as foraging area because of the

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accumulation of insects around the turbines.

For quite some time there have been indications of bat movements over the North Sea. Observers of bird migration at the Dutch coast record bats flying in from sea with some regularity (N. van der Ham in litt., M. de Lange in litt., R. van der Vliet in litt., S. Lagerveld, personal observation). Most sightings occur from late April to May and throughout September and October. Bats have also been observed during surveys at the North Sea in September (S. Lagerveld and H. Verdaat, personal observations) and have been found on oil platforms and ships (Boshamer & Bekker 2008, Russ et al. 2001, Skiba 2007, Walter et al. 2007, Petersen et al. 2014). In 2013 a *Nathusius' pipistrelle* was found in the Netherlands, which was banded three years earlier in the UK (T. Dolstra, personal communication). At the North Sea, bat activity was studied on Helgoland (Hüppop 2009) and on FINO 1, a research platform 45 km north of Borkum (Hüppop & Hill 2013). Both studies confirmed the occurrence of bats over the North Sea. In order to assess the occurrence of bats in offshore wind farms at the North Sea, we conducted a pilot study with ultrasonic recorders at two Dutch offshore wind farms. In addition, we gathered meteorological data. We used the occurrence patterns and meteorological data to establish why bats occur at sea. Another aim of this study was to assess the performance of the ultrasonic recorders under offshore conditions.

Material & methods

Study area

This study was conducted in the autumn of 2012 in two Dutch offshore wind farms (figure 1):

- Offshore Wind Farm Egmond aan Zee (OWEZ); consists of 36 Vestas V90-3MW wind turbines and a meteorological mast. The wind farm covers an area of 27 km²

and is located approximately 15 km off the Dutch coast. Monitoring was done from 29 August to 20 October 2012.

- Princess Amalia Windpark (PAWP); consists of 60 Vestas V80-2 MW wind turbines and a transformer platform. The wind farm covers an area of approximately 17 km² and is located 23 km off the Dutch coast. Monitoring was done from 4 to 23 September 2012.

Recording equipment and data analyses

Monitoring was performed with a Batcorder 2.0 (EcoObs GmbH); an automated ultrasonic recorder which can record sounds in the range of 16-150 kHz. The recorders were ruggedised for offshore conditions (Jonge Poerink et al. 2013). Both recorders were operating between 19:00 p.m. and 08:30 a.m. The recorders did not record continuously but only after being triggered by a bat call, or bat call-like ultrasonic sound. Bats can be recorded at a maximum distance of 15 - 50 meters from the recorder, depending on their specific sonar characteristics, the environmental conditions and the recorder settings.

At OWEZ a recorder was installed at the meteorological mast (figure 2); at PAWP a recorder was attached to the entrance platform of a wind turbine. Details of the locations are given in table 1.

All sound files were recorded in real-time onto a SD memory card. The sound files containing bat calls were separated from the noise files by BcAdmin 2.0 (EcoObs GmbH). Individual bat call recordings were analysed and identified using the automated identification software Batident 1.0 (EcoObs GmbH). In addition, all identifications were checked and evaluated using the criteria provided by Skiba (2009) and Barataud (2012).

Wind speed and wind direction were logged per 10-minute intervals by the weather station at the WTG08 wind turbine at OWEZ at a height of 70 m above sea level. The ambient pressure and precipitation data were meas-

ured at the OWEZ meteorological mast. The weather data were averaged per night for the analysis of the data.

Results

The ultrasonic recordings in OWEZ & PAWP

At OWEZ 189 bat call sequences containing 1477 individual echolocation calls were recorded in the period of 29 August until 20 October 2012. Within this period, bats were recorded during nine nights. Relatively high bat activity was observed during the nights of 3, 8, 22 September and 8 October (figure 3). Two species of bats were identified at OWEZ: *Nathusius' pipistrelle* and *noctule*. *Nathusius' pipistrelle* represented 98% of all call sequences and *noctule* represented 2%. *Noctules* were only recorded early September.

At PAWP 25 bat call sequences containing 110 individual echolocation calls were recorded from 4 to 23 September 2012. Within this period, bats were recorded during three nights. High bat activity was recorded during the nights of 8 and 22 September, which corresponds with high activity at OWEZ (figure 3). All observations at PAWP referred to *Nathusius' pipistrelle*.

At OWEZ 8% of the call sequences contained different echolocation calls that were emitted at the same time, proving that more than one individual was present. In one call sequence even three calls were recorded almost simultaneously, indicating the presence of three individuals. At PAWP there were no call sequences that indicated the presence of more than one individual. We recorded no social calls or feeding buzzes at either location.

In addition to the bat echolocation calls, the detectors recorded ultrasonic noise as well. At the OWEZ meteorological mast on average 50 noise files were recorded per 24 hours, whereas at the PAWP wind turbine on average 1500 noise files were recorded per 24 hours.

Bat activity and weather conditions

All observed bat activity occurred in nights with an average wind speed per night of less than 7 m/s with the exception of the night of 15 September when an average wind speed of 10 m/s was measured (figure 3). Furthermore, all observed bat activity occurred during nights with no precipitation and with an average atmospheric pressure >1010 hPa (figure 4).

Nocturnal pattern of bat activity

The time of the observed bat activity for *Nathusius' pipistrelle* was related to the time of sunset to assess the pattern of occurrence throughout the night (figure 4). Bat activity did not start immediately after dark: the peak activity occurred between 3-4 hours after sunset in both wind farms.

Performance of the recorder

The recorders have been functioning properly during the monitoring period. After the monitoring period the casings and microphones were inspected and found unaffected by salt spray, humidity or mechanical forces.

Discussion

Occurrence of bats in the offshore wind farms

It is hard to give an estimate of the actual number of bats based on the number of call sequences. An individual migrating bat may trigger the recorder only once, resulting in one recorded call sequence. Migrating bats however frequently travel in groups (Ahlén et al. 2009, Dietz et al. 2009, Mostert 2012) and a group of bats may also trigger the recorder only once. At OWEZ several recordings included more than one individual at the same time.

Ahlén et al. (2007, 2009) observed that migrating bats often interrupt their flight to

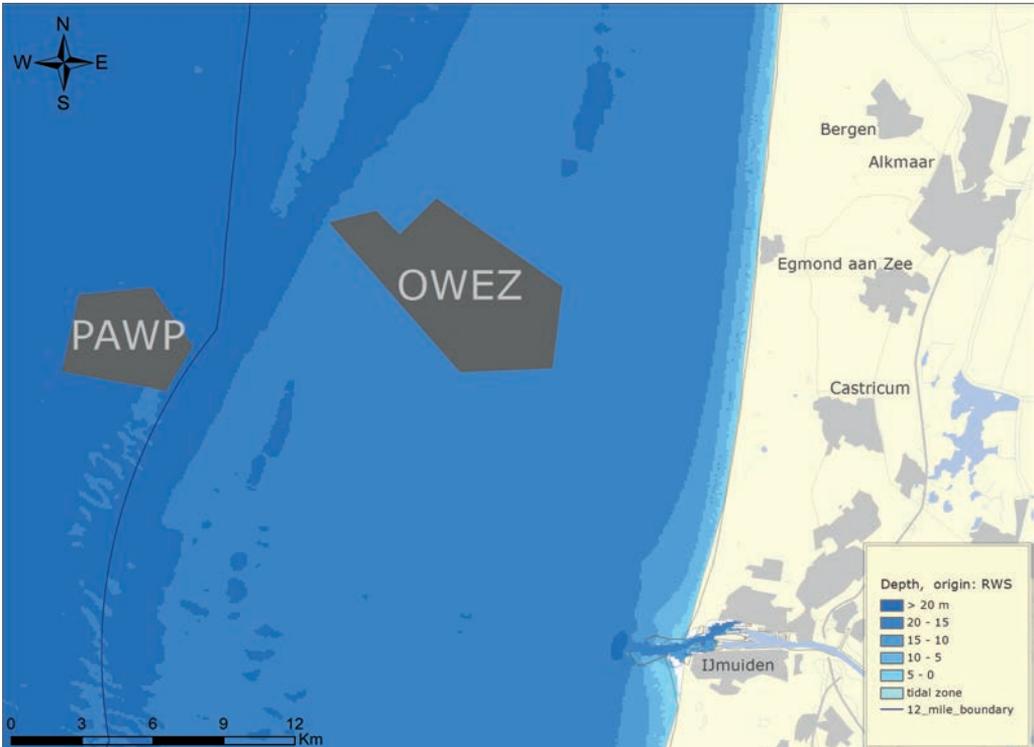


Figure 1. geographical locations of OWEZ and PAWP.



Figure 2. Ultrasonic recorder at the OWEZ meteorological mast. Photo: Hans Verdaat.

Table 1. Positions of the ultrasonic recorder.

Wind Farm	Geographical Position recorder	Distance to shore (km)	Height above sea level (m)	Direction of microphone
OWEZ	N 52° 36' 22.9" E 004° 23' 22.7"	15	15	East
PAWP	N 52° 34' 89.4" E 004° 15' 60.3"	23	15	East

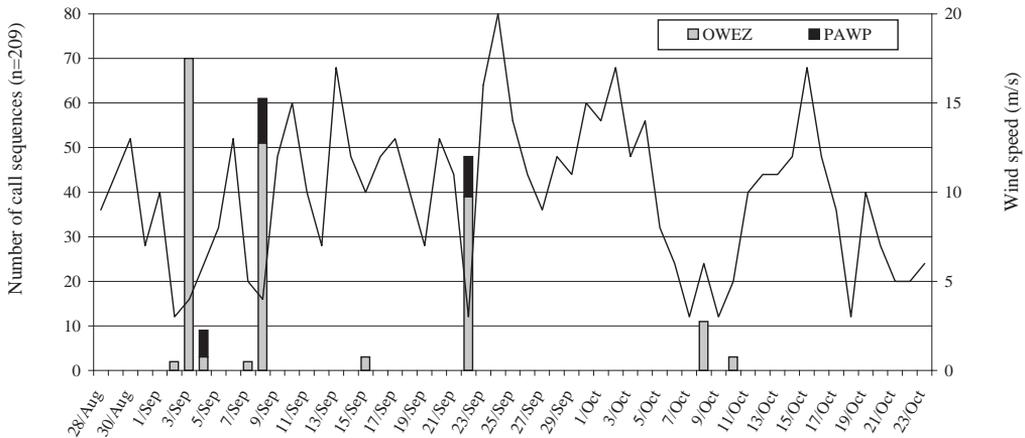


Figure 3. Number of call sequences of *Nathusius' pipistrelle* at OWEZ and PAWP and the average wind speed at OWEZ per night.

forage around offshore wind turbines because of the accumulation of flying insects. When foraging, an individual bat may fly multiple times in the vicinity of the recorder resulting in several recorded call sequences. Consequently, it is not possible to give an estimate of how many individual bats have been present in the vicinity of the recorders. The number of call sequences is therefore used as an indication of the bat activity.

Ahlén et al. (2007) observed that bats always use their echolocation during flight over the Baltic Sea at night. Whether they do so during the day is apparently not known. It is possible that they don't use their sonar (or that they use it to a lesser extent) during daylight hours at sea since at least some species of bat use visual cues for navigation over larger distances (Eklöf 2003). Consequently, they can be missed by the ultrasonic recorders.

Offshore wind turbines and other offshore structures attract bats (Ahlén et al. 2007, 2009). The observed abundance near the detectors

therefore is likely to be higher than the abundance over open sea.

The mounting height of the recorders was approximately 15 m above sea level. Bat calls are detected between 15 and 50 m from the recorder, which means that we recorded bats from sea level up to a height of 30 to 65 metres above sea level. It also means that higher-flying bats are likely to be missed. However, most bats that were observed at the Baltic Sea flew below 10 m altitude, including the normally high-flying species like noctule (Ahlén et al 2009). Bats observed during surveys at the North Sea ($n=3$) flew at altitudes between 5 and 20 m (S. Lagerveld and H. Verdaat, personal observations).

In OWEZ the number of recorded bat call sequences was much higher than in PAWP, also during the overlapping monitoring period. This can be due to a higher abundance of bats at OWEZ but there may be other explanations for the observed pattern:

- OWEZ is located 15 km off the coast, PAWP is located 23 km off the coast. The shorter

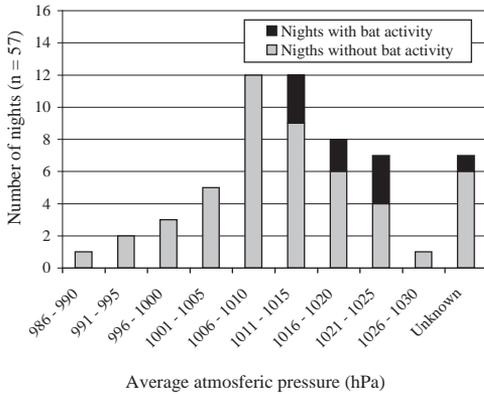


Figure 4. The number of nights with bat activity and the average atmospheric pressure at OWEZ.

distance to the coast of OWEZ can affect the number of bats in the wind farm. Also the location of the wind farms in relation to specific flyways can affect the abundance of bats in the wind farms;

- The higher number of recorded bat call sequences at OWEZ can be due to different behaviour (e.g. more activity due to a higher insect abundance);
- During our study the offshore wind turbine at PAWP produced 30 times more ultrasonic noise recordings than the OWEZ meteorological mast. Ultrasonic noise can mask bat calls and can lead to an underestimation of the bat activity;
- OWEZ covers an area of 27 km² and consists of 36 wind turbines and a meteorological mast. PAWP consists of 60 wind turbines including a transformer platform and covers a much smaller area of 17 km². The higher density of structures at PAWP might result in lower bat density per object compared to OWEZ.

Behaviour of bats in the offshore wind farms

Ahlén et al. (2007, 2009) mentioned that service engineers found roosting individuals of various bat species in the nacelles of off-

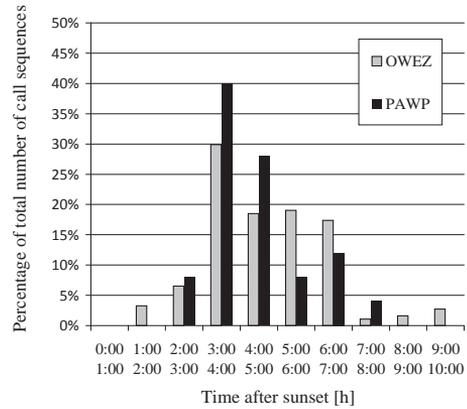


Figure 5. Percentage of call sequences of Nathusius' pipistrelle per hour after sunset at OWEZ and PAWP.

shore wind turbines near the Swedish coast. Those bats stayed there for several days and social calls were frequently observed. During our study there have been no indications that roosts were present in the vicinity of the recorders. Both noctule and Nathusius' pipistrelle leave their roost at dusk (Russ 2012, Dietz et al. 2009) and the observed bat activity started at least one hour after dusk and peaked between 3-4 hours after darkness had set in. In addition, we did not record any social calls, which can be indicative for the presence of roosts.

Noctule and Nathusius' pipistrelle pass through the Netherlands during migration, but are also fairly common residents at the Dutch mainland near the coast (Limpens et al 1997). The temporal pattern of occurrence during this pilot study suggests that the observed Nathusius' pipistrelles were migrating: their time of occurrence matches the species' migration season and both offshore wind farms are located well beyond their foraging range, which extends up to 6.5 km from their roosts (Dietz et al. 2009). The observations of noctules also coincide with their migration season, but we cannot exclude the possibility that foraging individuals of local populations from the mainland were involved. Distances up to 26 km between their roosts and foraging areas have been reported (Altringham 2003)

and therefore both offshore wind farms are located within their foraging range from the mainland.

This pilot study shows a strong link between bat activity in the two wind farms: when bats were observed in PAWP, they were always present in OWEZ as well. Bats were observed at wind speeds up to 10 m/s, but most activity occurred at wind speeds below 5 m/s. This result exactly matches the pattern observed in southern Sweden by Ahlén et al. (2007, 2009). In addition, bats were only observed during nights with high ambient pressures and no precipitation, shortly after periods of unfavourable weather conditions. This also corresponds with the findings of Ahlén et al. (2007, 2009) and Cryan & Brown (2007) who observed that migrating bats wait for favourable conditions to cross over sea.

Conclusions

It is possible to perform acoustic monitoring of bat activity at sea when ruggedised ultrasonic recorders are used.

This study indicates regular occurrence of bats in the Dutch offshore wind farms. Bats were only recorded during nights with low or moderate wind speeds, no precipitation and a high ambient pressure and it seems therefore unlikely that these observations refer to individuals who were blown off course by storms.

Virtually all recordings concerned *Nathusius' pipistrelle*. Noctules were recorded a few times. Both species are long-distance migrants but also occur as residents at the mainland near the coast. The observed occurrence pattern during this study indicates that *Nathusius' pipistrelle* occurred as a migrant in the offshore wind farms. The noctules were possibly migrating as well, but we cannot exclude the possibility that local populations from the mainland use the offshore wind farms as a foraging area.

Due to the restricted monitoring period and geographical scale of this pilot project it

is not possible to draw overall conclusions of the occurrence of bats at the North Sea. Our observations, however, combined with offshore sightings and findings of stranded individuals on oilrigs and ships, do indicate that bats regularly occur over the North Sea.

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Samenvatting

Vleermuizen in Nederlandse offshore windparken in het najaar van 2012

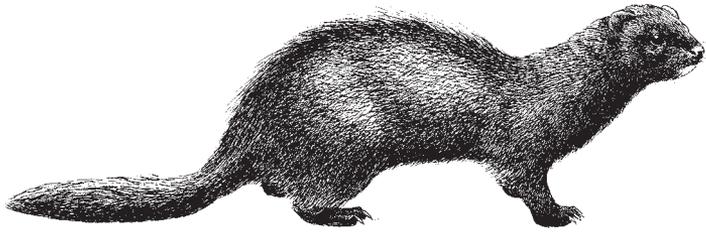
In de herfst van 2012 is een pilotstudie uitgevoerd met ultrasone recorders naar het voorkomen van vleermuizen op de Noordzee. Eén recorder werd geïnstalleerd op de meteorologische mast in Offshore Windpark Egmond aan Zee (OWEZ) en een andere recorder op

een offshore windturbine in het Prinses Amalia Windpark (PAWP). In OWEZ en PAWP werden respectievelijk 189 en 25 opnamen van vleermuis-echolocatiegeluiden gemaakt. Bijna alle opnames waren van ruige dwergvleermuizen (*Pipistrellus nathusii*); rosse vleermuizen (*Nyctalus noctula*) werden slechts enkele keren opgenomen. Vleermuizen werden vrijwel uitsluitend waargenomen tijdens nachten met een zwakke of matige wind, geen neerslag en een hoge omgevingsdruk. Het lijkt onwaarschijnlijk dat de dieren uit koers zijn geblazen door

hoge windsnelheden en er zijn geen aanwijzingen dat er verblijfplaatsen waren nabij de recorders. Het patroon van voorkomen van de ruige dwergvleermuis duidt er op dat het hier om migrerende dieren gaat. De waargenomen rosse vleermuizen betreffen mogelijk ook migrerende dieren, maar het kan niet uitgesloten worden dat het (ook) om foeragerende dieren gaat van lokale populaties in het kustgebied.

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Spatial ecology and reproductive biology of an invasive American mink (*Neovison vison*) population - new findings from the Czech-Moravian Highlands

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Abstract: The aim of this study was to obtain new information about the biology (spatial behaviour, circadian activity, reproductive ecology, etc.) of the American mink (*Neovison vison*) in the Czech-Moravian Highlands. A telemetry study was carried out with four males and three females in the Sazava River basin near Havlickuv Brod from 2004 to 2012. Several animals were monitored for more than a year, including the periods of mating, pregnancy and care of cubs. The telemetry study was supplemented with camera trapping and snow surveys during the winter. The research focused on sexual differences in the size and overlaps of home ranges, annual changes in spatial behaviour, circadian activity and reproductive and parental behaviour. Males and females differed in home range size, with the male home ranges being verifiably larger. The two sexes were also more active at different times: males were most active during the night, while the females were active during both day and night. The most striking sexual differences in spatial behaviour were found during the mating season (in March and April). During this period, the males occupied considerably larger home ranges than during the rest of the year. Female home ranges were stable for the whole year round. During April and May they intensively prepared burrows for parturition by bringing in organic material.

Keywords: American mink, *Neovison vison*, telemetry, circadian activity, spatial behaviour.

Introduction

The American mink (*Neovison vison*) is a medium-sized, semi-aquatic, mustelid species. In the 1920s it was introduced in Europe for fur farming (Bartoszewicz & Zalewski 2003). Some individuals escaped or were released and, over recent decades, the species has successfully established itself and spread over most of the continent. As an invasive species it has a significant impact on native European fauna, including the rare Euro-

pean mink (*Mustela lutreola*) (Maran et al. 1998, Sidorovich & Macdonald 2001). In the Czech Republic, the first American minks appeared in the wild at the beginning of the 1960s (Mazák 1964), but the main expansion did not start until the beginning of the 1990s. This has had a marked negative impact on the breeding success of water birds (Padyšáková et al. 2009). Minks also threaten populations of stone crayfish (*Austropotamobius torrentium*) and dice snake (*Natrix tessellata*) (Fischer et al. 2004). Analyses of the diet of American mink indicate it also predated certain species of bivalves, amphibians and mammals - mainly brown rat (*Rattus nor-*

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Figure 1. The location of the study area within the Czech Republic.

vegicus), water vole (*Arvicola terrestris*) and muskrat (*Ondatra zibethicus*) (Poledník & Poledníková 2010). To date there has been no study of its influence on native mustelid species, particularly Western polecat (*Mustela putorius*), stoat (*Mustela erminea*) and weasel (*Mustela nivalis*).

American mink's typical colour is dark brown-black with a white spot on the bottom lip and chin. The size and shape of this spot is very variable and, it is possible to recognise individuals from it (Dunstone 1993). Minks show sexual dimorphism in body size. The males are significantly larger than the females (Gerell 1970).

The distribution of the species is strictly connected to presence of water. Telemetry studies show, that minks generally have linear home ranges, situated along river banks or ponds (Gerell 1970). As such the population density is usually measured as the number of individuals per kilometre of watercourse. In Europe the density varies considerably, and probably depends on the characteristics of the environment.

The aim of this study was to contribute to the knowledge of the biology of this widespread and invasive species, which may negatively affect the populations of endangered animals. We used VHF telemetry to obtain detailed information about:

- a. the spatial requirements of American mink in the Czech-Moravian Highlands;
- b. the home range size and their basic characteristics;

- c. mink movements within their home range and distribution of activity during the day and night in both sexes, and;
- d. behavioural characteristics during reproduction and beyond.

Material and methods

Study area

The study was conducted in the Czech-Moravian Highlands around the town of Havlickuv Brod. The Sazava River and its main inflows form the hydrological axis of the area (figure 1).

The mink's occupancy of the central Sazava basin is not well documented and there are no records of when it first arrived. A large mink farm operated close to the town of Havlickuv Brod for several decades but closed down at the end of the 1980s. It is not known if the farm was responsible for the establishment of the local population or if the minks came from somewhere else. From our own data (finding tracks) it is obvious that minks were regular visitors to the Sazava River near Havlickuv Brod at the turn of the 1980s and 1990s. During the next ten years it became a common species.

Mink trapping

Trapping was carried out by using wire life traps, with dimensions of 50 x 16 x 16 cm and with one entrance (figure 2).

Low intensity trapping activities were carried out in January - February 2004 and December 2004 - January 2005. During these two periods only three traps were used and two male minks were caught. In 2006 - 2008 the telemetry monitoring was interrupted due to a lack of funds. Trapping activity was renewed on 31 October 2009 and continued, with short interruptions, until the end of March 2012. We had 15 traps at our disposal during this period. Trapping activities were



Figure 2. American mink caught in a wire trap. *Photoa: P. Hlaváčová.*



Figure 3. Variation in chin spots among trapped male minks. *Photos: V. Hlaváč.*



Figure 4. Variation in chin spots among trapped female minks. *Photos: P. Hlaváčová.*

regularly postponed in the summer, when there is an abundance of available food and the bait in traps is not a sufficient attraction for mink, so trapping success is very low. Low trapping success in summer and a high success rate in October (the time when juveniles disperse) and in winter (low food availability) are confirmed in other studies (see for example Yamaguchi et al. 2002).

Trapping was conducted in the following

periods:

- 31 October 2009 – 26 March 2010: 766 trap nights
- 15 August 2010 – 30 May 2011: 445 trap nights
- 30 October 2011 – 5 February 2011: 328 trap nights

One trap night equals one trap set for one night. Ten trap nights equal either one trap set for ten nights or ten traps set for one night.

Table 1. Characteristics of monitored minks.

Individual	Sex	Age	Weight (g)	Frequency MHz)	Monitored period	No. of fixes*
Albert (A)	M	Adult	1600	142.0040	21/3/2004-27/5/2004	181
					27/3/2005-14/6/2005	287
Bohous (B)	M	Adult	2000	142.3510	27/1/2005-10/8/2005	936
Cecilka (C)	F	Adult	600	142.2995	08/12/2009-22/1/2011	526
			700	149.3610	29/1/2011-10/5/2011	177
			700	149.7000	09/11/2011-11/2/2012	180
Dan (D)	M	Adult	1500	142.0135	07/1/2010-21/2/2010	47
Emilka (E)	F	Adult	900	142.0031	24/3/2010-11/4/2010	25
Fany (F)	F	Adult	800	149.3420	24/1/2011-28/4/2011	129
			800	148.9820	29/3/2012-5/8/2012	84
Gustav (G)	M	Adult	1700	142.0331	30/3/2012-26/9/2012	88

* The number of independent locations where a particular mink had been tracked.

Traps were installed along water banks at places where tracks or droppings had previously been found. Sardines from a can were used as bait. The traps were checked once a day at 6:30 a.m. The minks that were not used for telemetry were weighed, photographed and released back at the same place. Individuals were recognised by different spots on the chin (Dunstone 1993) (figures 3 and 4).

Mink marking

VHF transmitters were implanted into the abdominal cavity of chosen individuals. The operation was done by Dr. Pavel Vrbka in Ledeč nad Sázavou. The weight of the transmitters did not exceed 14 g, which is less than 2% of mink's body mass. This proportion is in line with recommendations from the specialised literature (Dunstone 1993, Kenward 2001).

The transmitters used were the M1230 from Advanced Telemetry Systems (Isanti, USA) and the TXE-2071 from Telenax (Playa del Carmen, Mexico) (with frequency ranges of between 142.0000 – 149.7000 MHz). We used AOR AR8000 and AR8200 scanning receivers (AOR LTD., Tokyo, Japan), which were connected to a three element Yagi antenna, or a twiglike omnidirectional antenna, which was placed on the roof of a car during triangulations. The characteristics of the monitored

animals are shown in table 1. The number of fixes refers to the number of independent locations of the mink.

Telemetry

The animals were located using classical VHF telemetry. In case of total loss of connection the animal was found by using an ultralight airplane. Records were taken of whether the mink was moving ('active') or resting ('inactive') at each location. The resting sites, which were found by day, were described. The exact locations were directly marked on a 1:10,000 map or were recorded on GPS map 76 (Garmin).

The Kernel method was chosen to express the home range. This was calculated in the Arc View GIS 3.2 programme with Animal Movement extension. Least square calculated value (LSQV) was used to provide a smoothing effect. These calculations gave the size and shape of home ranges, which include 95% of all animal locations.

The habitat of minks is restricted to water-courses and ponds, where minks use the immediate surroundings of the banks (most often within 2-3 m from the bank line). That is why the length of water banks is the main property of its home range. Along small streams the minks use both banks, while in larger streams they move along just one bank

(each bank creates a particular biotope). The banks of small streams (narrower than about 5 m) were counted only once (minks are able to visit both banks), whereas the banks of large watercourses (wider than about 5 m) were counted separately.

Daily VHF tracking also made it possible to determine the average travel distance during a single day in males and females. Furthermore, it enabled to set the ratio of day and night activities in relation to sex and the cause of death in the observed mink.

Camera traps

Two types of camera traps were used (Reconyx Rapid Fire – three units and Scout Guard – two units) in 2010-2013. Monitoring was carried out for 252 ‘camera trap days’. One camera trap day means one camera trap set for one day. The camera traps were usually placed in the home ranges of the radio-tracked animals, mainly under bridges of small streams flowing into the Sazava and on the river banks. Special monitoring was carried out also during a period when two females, C and F, were taking care of their cubs. The camera traps were situated next to the dens to enable daily observation of parental behaviour.

Although no detailed analysis of the diet was carried out, the combination of the telemetry and camera traps study helped to estimate the trophic niche of the American mink on the Sazava River.

Results

Mink trapping

There were 29 trappings of 19 different individuals between 2004 and 2012. In the first period (2004-2005) one mink was trapped within 66 trap nights. During this period another mink in a concrete culvert was unexpectedly caught by hand. In the period 2009-2012 15 traps were



Figure 5. It is extremely difficult to get a distinguishable picture of minks' chin spots in nature. Photo: V. Hlaváč.

used and in the course of 1579 trap nights 17 individuals were caught. One mink was trapped five times during one winter. Males were trapped much more often than females: Overall 16 different males (in 22 cases) and three different females (in 7 cases) were caught. Seven individuals were chosen for the telemetry study in order to have information from a similar number of animals of both sexes.

Use of chin spots for the identification of individuals

The chin spots of all the captured animals were documented. The large variability of spots allowed us to distinguish individual animals (figures 3 and 4). However, it was very difficult to obtain a clear image of spots in the field. During our research we obtained only few camera trap shots or pictures taken during direct observation where the spots were clearly distinguishable (figure 5). To document the spots for a reliable assessment it was usually necessary to catch the animal.

Home range characteristics

The monitoring showed a difference between males and females in home range size and spatial behaviour. The male minks' movements and spatial behaviour were more differ-

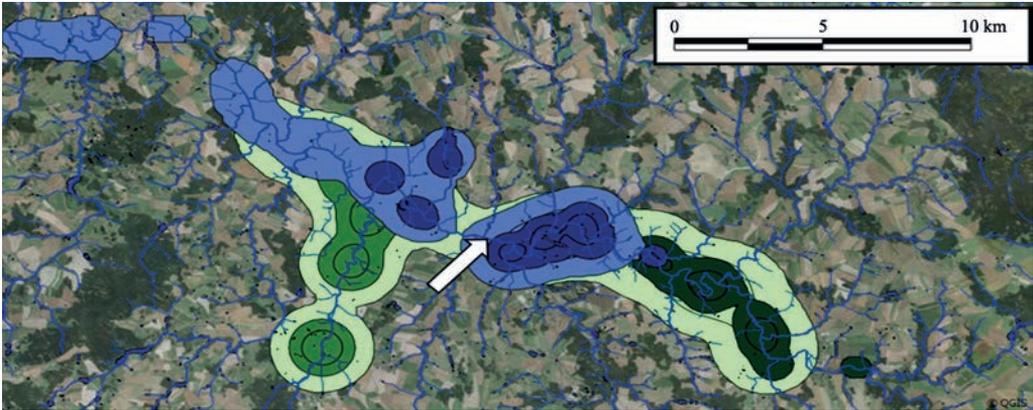


Figure 6. The home ranges of males A (green) and B (blue) during mating periods and during the rest of the year. The arrow indicates the location where both males were seen mating with the same female. Green indicates the home range of male A outside the mating season in 2004 (medium green) and 2005 (dark-green) and during the mating season (March and April) of 2005 (light-green). Blue indicates the home range of male B in 2005 during (medium blue) and outside (dark-blue) the mating season.

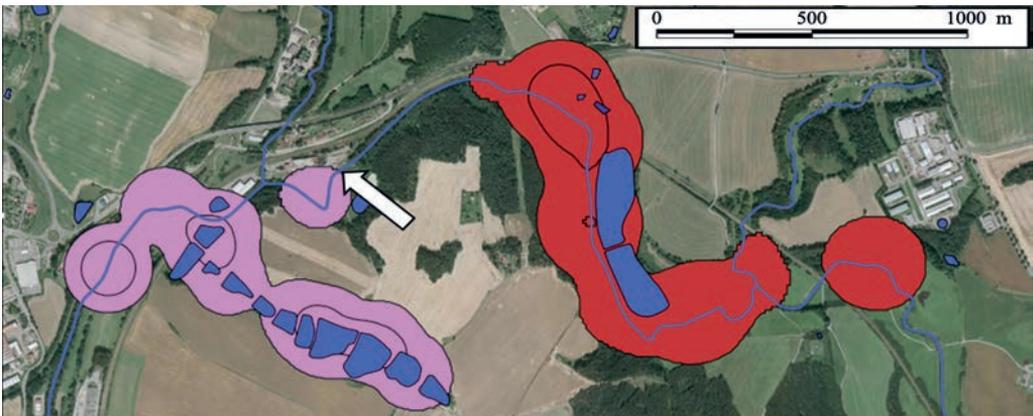


Figure 7. The home ranges of females C (red) and F (pink) in the 24 January 2011- 28 April 2011 period. The location where both females were caught is indicated by an arrow. Fish ponds and watercourses are indicated in blue.

ent during the mating season (March, April) than in the rest of the year. During the mating season males increased their home ranges and started to occupy much larger areas. They did not defend their territories at all. The males A and B used the same section of the river, having occupied large areas: male A used 137 km of banks and male B 178 km. During the mating season they met each other several times, used the same resting sites and were even seen to mate with the same female during one night. They moved quickly along the river

bank until they found a female. They then stayed there for several hours or even days. The males were able to move for long distances during one night. The maximum distance of the day/night movement was 21.3 km for male B and 20.5 km for male A. The overlap of the area which they used in the mating season was approximately 70%. Tracking on the fresh snow cover allowed us to compare the movement of the radio-tracked animals with the movement of other minks in the area. It was obvious from the track findings that this



Figure 8. The home ranges of female F (purple) and male G (green) between 30 March 2012 and 26 September 2012. Fish ponds and watercourses are indicated in blue.

area was shared also with other males.

The male home ranges were stable, apart from the mating period. However, the ranges could change after the mating season. Male A, which was monitored for two years, spent the first year (2004) on the Sazava River downstream of Havlickuv Brod and on the Usobsky stream, then after the mating season (May 2005) it moved and settled 17 km upstream along the Sazava River (measured as the length of the riverbank between the centers of the home ranges) (figure 6).

The home ranges of the females C and F were situated next to each other. Even though both females were trapped during one night at the same place, no home range overlap was recorded during the period when both females were radio-tracked simultaneously (figure 7).

Male D, which was followed at the same time, occupied a much larger area, which included the home ranges of both females.

Several weeks after female C was killed by a hunting dog, female F moved into the territory that had become free. This female (F) had a litter 36 days after transmitter implantation and her release. Her four cubs were born on 5 May

2012 and stayed in the same den until 6 June 2012 (recorded by the camera trap survey). The male G was a regular visitor to the same pond where the female had her cubs (figure 8).

There were large differences in the home ranges of males and females. The males' home ranges were smaller in 2011-2012 than in 2004-2005 (we do not have information on female home ranges for this earlier period). However, this difference was not significant (Wilcoxon Rank sum test, $P=0.2$), so the earlier data for the males could also be used for comparison. Overall, the home ranges of males were significantly larger (t -test; $P=0.01013$): on average they covered 30.4 km of banks (except during the mating season), while the females' home ranges covered just 7.5 km of banks (figures 9A and 9B). The characteristics of the home ranges are described in table 2.

Circadian activity

There was a remarkable difference in the circadian activities of males and females. The males were mostly active in the evening and

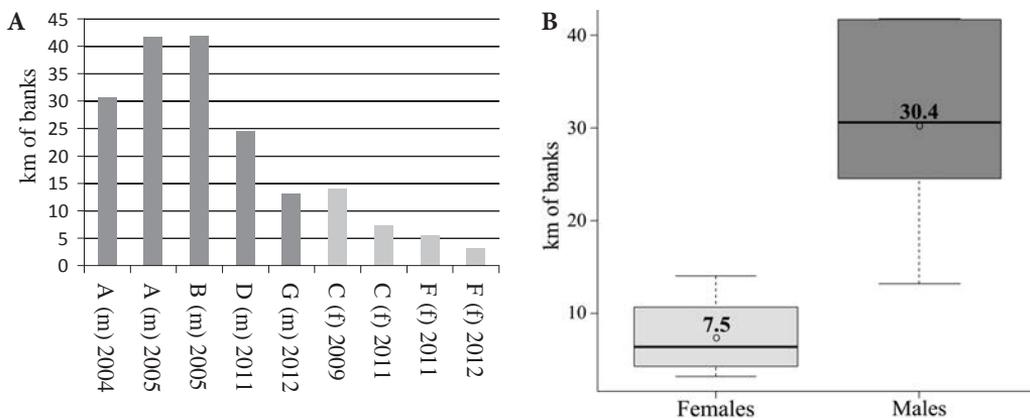


Figure 9. A. Home range size (km of banks) of individual (A, B, etc.) male (m; dark-grey) and female (f; light-grey) minks. 2004, 2005, etc. refers to the year in which the data were taken. B. Home range size (km of banks) of females and males. Mean values are marked by circles.

Table 2. The characteristics of the minks' home ranges.

Individual	Male / female	Length of waterflow in home range (km)	Length of Sazava River (km)	Length of other streams (km)	Number of water basins	Area of water basins (ha)	Length of banks of water basins (km)	Length of all banks (km)
A 2004	Male	16.163	7.135	9.028	60	7.228	7.287	30.585
A 2005	Male	19.872	13.920	5.952	32	9.252	7.902	41.694
A - including mating season	Male	80.218	35.542	44.676	91	37.212	21.743	137.503
B 2005	Male	18.260	11.145	7.115	57	24.177	12.431	41.836
B - including mating season	Male	56.799	29.819	26.980	42	148.210	93.264	179.882
C 2009	Female	5.950	4.175	1.775	12	7.800	3.965	14.090
C 2011	Female	2.930	2.719	0.211	5	5.6191	1.736	7.385
D 2010	Male	9.119	6.180	2.939	28	14.5511	9.304	24.603
F 2011	Female	1.019	1.019	0	12	67.896	3.415	5.453
F 2012	Female	0.950	0.911	0.039	2	4.852	0.851	2.750
G 2012	Male	4.215	4.121	0.094	16	73.231	4.915	13.251

night time while the females were equally active during the day and night (figures 10 and 11). Since the number of the animals involved is rather low, these findings should be verified by further research.

Movements

The longest distance travelled in 24 hours was 21.6 km (achieved by mink A). Among

females the longest distances travelled were by females E and C (5.10 km and 5.04 km respectively). Female F was the least mobile: her longest movement was just 0.85 km in one day. The average daily movements in each month significantly differed between males and females (nested ANOVA, $P=0.017$). The greatest difference was recorded during March and April, when the males' mobility greatly increased (figure 12). A higher level of mobility, in individuals of both sexes (B and

Table 3. Causes of mortality of monitored individuals.

Individual	Cause of mortality
Male A	Was found dead in his resting site – unknown reason
Male B	Did not die during monitoring
Male D	Shot by a hunter
Male G	Killed by a car on the road
Female C	Killed by a hunting dog
Female F	Killed by a hunting dog
Female E	Died 10 days after releasing – unknown reason, maybe trouble with implantation?

C), was recorded in August, the period when young animals start occupying new home ranges.

Mortality factor

The causes of mortality in the monitored individuals are summarised in table 3. While the monitoring sample was too small to evaluate mortality factors in general, it is interesting to summarise the reasons of death of the radio-tracked animals.

Six animals died during the research period: half of them were killed by a hunter or

a hunting dog. It seems that hunting may have some influence on the population density on the Sazava River. One animal was killed by a car on the road and one female died ten days after being released, probably due to troubles arising from the implantation.

Diet

The information about the minks' diet was obtained by camera trap records, direct observation and prey remains at the feeding sites. The most frequent prey included rodents - mainly water voles (*Arvicola terrestris*) (eight records) and brown rats (*Rattus norvegicus*) (five records) with, on one occasion, a muskrat (*Ondatra zibethicus*) (caught by a male mink) (figures 13 and 14). Another important prey group were fish, usually smaller individuals (five records), although one male mink caught a 7 kg silver carp (*Hypophthalmichthys molitrix*). Water birds were also recorded in the minks' diet (a female mink was pictured on a camera trap with an adult wild duck (*Anas platyrhynchos*) as her prey (figure 15). Considering the spatially limited data and the

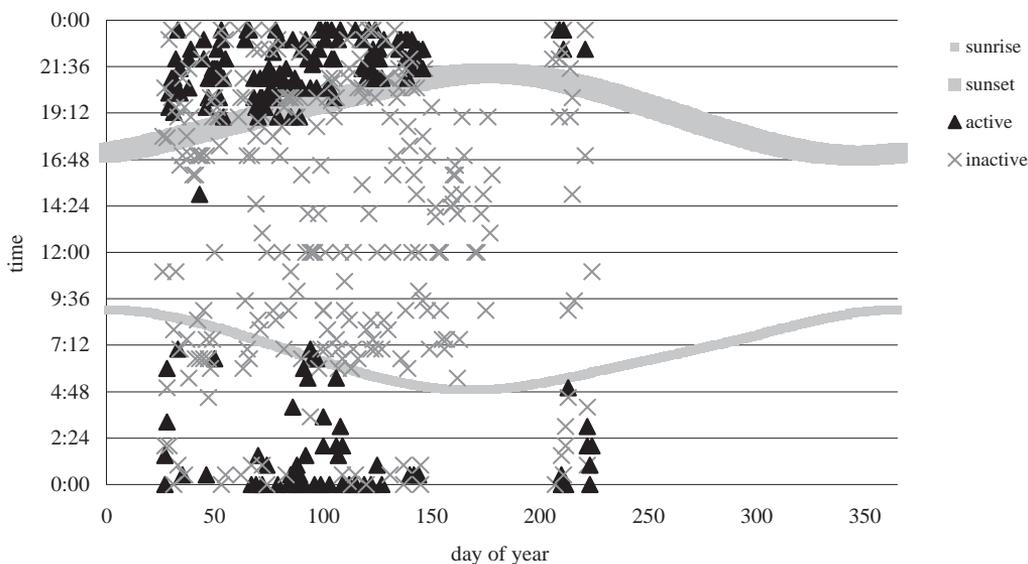


Figure 10. Distribution of active and inactive male locations during a year (1 January - 31 December), by hour of day.

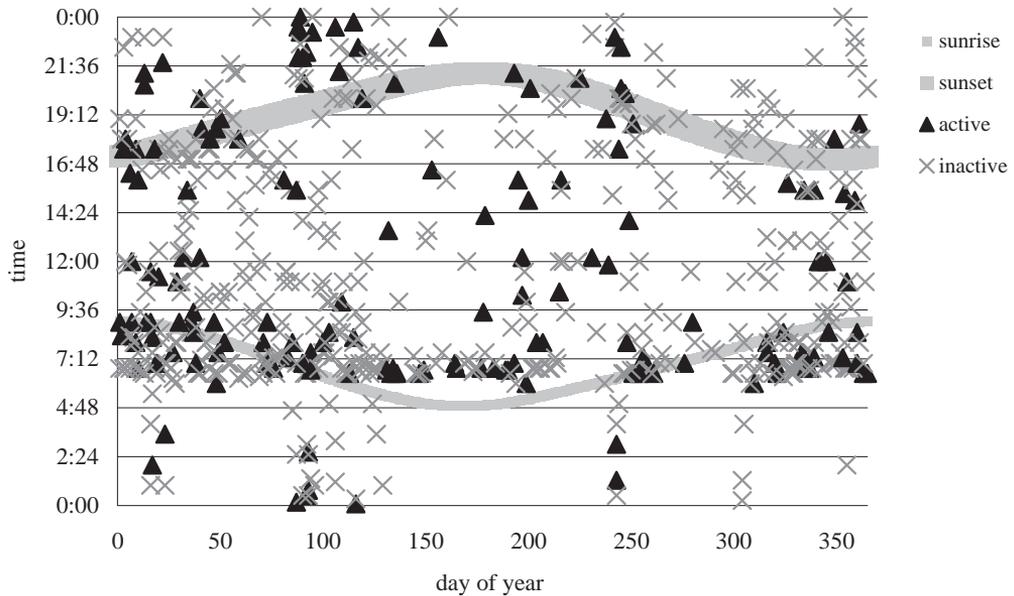


Figure 11. Distribution of active and inactive female locations during a year (1 January - 31 December), by hour of day.

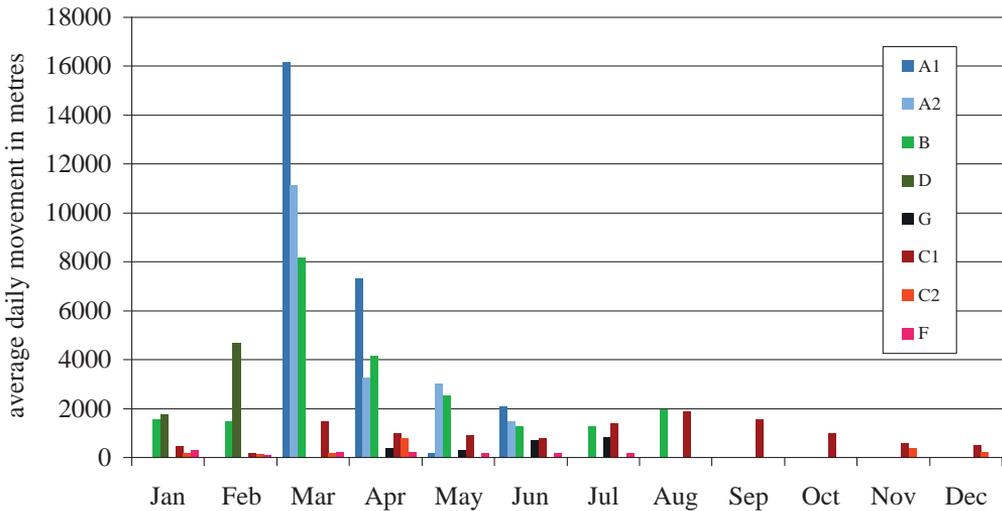


Figure 12. Average daily movements in metres by particular individuals. A1 = male A in 2004, A2 = male A in 2005, B = male B, D = male D, G = male G, C1 = female C during the period 08 Dec 2009 - 22 Jan 2011, C2 = female C during the period 29 Jan 2011 - 11 Feb 2012, F = female F.

effect of site-specific variations on the supply of prey, the spectrum of the mink diet is probably wider in range than these observations suggest.

During the monitoring period two pairs

of marsh harrier (*Circus aeruginosus*) nested within a mink's territory. The minks went past the nest, within a short distance, several times, the male G slept three times within 15 m from the nest, when the chicks were about



Figure 13. Female mink with a caught brown rat. Photo: V. Hlaváč.

14 days old. However their nest was not damaged by mink and all the chicks successfully raised.

Parental behaviour

Two females, C and F, were monitored while preparing the nesting den and raising their cubs. One of the two females was radio-tracked for two years and the other for three years. The parental behaviour of each of these females was recorded twice: female C in 2010 and 2011 and female F in 2011 and 2012.

The first record of female C settling was made 28 April 2010. She chose a place in the middle of her home range in an embankment between a river and a fishpond, surrounded with sedge (*Carex buekii*). She stayed in the den without leaving the place at all but then left it after ten days.

The next year the same female settled in a root cavity of an elder tree (*Alnus glutinosa*) on 29 April 2011. She intensively prepared the den, bringing in grass and stayed there at least till 10 May 2011. No subsequent data are available because of the failure of the transmitter battery.

Female F was seen preparing her den in a similar way (though bringing in twigs) on 30 March 2011. The following year she found the



Figure 14. Water vole is a common prey of American mink. Photo taken by camera trap.

place in the embankment between the river and the fishpond that was previously occupied by female C. She settled there on 5 May 2012 and had at least four cubs, which were firstly seen outside the den on 20 July 2012. This female was monitored throughout the whole rearing period. A great amount of data about cubs' behaviour was generated from the camera trap survey and telemetry.

The cubs were first observed outside the den at the age of 45 days. Ten days later the family moved to another den on the banks of the pond (about 100 m from the original nest). After eight more days they moved again, this time to an old pile of branches near a concrete culvert. They stayed there for a month (until 3 August), when the female was killed by a dog. By this time the cubs were fully grown. After the death of their mother they were not observed again. The last site was very suitable for animal observation, as all the animals had to use a concrete culvert to access it (figure 16). Whilst monitoring an otter regularly went past this den (figure 17) and a muskrat was also often seen on the site, although there were no interactions between them and the minks. The male G occupied the same area (the same fishpond) during the monitoring period although it was not clear, whether this male was the father of the cubs. It was, how-



Figure 15. A female mink bringing a duck to her cubs. *Photo taken by camera trap.*



Figure 16. The concrete culvert created good conditions for observing minks and other animals near the den. In this picture the mink family is returning to their den along the concrete culvert. *Photo taken by camera trap.*

ever, evident that he never contacted the cubs in the nesting den.

Discussion

Home ranges

The differences in home range size between the sexes and the overlap of male and female home ranges could be related to the distinctive sexual dimorphism in body sizes (Thom et al. 2004). The intrasexual territoriality in connection with overlaps in home ranges between the males and the females is also found in other mustelids (Dunstone 1993). This system of territoriality could minimise competition between the sexes. Sexual dimorphism in body size and the intersexual competition could result in the sexes having different behaviour and different ecological strategies.

Circadian activity

Several studies have explored the circadian activity of the American mink but their results

have differed considerably. Diurnal activity of minks was proven by Harrington and Macdonald (2008) and Garcia et al. (2009), while nocturnal activity was found by Gerell (1970), Birks and Linn (1982) and Yamaguchi et al. (2003). A study by Zschille et al. (2010) showed circadian activity to be different between males and females, with females being quite active during the day and males primarily active during the night. By contrast a study by Niemimaa (1995) found no sexual difference in circadian activity.

Our results, based on observations of four males and three females, do show differences between male and female circadian activity. The males were strictly nocturnal, while the females were both diurnal and nocturnal. What might be the reason(s) for such obvious differences in behaviour?

One hypothesis could be that the (smaller) females seek to minimise body heat loss during cold nights. However, this hypothesis cannot be supported by the evidence, as females' nocturnal activities were the same during summer and the winter periods (with colder nights).

Intra-specific competition is another possible reason why males' and females' circa-



Figure 17. An otter regularly went past the mink den, at close distance, without any interspecies interactions. Photo taken by camera trap.

dian activities differ. As there is an overlap between the home ranges of males and females, it is possible that the activity of the smaller females is shifted to the daylight hours to avoid competitive pressure from the males.

Movements

The recorded average daily movement of females was approximately 1 km, while for males it was 4.5 km. The largest difference in movements was recorded in March and April, when males travelled up to 22 km during one night, the females showed the same mobility pattern as in other months and the longest distance they covered was 3.5 km/day in this period.

Male behaviour during March and April was strongly affected by their instinctive search for new females for mating. The females were quite sedentary and stayed in their territories during the mating period. This behaviour has also been confirmed in studies in other parts of Europe (Dunstone & Birks 1983, Ireland 1990, Yamaguchi et al. 2003).

Another increase in mobility was recorded during August and September. This behaviour may be caused by the dispersion of cubs and the

efforts of older minks to protect their territories against the newcomers. This pattern was also observed by Beran (2005) and a higher trapping success (caused mainly by higher mobility) was recorded by Yamaguchi et al. (2002)

Summary and conclusions

Seven individuals of American mink (four males and three females) were radio-tracked on the Czech Moravian Highlands near Havlickuv Brod between 2004 and 2012. The animals were tagged with VHF transmitters, which were implanted into the abdominal cavity. The Kernel method was used to determine their home ranges, which were restricted to rivers, streams and ponds in the area.

The home ranges of males were significantly larger than those of females. The average size of male home ranges were 30.4 km of banks (more in the mating season), whereas the ranges of females were just 7.5 km. Overlaps between home ranges were recorded between males and females, with male ranges covering several females' ranges. Clear overlaps in same sex ranges were not recorded, except during the mating season, when males abandoned their territorial behaviour and occupied a larger area, probably with the aim of finding as many females as possible.

There were differences in circadian activity between males and females. Females were equally active during the day and night, whereas male activity was mostly limited to the night.

Differences in the movements of both sexes were also recorded. The males were able to cover a distance of up to 22 km during one night, while the longest distance covered by a female was just 5 km in 24 hours. The males were most mobile during March and April, while the females' mobility was relatively stable during the whole year. The mobility of both sexes was rather low during the winter.

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Samenvatting

Ruimtegebruik en voortplantingsbiologie van de Amerikaanse nerts in de Moravische Hooglanden (Tsjechië)

Zoals op veel locaties in Europa kreeg de Amerikaanse nerts (*Neovison vison*), oorspronkelijk ingevoerd als kweek-pelsdier, ook in de Tsjechische Republiek vaste voet aan de grond. Vanaf het begin van de jaren 1990 was er sprake van een duidelijke expansie. Doel van deze studie was informatie te verzamelen over de biologie en de ecologie (ruimtelijk gedrag, dag-nachtritme, voorplanting enz.) van deze invasieve exoot. Daartoe werd een beroep gedaan op klassieke radiotelemetrie (VHF-zender-onderzoek), aangevuld met de inzet van cameravallen en sporenonderzoek. De studie werd in de periode 2004-2012 uitgevoerd in de Moravische Hooglanden nabij Havlickuv Brod. Bij zeven Amerikaanse nertsen, vier mannetjes en drie wijfjes, werd een VHF-zendertje ingebracht. De home ranges werden globaal bepaald via de Kernel-methode en vervolgens herleid tot het totaal

van waterlopen en ander aanwezig open water. De home ranges van de mannetjes waren significant groter dan die van de wijfjes. Bij de mannetjes bedroeg de gemiddelde oeverlengte binnen de home range 30,4 km (buiten de paartijd), terwijl dit bij wijfjes 7.5 km was. Home ranges van mannetjes bleken daarbij te overlappen met die van meerdere wijfjes, terwijl dit binnen hetzelfde geslacht niet het geval was. Uitzondering op dit laatste vond plaats tijdens de paartijd (maart – april), wanneer de mannetjes hun territoriaal gedrag verloren en grotere gebieden gingen gebruiken, kennelijk om zoveel mogelijk wijfjes te kunnen vinden. Een opmerkelijk verschil tussen mannetjes en wijfjes kon ook worden vastgesteld in het dag-nachtritme: terwijl wijfjes zowel overdag als 's nachts actief bleken te zijn, waren de mannetjes enkel nachtactief. Verder verschilden beide geslachten ook duidelijk inzake hun bewegingspatroon. Mannetjes waren in staat om in één nacht afstanden tot 22 km te overbruggen terwijl voor een wijfje de grootste geregistreerde verplaatsing binnen 24 uur vijf km bedroeg. De grootste mobiliteit bij de mannetjes werd in de paartijd waargenomen, terwijl deze bij de wijfjes relatief stabiel was over het hele jaar. Tijdens de winter was de mobiliteit van beide geslachten relatief laag.

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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 interflaves 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

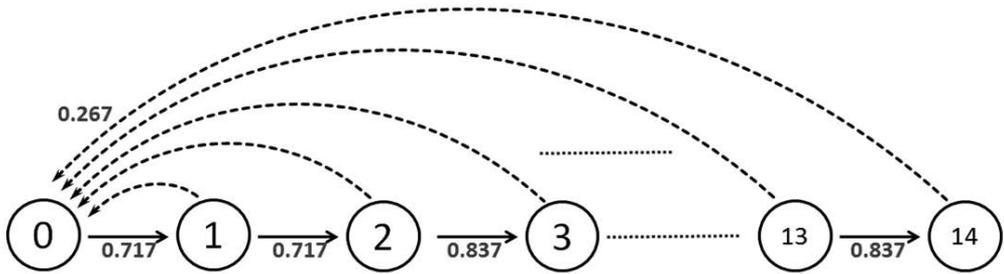


Figure 2. Matrix projection model for a European badger population near Oxford (Macdonald et al. 2009), based on post-breeding census data. The first stage therefore represents newborn cubs (zero-year olds). The population model consists of five parameters: age of first reproduction (2), age of last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

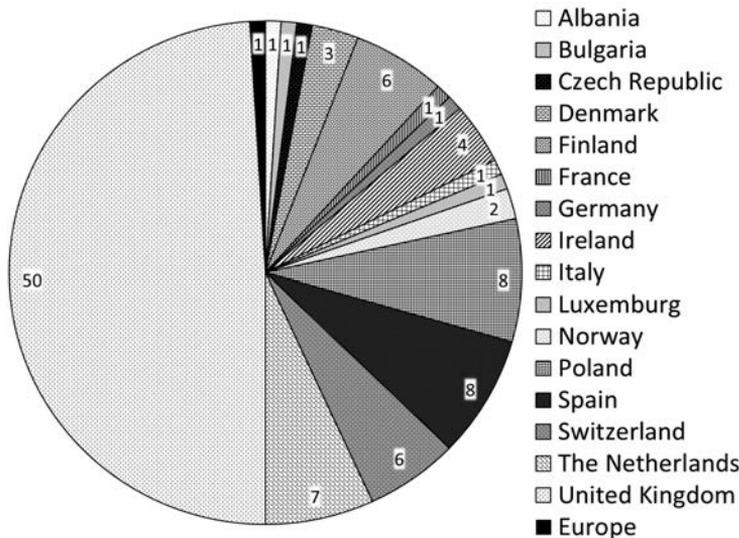


Figure 3. Countries where the studies containing data relevant to the search topic were performed, i.e. the factors influencing distribution and density of the European badger as presented in this review.

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		
Terrain characteristics and sett site availability	Rain, temperature between 5- 15°C and high air humidity	Favours earthworm availability.	Badger presence, size and shape of occupied territory and spatial organisation.	Positive	4-8	
	Cold winters, dry summers and wind	Decreases earthworm availability.		Negative		9
	Spring rainfall and high temperature	Increase cub parasitic susceptibility.		Negative		
	Suitable geology	Facilitates digging and drainage.		Limiting factor		
Slope	Slope	Favours earth removal.	Badger presence, size and shape of occupied territory and spatial organisation.	Positive	10-21	
	Aspect	Selection of sites on south to west-facing slopes.				
Habitat type	Terrain heterogeneity	Visual hiding	Population density, group size and territory size.	Positive	22	
	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.				
Food availability	Woodland	Offers cover, shelter, structural support for sett building and additional source of food items.	Population density, group size and territory size.	Positive	1, 4-5, 10-15, 23-32	
	Hedgerows and scrub	Cover and shelter				
	Grassland and pasture	Foraging, source of earthworms. Short grass is more suitable.				
Food availability	Arable fields: e.g. maize, wheat, barley	Food source: cultivated food and earthworm content.	Population size and density, territory size and shape and spatial organisation.	Limiting factor	1, 11, 24, 29, 33, 43	
	Large variety of items: e.g. earthworms, other invertebrates, birds' eggs and chicks, rodents, carrion, fruits, cereals	Food source.				

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) and triggers poaching.	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 & Barrettn 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.

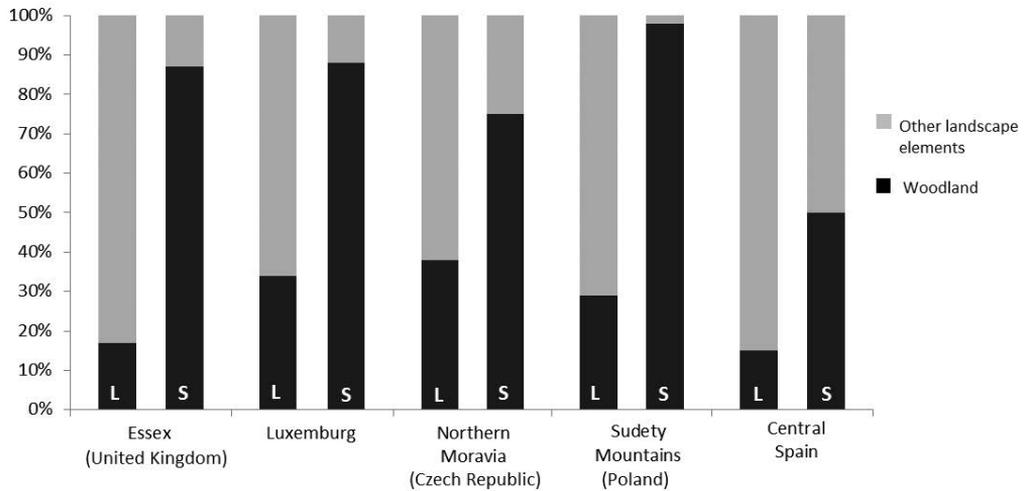


Figure 4. European badger sett site selection for either woodland or other landscape elements. Each pair of columns shows the results, respectively, from ecological studies in Essex (United Kingdom, Skinner et al. 1991a), Luxemburg (Schley et al. 2004), Northern Moravia (Czech Republic, Matyáščík & Bičík 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

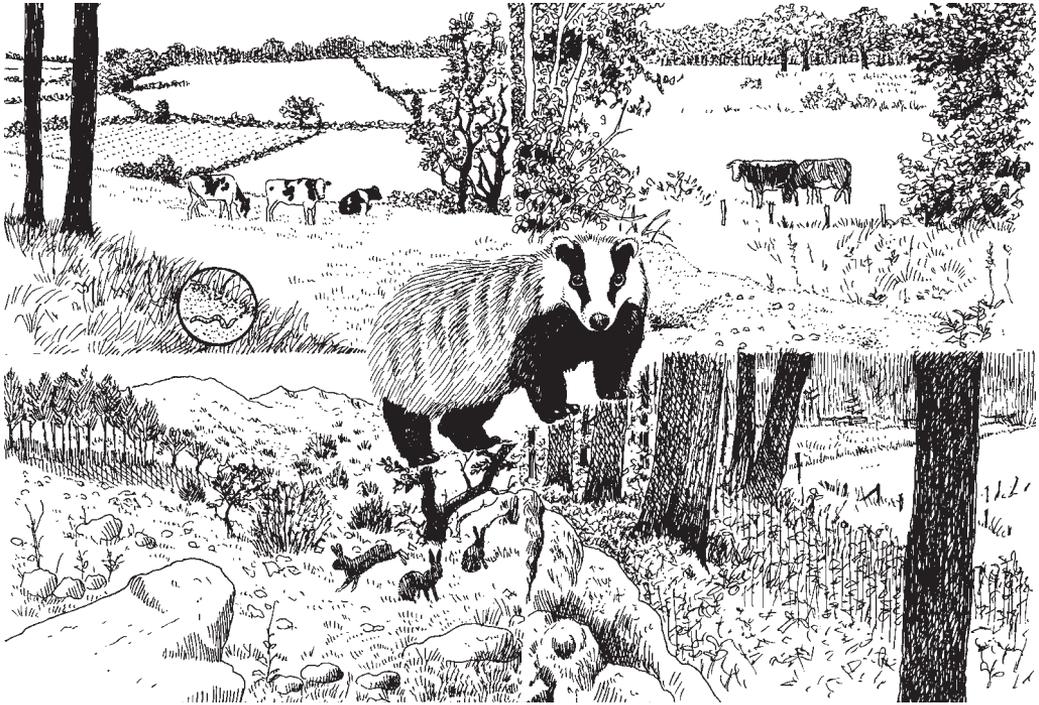


Figure 5. Illustration of four different landscapes that the European badger inhabits across its geographical range, each showing the elements that the badger preferably selects from. The very different landscape compositions illustrate the adaptability of the species. Upper-left, the landscape in the 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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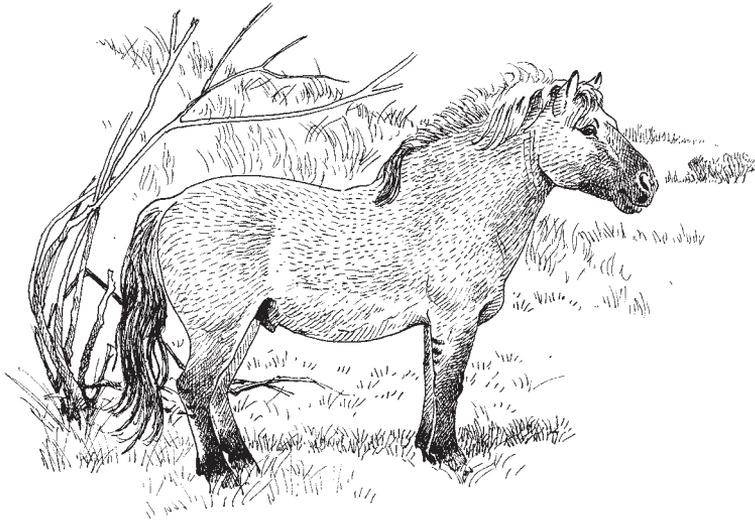
Samenvatting

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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On the origin of the Polish konik and its relation to Dutch nature management

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Abstract: After the end of the last ice age, relatively small numbers of the wild horse managed to survive throughout much of the Holocene in the heavily forested parts of Western and Central Europe. Hunting and being driven from its feeding grounds by man diminished the numbers of these animals. Probably, the last population of these horses survived in the wild in the borderland of East Prussia, Poland and Lithuania, until the 16th Century. The last specimens were housed by Jan Zamoyski in his zoo at Zwierzyniec (SE Poland). There, this (sub)species came to an end, at the end of the 18th Century. On the basis of a report by Julius Brincken in 1826, which stated that the last wild horses would have been crossed with farm horses about 1806, the Pole Tadeusz Vetulani started a breeding-back experiment in the Forest of Białowieża in 1936. It was his intention to get back the wild ancestor by selecting and crossing farm horses from the vicinity of Biłgoraj. After Vetulani's death in 1952, this experiment was taken over by the Polish state, and was moved to Popielno (NE Poland). After the cessation of the breeding-back experiment, around 1970, the konik is still bred there, but these days only as a 'primitive horse breed'. There are several pieces of evidence that show that the Brincken's report on the wild horse was misleading and inaccurate. In addition, Vetulani conducted his experiment in a careless way and, as such, his breeding-back experiment should be considered to have been unsuccessful. In the 1980s, koniks were put out in the Netherlands – first on the Ennemaborgh Estate in 1981 and later in 1984 in the Oostvaardersplassen Nature Reserve - as part of a cheaper and more 'natural' nature management in the Netherlands. There was (and still is) a perception that the konik is 'the most recent descendant' of the European wild horse. Through using specific phrases (such as 'letting nature have its way', 'primeval landscape' and 'Serengeti') managers of the Oostvaardersplassen and some media frame the Oostvaardersplassen area as an untouched and natural ecosystem, which is far from the case.

Keywords: wild horses, feral horses, archaeology, (cultural) history, ecology, morphology, nature management, perceptions.

Introduction

In the course of the 1970s, Dutch nature management adopted new approaches that are still being followed today. Previously, nature reserves were managed by periodic mowing, burning or cutting vegetation. From the 1970s onwards cattle, horses and sheep were increasingly used to manage nature reserves, as this was a cheaper method. This was influenced by the

ideas of the *Stichting Kritisch Bosbeheer* (Critical Forest Management Foundation), which advocated the (re)introduction of lost animal species (elk, wisent and wolf) or substitutes of extinct species (aurochs and wild horse). The underlying thinking was that 'nature' would become more 'natural' by using these animals. This in turn might help to evolve what some saw as more natural, half-open, park-like landscapes. In the long run, human intervention might not even be needed anymore. This line of thinking led to the konik being introduced into the Netherlands in the 1980s.

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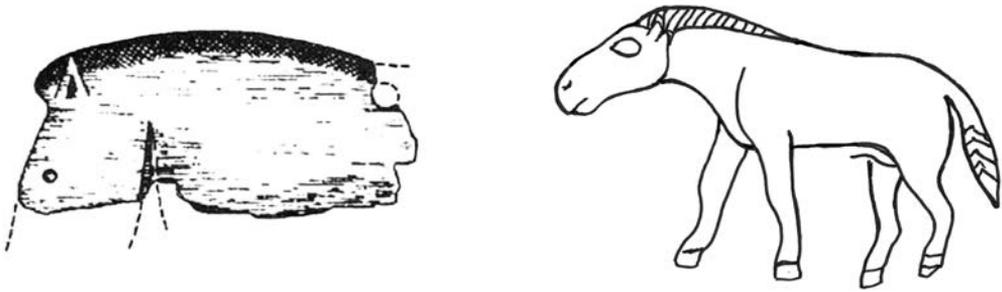


Figure 1. Images of wild horses, from the former steppes of south-east Europe. The left hand one was carved out of bone and dates from the 5th millennium BCE (Kvalynsk culture) (Kuzmina 2003). The right hand one dates from the 4th millennium BCE (Maikop culture). It was engraved on a silver beaker and forms a part of a hunting scene, together with several other game animals (Anthony 2007).

Personal doubts on the part of the author of this article, about the status of the konik as being the most recent descendant of the European wild horse, were the initial underlying reason for the study on which this paper is based. In spite of what was claimed, koniks show nearly no striking characteristics of the wild horse, as regards coat colour, mane form, etc. Later, the research was stimulated and further expanded as a result of the commotion over the mass winter starvations of large herbivores in the Oostvaardersplassen area (Province of Flevoland, between the towns of Almere and Lelystad), that have occurred since 2003. The research concerns the history of the European wild horse, the origin of the Polish konik, and its current use in modern day nature management, and perceptions about these horses.

Methods

The research on which this article is based was done as a PhD thesis at the Vrije Universiteit in Amsterdam and was mainly based on literature reviews and other sources (bones, interviews, field visits). The study draws on historical (archaeological and cultural-historical data), biological (animal morphology, ecology, DNA) and philological data. To access this material, libraries and archives in

the Netherlands, Germany and Poland were visited. In addition, field data was gathered from field visits to nature reserves, including the Oostvaardersplassen Nature Reserve, the primeval forest of Rothwald (Austria) and the Vltava flood plains (Czech Republic) to find data on natural processes, and the Sieraków Stud Farm (Poland) to learn more about the ins and outs of konik breeding.

Results

The Holocene horse of Western and Central Europe

During the last ice age, a wide steppe belt extended from Ireland through Europe and Asia as far as North America, mainly consisting of grassland. About 12,000 years ago, the climate changed drastically. Under the influence of increased precipitation and higher temperatures, in Western and Central Europe this steppe belt turned into a mostly forested area (Guthrie 1990, Mitchell 2005, Mol et al. 2006). Large herbivores were not able to prevent this forest growth (see van Vuure 2005 and the references in note 3). Horses were very common on the steppes; there they had plenty of room and grass at their disposal. From the Miocene onwards, the horses developed several bodily adaptations, concerning



Figure 2. The shaded part shows the probable distribution area of the wild horse in Western and Central Europe during the Holocene. This horse died out in southern Sweden and England halfway through the Holocene. It was probably absent from Italy and the Southern Balkans during this time, given the lack of bone finds there (from van Vuure, in press). The former Holocene distribution area of the wild horse in Eastern Europe and Asia is not well known. 1. Dereivka 2. Botai.  Distribution area of the Przewalski's horse, during the 19th and 20th Centuries.

locomotion (limb and muscle constructions), dentition and energy management, that enabled them to better cope with grassy vegetation and predators (Franzen 2010). After the climate changed and forests grew in Western and Central Europe, the horses found themselves in a much less suitable habitat. In North America, the wild horse died out, but in Europe it managed to survive. During the Holocene, in the steppes of Southeastern Europe (e.g. Ukraine) and Central Asia, wild horses survived for a long time in large numbers. The archaeological sites of Dereivka (Ukraine) and Botai (Kazakhstan) (see figure 2), show that wild horses constituted 70-80% of the animals caught by man, at this time (Levine 1999, Anthony 2007). The Przewalski's horse is the remnant of these former large horse populations. About 3500 BCE, the horse was domesticated in the steppe areas of

Ukraine and Kazakhstan (Outram et al. 2009).

After the transition to the Holocene, the numbers of wild horses¹ in Western and Central Europe drastically decreased. Judging from the limited number of sites and bones of this horse, it must have become a relatively rare animal by then (Clason 1986, Uerpman 1990, Benecke 1993, 2006, Döhle 1999, Lõugas 2006, Sommer et al. 2011, Bendrey 2012). Wild horse generally constituted less than 5% of human catches; very often it was lacking. For red deer (*Cervus elaphus*) the opposite holds: during the last ice age it was rare, but during the Holocene it became very common (Zeiler & Kooistra 1998, Hüster-Plogmann et al. 1999, Lauwerier et al. 2004, Louwe Kooijmans 2013). The many thousands of retrieved bones of red deer from the Holocene contrast sharply with the few wild-horse bones. We also know that wild horses, if available, have

always been a sought-after catch (Mager 1941, Levine 1999, Anthony 2007). In the Netherlands too, some Holocene sites such as Hoge Vaart, Swifterbant, Hekelingen and Schokland provide bones of wild horse (Modderman 1953, Clason 1986, Gehasse 1995, Laarman 2001). In the predominantly forested habitat of Western and Central Europe², the wild horse was apparently able to find just sufficient opportunities to survive. In the forest itself, there must have been too little grass available for them to feed on. The only areas that probably were suitable for horses to live in, were marshy areas, where trees could not grow (van Vuure, in press). These would have been the grass and sedge marshes along rivers and at lakes and coasts. The bodily adaptations that were required to live in small, scattered grassy habitats in a large wooded area, would have included a reduction in body size and an adaptation of the coat colour (van Vuure, in press). A (relative) broadening of the hooves also appears to have been an adjustment to life on soft soils. This latter adjustment arose at the transition from the Pleistocene to the Holocene (Kuzmina 1997, Baales 2002, Bignon & Eisenmann 2006, Van Asperen 2010, Boeskorov et al. 2014). As far as it can be currently ascertained, the wild horse of Western and Central Europe was relatively small, with a shoulder height of 120 -130 cm. It had a dun to dark brown coat colour, with a very dark dorsal stripe on the back. The short erect mane was also a very dark colour.

As man hunted the wild horse and brought land into cultivation, wild horse numbers decreased. Because it is difficult to distinguish bones of the wild horse from bones of the domestic horse, it is difficult to ascertain how quick this decline was, and to what extent in which areas. Mentions of 'wild horses' have been handed down to us from both classical antiquity and the Middle Ages. It is often difficult to make out whether these concerned originally wild horses or feral domestic ones. However, one area in Europe stood out in terms of number and nature of the mentions

of 'wild horses' (van Vuure, in press). This was the area of the Great Wilderness. This wilderness area of forests and marshes, hardly influenced by man, was largely situated in former East Prussia, and partly in neighbouring Poland and Lithuania (figure 3). Wild horse probably still existed there from the late 13th to the early 16th Centuries (Mager 1960). The descriptions of the horses living there in the wild, of their physical appearance (body size, coat colour), their nature (ability to be tamed, shyness), and the way man regarded and treated them (they were sought-after by the nobility for their private zoos, but regarded as useless for production), might be considered as valid arguments to believe that this really was the last population of wild horses of Central Europe. Alongside the wild horse, aurochs (*Bos primigenius*), wisent (*Bison bonasus*), elk (*Alces alces*) and wolverines (*Gulo gulo*) also held out for a relatively long time in the Great Wilderness. At the end of the 16th Century, mentions of the wild horse in the wild abruptly ceased. From that time on, (reliable) mentions of the wild horse have been connected with Jan Zamoyski, an influential Polish count, and his family. In the late 16th Century, Jan Zamoyski founded a large and prestigious zoo and wildlife park near the village of Zwierzyniec, in SE Poland (see figure 3). Mentions and descriptions of wild horses in this zoo have been handed down from the late 18th Century. Hacquet (1794), who visited this zoo, mentioned that the last wild horses were either shot there, or found their end in the wild-animals theatre (*Hetztheater*) in Lemberg (now Lviv, Ukraine). Descriptions of 'wild horses' in the Russian steppes were recorded well into the 19th Century, but there are large doubts about their reliability (van Vuure, in press).

The origin of the Polish konik

An important influence on current thinking on the European wild horse is the book pub-

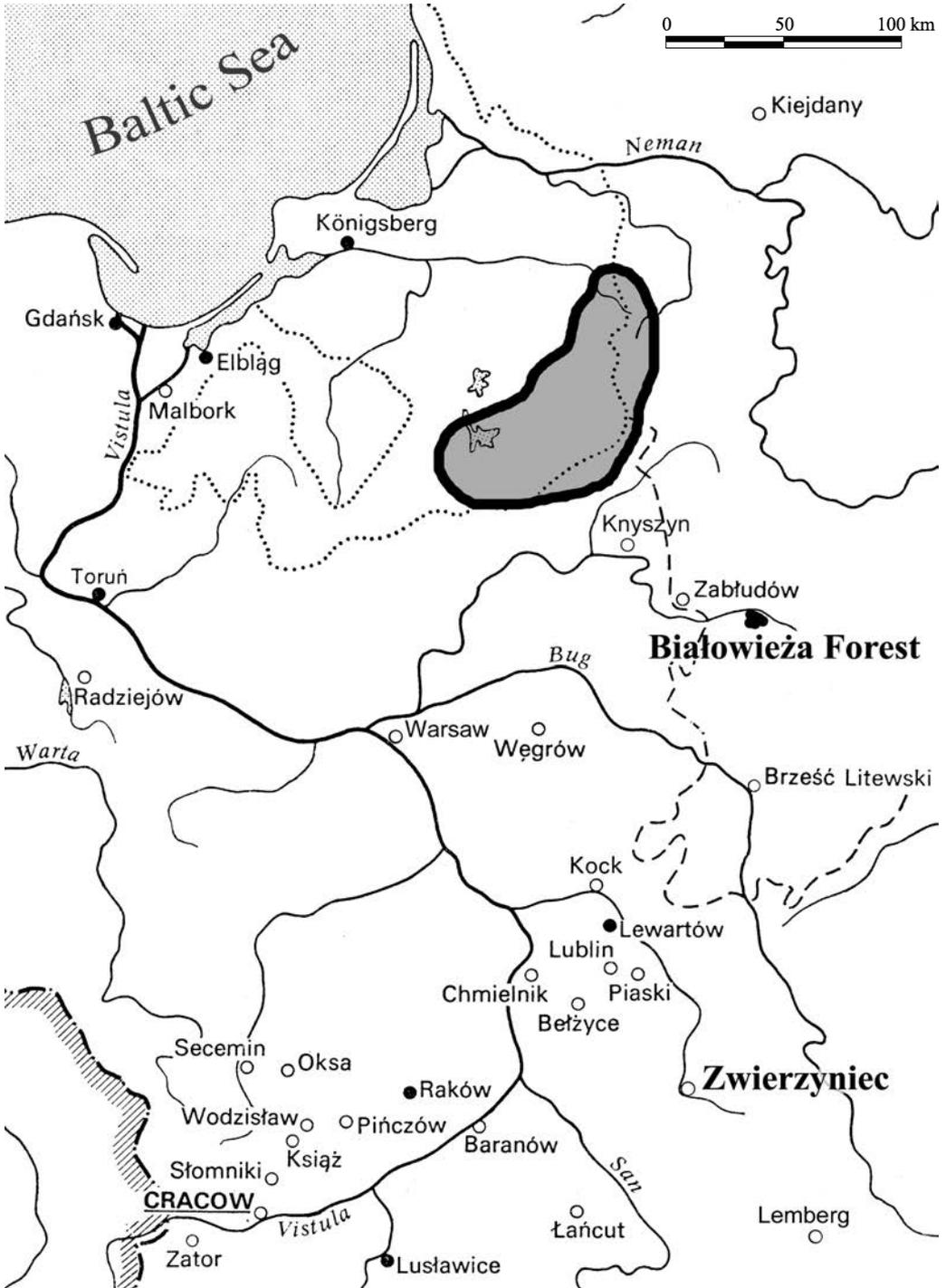


Figure 3. Map of East Prussia (capital: Königsberg) and a part of Poland and Lithuania, in the 16th Century, showing the supposed last living area of the wild horse of Central Europe, the Forest of Białowieża and the village of Zwierzyniec.

lished by the German forester Julius Brincken in 1826, in which Brincken described the flora and fauna of the Białowieża Forest, a large primeval forest situated on the border between Poland and Belarus (see figure 3), and also paid attention to the lost wild horse. The descriptions he gave of this animal and its disappearance continue to be central to the 20th Century perceptions about this horse and the Polish konik, bred halfway through that century. Brincken wrote that the Białowieża Forest had formed the last living area of the wild horse. During the late 1780s, the last wild horses would have been captured there and transported to the zoo of the Zamoyski family. About 1806, he claimed that they were distributed among local farmers, who then crossed them with their own horses. According to Brincken, in his time 'these wild horses would be still recognisable among the horses of the farmers'. However, Brincken did not state well what these horses looked like, nor where he got his information from (which is a common shortcoming of Brincken's style of researching and reporting).

Some years after the publication of Brincken's book, considerable criticisms were made of it by contemporary local scientists (see Daszkiewicz et al. 2004). According to these critics, Brincken was often very inaccurate in collecting and checking data about plant and animal species. The book was "teeming with errors, inaccuracies and fabrications" (Daszkiewicz et al. 2004, p. 25). For instance, Brincken mentioned the occurrence of *Tilia platyphyllos*, *Acer pseudoplatanus*, *A. campestre*, *Alnus incana*, *Sambucus nigra*, *Populus alba*, *Prunus spinosa* and *Crataegus oxyacantha*, tree species that - according to contemporary and current experts (Daszkiewicz et al. 2004, Błoński et al. 1888, Faliński 1986) - did not grow in that forest. As for animals, Brincken mentioned the occurrence of the Russian flying squirrel (*Pteromys volans*), three different 'species' of brown bear (*Ursus arctos*) (a large, nearly black bear, a medium-sized brown one and a silver col-

oured small one), wolverines (*Gulo gulo*), two different 'species' of red squirrel (*Sciurus vulgaris*) (a white one and a gold coloured one) and steppe polecat (*Mustela eversmanii*); certainly not all of which occurred there at that time. In addition, he gave several incorrect data on wisent (European bison) numbers, and on local geography and history. These are just a few of Brincken's many errors. However, the criticisms, expressed by experts like S.B. Górski, F.P.S. Jarocki and E. De Ronca, were soon forgotten. Later, various authoritative writers, especially from abroad, referred to Brincken's book as a reliable source of knowledge about the Białowieża Forest. In the 20th Century, Brincken's version of the physical appearance and the disappearance of the last wild horses began to play an influential role in the debate on whether descendants of the last wild horses actually still existed. The next step in this development was a research, by Grabowski & Schuch in 1921, done on farm horses (called 'koniki') in the vicinity of the village of Biłgoraj, about 20 km west of Zwiierzyniec. Their research described the local farm horses and how they were linked to the last wild horses from the Forest of Białowieża. This research motivated Tadeusz Vetulani, an animal breeder, to start his own research on farm horses near Biłgoraj.

Vetulani carried out his research on the koniks of Biłgoraj in the course of the 1920s. The research consisted of measuring a series of skull characteristics in these horses, e.g. lengths and widths of the different parts of the skull, the form of the forehead and that of the profile line of the skull. These characteristics were compared with the skull characteristics of two supposedly wild horses (known as the Cherson tarpan and the Tauric tarpan). These two 'tarpans' were caught in the Russian steppes halfway through the 19th Century. He did this comparison on the basis of a statistical method, which at that time was known as the 'differential method of Czekanowski'. This method was based on determining the differences between each skull and every

other one, with regard to x number of characteristics. Per skull pair, these differences were added up and divided by x to obtain the overall average. The smaller this average, the greater the relationship between the skulls, reasoned Czekanowski.

During the 1930s, Vetulani believed he had obtained sufficient evidence to label the koniks of Biłgoraj as recent descendants of the last wild horses of Central Europe. He then conceived the plan to try and breed back that wild ancestor, using a selection of horses from (mainly) Biłgoraj. In his breeding experiment, Vetulani focused on characteristics such as the 'mouse-grey' summer coat, the white winter coat, the dorsal stripe and the erect mane. In 1936, he started such a breeding-back experiment in a small reserve in the Forest of Białowieża (Vetulani 1936) where, according to Brincken, the last wild horses would have lived³. When the second World War broke out in Poland, in September 1939, the experiment was taken over: first by the Russians, and subsequently by the Germans in June 1940. The Russians had a strong interest in Vetulani's experiment and wanted to continue it. The German management of the experiment practically dismantled it, through the agency of Lutz Heck. After the war, Vetulani was able to continue his experiment with the remnants of the experiment, supplemented with newly acquired horses – even though the newly-installed communist government increasingly frustrated his work. After the death of Vetulani, in 1952, the experiment was moved from Białowieża to Popielno, in NE Poland, where the state drove it in two directions from 1955 onwards (Pruski 1959). One part of the koniks was put out in a large reserve, to run wild. The other part went on as the 'stable group'. The latter group was bred to acquire a better agricultural horse. In subsequent years, regular exchanges occurred between the two groups of horses to prevent inbreeding. About 1970, the authorities came to the conclusion that the breeding of agricultural horses was no longer necessary as the tractor would take

over the role of the farm horse. It was also decided that it was not possible to breed back the wild horse, and the breeding was turned to "a kind of preservation breeding of a primitive horse breed" (Jeziernski & Jaworski 2008). Today, the Polish konik is used in various branches of equestrianism, crossed with other horse breeds, and exported. The koniks that were bought to the Netherlands in the early 1980s came from Popielno.

Criticisms of Brincken and Vetulani

As already mentioned, the contemporary criticisms of Brincken's book were soon lost to oblivion. Thanks to the publication by Daszkiewicz et al. (2004), there is once again more awareness of these criticisms. A closer study of Brincken's book, made as part of this PhD research, showed that it contains many more errors and fabrications in the reporting of the extant flora and fauna than initially thought. In particular Brincken's report on the wild horse had never been criticised by anybody. His report turned out to be very shaky (van Vuure, in press), because he wrongly quoted or interpreted texts from a number of authors. For instance, Brincken's assertion that the last European wild horses lived in the Forest of Białowieża in the 18th Century is inaccurate. He misinterpreted texts by the Polish authors Rzączyński (1742) and Czacki (1801). Rzączyński wrote about wild horses in the 16th Century and these were not located in the Forest of Białowieża. In fact, Czacki's text also concerned wild horses in the 16th Century and a careful reading of his text suggests that a printing error is responsible for a wrong time indication. Secondly, there are no reliable 18th-century authors, who mention this horse being extant in Poland or Lithuania in the wild, in the 18th Century; neither Connor (1700), nor Rzączyński (1742), nor the Forst-Ordnung für Ost-Preußen und Litthauen (1775), Kluk (1779), Büsching (1788), Gilibert (1796) or Czacki (1801) mentioned it. Thirdly,

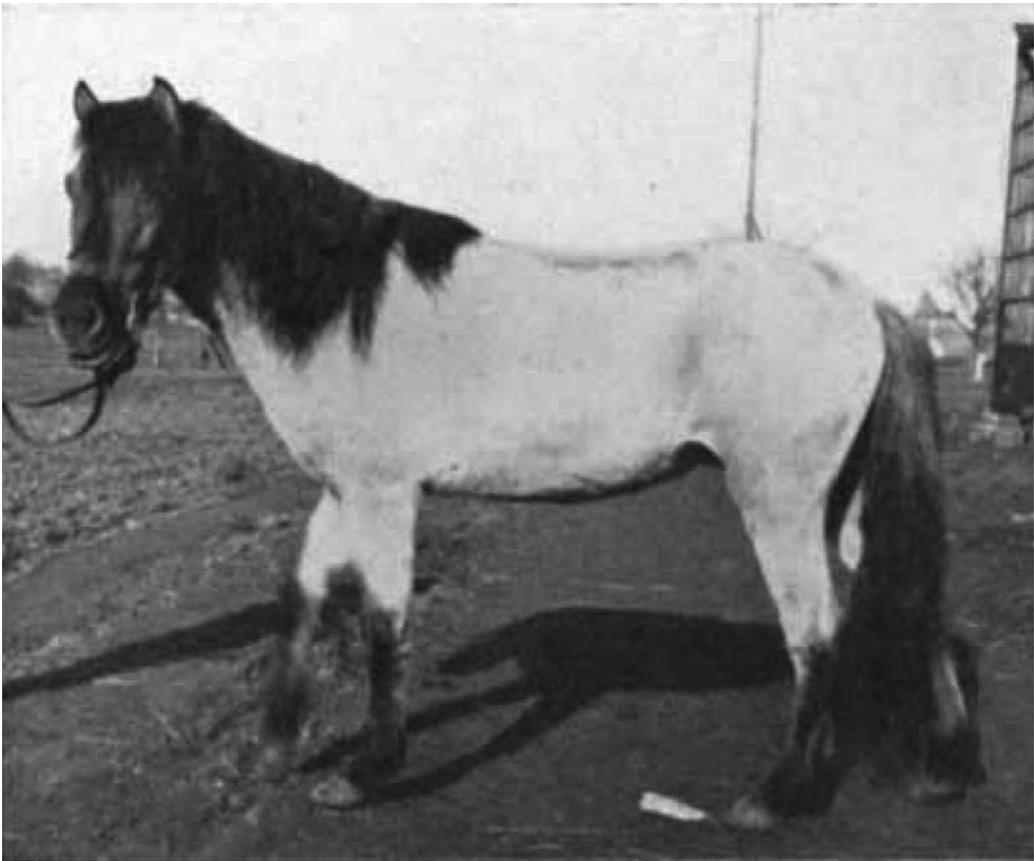


Figure 4. The konik stallion Tref in its white winter coat in March 1936. For Vetulani, Tref was one of the most important breeding horses in his experiment (from Vetulani 1938).

there are good political reasons to assume that the last wild horses were not transported from Białowieża to Zwierzyniec in the 1780s, as Brincken described. Firstly, the then Polish king was very interested in hunting and big game and would probably have done everything in his power to keep these horses at Białowieża. Secondly, these horses would have been transported to enemy territory: at this time Zwierzyniec was situated in Austria, which annexed a large part of Poland in 1772. Moreover, there are already mentions of wild horses at Zwierzyniec from the early 1770s. Finally, it seems unlikely that the last wild horses would have been distributed among local farmers, as Brincken described, as ‘farmers’ were the lowest social class. They

were called serfs, but were in fact slaves, without any property and at the mercy of the arbitrariness of the estate owner. During the 1780s and 1790s, an economic crisis raged in that region (Galicia, in SE Poland), there was great social unrest and the Zamoyski family was regularly on war-footing with these ‘farmers’. It is unlikely that the Zamoyski’s would have fêted these ‘farmers’ with great gifts. And even if these farmers were given the wild horses, it would have been counter-productive for them to cross them with (relatively highly bred) farm horses. Because of their ‘weak’ constitution and ‘bad’ character these wild horses were “of no use at all” (“*nullum ad usum*”) for agriculture, as several 16th-century authors had observed (e.g. Stella 1518, Gra-

tiani 1669). Moreover, horse breeding was at a high level at Zwierzyniec, from the late 18th century onwards, and expensive horses were being imported from Prussia, Turkey, England and Italy for breeding purposes. It seems more likely that the last wild horses were, as Hacquet (1794) wrote, deliberately killed in the early 1790s. Lack of interest and economic cutbacks must have been the reason for this.

The untenability of Brincken's account is reason to criticise Vetulani's work. Another relates to the methods employed by Vetulani, while researching the koniks of Biłgoraj, and the execution of his breeding-back experiment. His experiment was not objective, he selected the animals to measure from those that already met his expectations. Because well-known hippologists of the time, such as L. Adametz and O. Antonius, considered the wild horse as being of the eastern (oriental) type, Vetulani removed all western type Biłgoraj horses from the basic material to be researched, in favour of oriental ones. Afterwards he concluded, understandably, that the wild horse was of the oriental type. To compare these horses, he also departed unconditionally from the originally wild character of the Cherson tarpan and the Tauric tarpan, whose skull measures were included in the experiment. In addition, Vetulani used some other horse skulls, found in archaeological sites, which he assumed to have belonged to wild horses; however, afterwards they turned out to be from domestic horses (Herre 1939). Vetulani's use of the differential method of Czekanowski was also made arbitrarily (Skorkowski 1934). Other researchers, using the same data, came to different conclusions. Moreover, Czekanowski himself changed his method, because of criticisms, while Vetulani continued to use the method that Czekanowski had devised initially. Later, Czekanowski's method became entirely obsolete and was abandoned, because of its unsoundness. By giving so much focus to certain skull characteristics (e.g. the concave profile line of the head), as being typical of the Central Euro-

pean wild-horse (sub)species, Vetulani failed to realise that these could fall within the natural range of variation of a horse species (Herre 1939). For example, Przewalski's horse can also have a concave head profile line. Moreover, according to Herre, Vetulani had been overly influenced by the dubious assumptions of authorities of the time, such as Adametz and Anthonius, who not only considered the Cherson and Tauric tarpans as being originally wild horses, but also considered certain horse breeds, including the Arabian and Bosnian breeds, to be 'descendants of the tarpan'. Moreover, both disagreed with each other as regards the exact appearance of the 'tarpan' skull.

After the breeding of koniks was moved to Popielno, in 1955, the initial breeding objectives of Vetulani were partly abandoned (Pruski 1959). The white winter coat (see figure 4) was no longer aimed for, nor were the concave profile line of the head and the short erect mane. Inbreeding, sometimes used by Vetulani, was prevented as much as possible, from 1955 onwards. Eventually, as mentioned above, the actual back-breeding ceased. Today, the konik with its blue dun coat colour, its shoulder height of 130-140 cm and its long hanging mane bears little resemblance to the wild horse.

The introduction of the konik in the Netherlands

In 1981, the konik was introduced to the Ennemaborgh Estate (in the Province of Groningen) as a substitute of the extinct European wild horse, to be used in the new approach to nature management (Poortinga 1981). It was considered to be the closest living relative of the extinct Western and Central European wild horse and to be well suited for re-establishing the former natural landscape. Three years later, in 1984, the (Dutch) Forestry Commission also purchased koniks from Poland, which were put out into the



Figure 5. Konik horses in the Blauwe Kamer Nature Reserve, near Rhenen, the Netherlands. Photo: T. van Vuure.

Oostvaardersplassen Nature Reserve in the same year. In the previous year the Dutch Forestry Commission had introduced Heck cattle in the same area with the aim of establishing short grassy vegetations for the benefit of the many greylag geese (*Anser anser*) occurring there. In addition, the commission was also regulating the water level for the geese's benefit (Poorter 1982). The, then already, massive occurrence of these geese was and is considered by many as a genuine primeval phenomenon in north-western Europe. However, in the Netherlands there are no historic descriptive accounts or evidence from archaeological excavations (Zeiler 1997, Lauwerier et al. 2005, Brinkkemper et al. 2010; mallards - *Anas platyrhynchos* - turned out to be much more hunted) to support this belief. Nevertheless, a high priority is given to preserving large geese numbers in the Oostvaardersplassen Nature Reserve yet.

The idea was that the deployment of horses, which graze in a somewhat different way

than cattle, would create a more varied vegetation. The Forestry Commission had chosen the konik, not only because it was considered as a primitive and hardy horse breed but also because it was considered to be "the most recent descendant of the wild horse" (Vera 1984). They also thought it important that the konik would not immediately remind people of a common domestic horse, and arouse the public's pity when it lost a lot of weight in winter. The target that was applied to the Oostvaardersplassen: 'realising short grassy vegetation for geese', has since been expanded. There was a view that it was important to show that the 'natural' Holocene landscape of Western and Central Europe was actually a semi-open landscape, emerged under the influence of grazing and browsing by large herbivores such as wisent, aurochs, wild horse and others. By the late 1970s, this idea had already been developed by the Critical Forest Management Foundation and others (e.g. van de Veen & van Wieren 1980, Poortinga

1981, van der Lans & Poortinga 1986). Later, Vera (2000) tried to give this view a broader scientific basis, by means of palynological and other data. The idea that the original natural landscape of the Holocene was half-open, has found a lot of support among biologists and nature lovers (e.g. Bunzel-Drüke et al. 1994, Olf et al. 1999, Wigbels 2002). On the other hand, there has been criticism of it from archaeologists (e.g. Zeiler & Kooistra 1998, Louwe Kooijmans 2012) and silviculturists (e.g. Borgesius & van Tol 1998, Feijen 2003, Bobiec et al. 2011, Tanentzap et al. 2012), who argue that that landscape was heavily and densely forested and that this would have limited the numbers and impact of large herbivores. The debate on this continues to this day.

Koniks have successfully developed both on the Ennemaborgh Estate and in the Oostvaardersplassen and have also been introduced to other Dutch nature reserves (figure 5). On the Ennemaborgh Estate, human intervention limits the number of koniks to around 30-35 living on an area of 170 hectares. By contrast, in the Oostvaardersplassen area, nature determines the size of their population, through natural food availability and climatic factors. In recent years, the number of koniks there has fluctuated at around 900. A few years ago, there were around 4000-5000 Heck cattle, koniks and red deer on this site, which means one large herbivore per 0.5 ha. Since the winter of 2002/2003, and especially in late winter, large scale starvation of Heck cattle, koniks and red deer have regularly occurred. Such a level of mortality was hitherto unknown in the Netherlands. This mortality, and possible management measures to control it, have been (and continue to be) fiercely debated, and return with some regularity in the mass media (van Vuure, in press). Under the current management regime of the Oostvaardersplassen animals that are near death are shot, to avoid animal suffering and public outrage. Dead Heck cattle and koniks also need to be removed as much as possible from the area, to prevent possible outbreaks

of animal diseases that might be harmful to nearby commercial livestock units.

Perceptions surrounding the wild horse and the konik

Historically, the horse has occupied a very special place in human society. Initially, it formed a major catch, attractive because of the meat and the hides it provided. Once the horse was domesticated, other material, and immaterial, values were added. The horse not only played an important role in transport and warfare, but also in religion, folklore and in providing social status. By being able to ride horses, people were able to move rapidly over large distances. This greatly contributed to the spread and influence of the Indo-European tribes from their area of origin, the Eurasian steppes (Anthony 2007).

The views on the last wild horses in the Great Wilderness varied quite a lot. In general, people had little appreciation of them. These horses would have been too weak and have had too 'bad' a character to be deployed for the army or agriculture. The nobility, on the other hand, were very interested in them. To them, this horse, like the aurochs, the wisent and the elk, was a sought-after zoo animal in the 16th Century. Nobles did not spare trouble nor expense to get such special animals from afar into their zoos, to show them to family members and high society, and acquire a lot of prestige. For such reasons, the powerful Polish nobleman Jan Zamoyski had wild horses in his zoo around 1600, alongside other unusual animals including even aurochs, an animal that then only occurred in the Royal Forest of Jaktorów, in Central Poland. In the 1560s, the wild horse had already become so rare in the Great Wilderness, that it was no longer possible to supply the demand from foreign nobility.

Initially, the research on, and the breeding of, koniks in Poland, by Vetulani and later the Polish State, had nothing to do with nature

management. It started as a morphological study of a group of 'primitive' horses, in an agriculturally backward region. Grabowski & Schuch (1921) linked these horses, through Brincken's account, to the extinct Central European wild horse. Vetulani, in particular, added an aspect of national pride to this story. In a speech in 1927, he was proud that the 'tarpan', as he called the extinct European wild horse, had retained its superior features, not only in the koniks of Biłgoraj, but in more Polish horses (Vetulani 1927). According to him, this would open up unprecedented possibilities for breeding horses especially for agriculture, and even for equestrian sports. With financial support from the Ministries of Agriculture and of War, which hoped for better horses for agriculture and the army, he began his breeding-back experiment in 1936 (Vetulani 1938). For financial reasons, Vetulani seems to have pretended, or to have even thought to himself that a bred-back wild horse would also be fit for agriculture and the army. Another aspect of back-breeding the konik had to do with Poland, becoming an independent country again in 1921 after 126 years. Breeding the konik contributed significantly to national pride (Czarnowski 1957, Lizet & Daszkiewicz 1995, Wajrak 2000, Daszkiewicz 2003). Poland was 'back on the map' and had been able 'to breed back the European wild horse', a horse that was so strongly associated with Polish nature and Polish history.

The role allotted to the konik in the Netherlands was of a very different nature. Here, the 'resurrected wild horse' was chosen to give nature its 'original appearance'. This was one of the reasons why it was introduced to the Oostvaardersplassen. The image of the konik as 'bred-back primeval horse', along with Heck cattle as 'bred-back aurochs', greatly contributes to the current perceptions of the Oostvaardersplassen (Markerink 2002, Vera et al. 2007, Smit et al. 2010). Nature managers and the media regularly describe this nature reserve as a 'primeval landscape, such as those that could be seen in the Netherlands thou-

sands of years ago' (Staatsbosbeheer website, F.W.M. Vera in Kolbert 2012). By many it is seen as decisive evidence of the proposition that large herbivores are capable of counter-acting forest growth by nature, and giving the landscape a park-like appearance. Terms like 'letting nature have its way', 'primeval landscape', 'Serengeti' and 'untouched wilderness' are often used to describe the Oostvaardersplassen (Bethge 2001, Wigbels 2002, Veer et al. 2005, Linnartz & Helmer 2009, van de Klundert 2012, Kolbert 2012, Reed 2013): as such we are dealing with a case of, conscious or unconscious, framing (van Vuure, in press). That means, by a particular choice of words and way of reasoning, an image is evoked, which in its clarity and simplicity can be highly convincing, and finds easy acceptance by the general public. The widespread fascination for wildernesses and extinct animal species may contribute further to this. Yet, the Oostvaardersplassen does not form a complete and primeval ecosystem, as would have existed in Mid-Holocene Europe (van Vuure, in press). It is a biologically-artificial ecosystem, where some large herbivores are allowed to be present and others (e.g. elk (*Alces alces*), wild boar (*Sus scrofa*)) are not, and moreover under restrictive conditions imposed by man. Roe deer (*Capreolus capreolus*), an indigenous deer species in the Netherlands, were initially present in the Oostvaardersplassen, but have been out-competed and have since disappeared there (van Manen 2013). Large predators, such as wolf (*Canis lupus*), brown bear (*Ursus arctos*) and lynx (*Lynx lynx*) are also missing. The general public is not really aware of the appearance or functioning of an 'untouched' European ecosystem, and is easily influenced by the choice of words used to describe the Oostvaardersplassen. Moreover, the promotion of grazers and grazing projects leads to people to assume *a priori* that large herbivores are always able to have a strong impact on tree growth. On the other hand, human empathy is put to the test by the regular massive starvation of these large herbi-

vores in late winter. The absence of large predators leads to a concentration of starvation in late winter (instead of throughout the year) and the absence of scavengers counteracts the rapid decay of dead bodies, moreover. The open treeless landscape makes these deaths even more visible. Here, the romanticism of nature conservation and human empathy conflict with the harsh reality of nature.

Discussion

Although we have learned more in recent years about the appearance and habitat of the lost wild horse of Western and Central Europe, not all details about them are yet clear. More data from more bone finds, supplemented with ancient-DNA research on these bones, may possibly shed more light on them in the future. Bone research on wild horses should focus on limb bones and dentition, to learn more about niche adaptations. A decline in body size and the development of (relatively) broader hooves were possibly among such adaptations. Comparative bone research, to discriminate wild horses from domestic horses, should preferably be done on large numbers of horse bones, since different horse breeds can be osteologically similar (Benecke 2006, Cieslak et al. 2010) and wrong conclusions can be easily drawn. As regards DNA research, mitochondrial DNA may elucidate relationships between horse breeds, but does not allow us to determine a possible close relationship with originally wild horses. Many current horse breeds possess mitochondrial DNA of their wild ancestors (Cieslak et al. 2010). Nuclear DNA, on the other hand, will reveal more details about horse morphology and relationships. However, hardly any nuclear DNA research on (Holocene) Western and Central European wild horses has yet been done.

It has been shown that konik horses are able to maintain themselves in certain nature reserves all the year round, but other 'primi-

tive' horse breeds are probably able to do the same. In this respect, some also suggest the Exmoor pony is an original wild horse - and in some respects this horse breed resembles the wild ancestor even more (Hovens & Rijkers 2013). However, the Exmoor pony too is not the original European wild horse; historical records, bone comparisons and DNA research have not been able to demonstrate this so far (Green 2013, van Vuure, in press). When looking to create large nature reserves in Europe ('*Rewilding Europe*'), in which (nearly) all original (Holocene) animal species are introduced, the pros and cons of the (primitive) horse breed to be used need to be carefully considered. The fact is, in real-life natural situations these horses would also have been confronted with large predators such as wolves and bears, which will make high demands on the horses as regards defensibility, running speed and sensory abilities.

Despite all the commotion about the konik, we can conclude that the efforts of Vetulani did lead to the saving of the konik - which was an old breed of farm horse. But there is less unanimity about the konik's 'unique' role in nature management. In the Oostvaardersplassen, the disappearance of elder (*Sambucus nigra*) and willow (*Salix* sp.) forests, the close-grazed grass vegetations and the decline of 36% of bird species since 1997, have led many people to argue that there is overgrazing and ecological devastation (e.g. Bijlsma 2008, Van Manen 2013, van Beusekom 2014). The discussion about the impact that large herbivores exert on the vegetation is still ongoing, but is currently at an impasse and it is the question how it will be resolved.

One suggestion is enlargement: connecting the Oostvaardersplassen to the south with the Horsterwold Forest or the Veluwe area. But this would only provide a temporary relief from the shortage of food for the large herbivores. After a few years, overpopulation would reoccur, leading to the same discussions that are being heard now. In addition, in the Veluwe area the approach to game man-

agement is totally different than that in the Oostvaardersplassen. Also, there are veterinary reasons for restricting the admission of Heck cattle and konik horses into the Veluwe. The numbers of large herbivores in the Oostvaardersplassen seem to be decreasing, especially the number of red deer⁴. This opens up an interesting new phase. Will their numbers continue to fall further? Will willows and elders extend over the area, as a result of this? And why are the numbers of large herbivores only decreasing now, and not, say, five years before? Physiological research on these large herbivores might explain how these animals adapt themselves to changing food levels and how they function in an ecosystem without predators. If the population decline, especially that of the red deer, does not continue, it could be possible to experimentally introduce wolves into this area. Wolves are specialised deer hunters and should strongly reduce the numbers of deer. Elsewhere, it has been shown that wolves really are capable of this (Jędrzejewska & Jędrzejewski 1998, Flueck 2000, Ripple and Beschta 2012). The questions of how wolves would behave socially in the Oostvaardersplassen area (would they form one pack or more?), and how the public would react to the presence and the impact of wolves, would also be interesting issues.

Summary and conclusions

This research reveals more about the physical appearance and the habitat of the lost Holocene wild horse of Western and Central Europe. This horse sub-species had a shoulder height of 120–130 cm, had a dun to dark brown coat colour and a short erect mane. It probably lived in small groups in low densities in marshes along rivers and lakes. This paper also clarifies the facts about the demise of this wild horse: how and where it came to an end. The analysis of the report by Brincken on the wild horse has shown that this report is totally unreliable. The analysis of Vetulani's

working methods has shown that his breeding-back experiment did not reach its objective. With these analyses, the myth of the konik, as being the closest existing descendant of the European wild horse and the breed most similar to it should be laid to rest.

In itself, the konik performs well as a grazer in some nature reserves in the Netherlands, but its role might be taken over by (various) other horse breeds. Other 'primitive' breeds are also able to survive in such a situation all year round. The perception of the konik, as the breed most similar to its extinct ancestor, played a major role in the preference for this horse breed in the early 1980s.

The framing of the Oostvaardersplassen as an 'untouched natural ecosystem' is unjustified, because of its incompleteness and artificiality. The discussion on the appearance of the Holocene natural landscape of Western and Central Europe will doubtless continue unabated.

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Samenvatting

Over het ontstaan van de Poolse konik en de relatie ervan met het natuurbeheer in Nederland

Nadat de laatste ijstijd was geëindigd, heeft het wilde paard gedurende een groot deel van het Holoceen als relatief zeldzaam dier weten te overleven in het sterk beboste West- en Centraal-Europa. Jacht en verdrijving van zijn voedselgronden door de mens hebben de aantallen van deze paarden steeds meer doen afnemen. Waarschijnlijk heeft de laatste populatie van deze paarden tot in de 16^e eeuw in het wild kunnen overleven in het grensgebied van Oost-Pruisen, Polen en Litouwen. De laatste exemplaren zijn door Jan Zamoyski ondergebracht in zijn dierentuin in Zwierzyniec (ZO-Polen). Daar is deze (onder)soort op het eind van de 18^e eeuw aan zijn eind gekomen.

Op basis van het verslag van Julius Brincken in 1826, waarin vermeld werd dat de laatste wilde paarden rond 1806 gekruist zouden zijn met boerenpaarden, is Tadeusz Vetulani in Polen in 1936 een terugfokexperiment in het Bos van Białowieża begonnen. Het was de bedoeling om, door selectie en kruising van boerenpaarden uit de omgeving van Biłgoraj, de wilde voorouder terug te krijgen. Na Vetu-

lani's dood in 1952 is dit experiment door de Poolse staat overgenomen en verplaatst naar Popielno (NO-Polen). Na staking van het terugfokexperiment, rond 1970, wordt de konik daar tegenwoordig alleen nog als 'primitief paardenras' gefokt.

Op grond van diverse argumenten is aangetoond dat het verslag van Brincken over het wilde paard niet op waarheid berust. Om deze reden, en omdat Vetulani zijn experiment op een onzorgvuldige manier heeft uitgevoerd, moet diens terugfokexperiment als niet geslaagd worden beschouwd.

In het kader van een goedkoper en 'natuurlijker' natuurbeheer, zijn in 1981 koniks in Nederland op het landgoed Ennemaborgh uitgezet, en in 1984 in het natuurreservaat Oostvaardersplassen. De konik werd en wordt in de beeldvorming namelijk beschouwd als 'de meest recente afstammeling van het wilde paard'. Door een bepaalde woordkeuze door de beheerders van de Oostvaardersplassen en sommige media, zoals 'de natuur haar gang laten gaan', 'oerlandschap' en 'Serengeti', is er sprake van het *framen* van de Oostvaardersplassen als een ongerept en natuurlijk ecosysteem.

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Notes

1. There is disagreement on the scientific naming of this horse. Some use the name *Equus ferus* for it, as distinct from *Equus caballus*, the domestic horse. Others use the name *Equus caballus* or *Equus caballus ferus*. The name *Equus ferus* was first given by P. Boddaert (1785), based on the data by S.G. Gmelin (1770). However, there are doubts about the original wildness of the horses described by Gmelin (van Vuure, in press). For the Holocene wild horse of Western and Central Europe, I use the term 'wild horse', by analogy with 'wild cat' (*Felis silvestris*) and 'wild boar' (*Sus scrofa*). In the course of the 18th Century, the name 'tarpan' popped up in the literature on the Russian steppes. It is not clear

whether 'tarpan' was a designation for originally wild horses or for feral domestic ones.

2. Arguments for this point of view can be drawn from research on pollen, bones and plant macrofossils (e.g. Zoller & Haas 1995, Mitchell & Cole 1998, Zeiler & Kooistra 1998, Litt 2000, Svenning 2002, Mitchell 2005), from insect research (e.g. Girling 1989, Dinnin & Sadler 1999, Ponel et al. 2000, Svenning 2002) and research on land molluscs (e.g. Gedda 2001, Svenning 2002, Davies 2008). This is supported by the works by Roman writers like Caesar (58-52 BCE) and Tacitus (98 CE) (for both: see Timpe 1989). Other evidence can be found in the history of the primeval Forest of Białowieża (Błoński et al. 1888, Hedemann 1939), from descriptions and palynological research of the Great Wilderness in what was formerly East Prussia (e.g. Hirsch 1863, Schlüter 1921, Mortensen 1938, Mager 1960, Kupryjanowicz 2004, 2007, Wacznik 2009, Pluskowski 2013), from research on the Mesolithic and Neolithic 'submerged forests' on the British coasts (Timpany 2005), and from Louwe Kooijmans (2012).
3. In Germany, the brothers Heinz and Lutz Heck, according to their account, got there before him by a few years. In 1933 already, they claimed to have bred a 'Waldpferd' ('forest horse') (Heck & Heck 1934). They had done this by crossing Przewalski's horses with Icelandic horses and koniks. Later, especially during World War II, they would cross in even more koniks, most of them illegally obtained from Vetulani's experiment at Białowieża.
4. After a continuous increase since 1992, from 2011 on the number of red deer started to fall. On 1 May 2011, the number of red deer was around 2870, on 1 May 2012 it was around 2490, and on 1 May 2013 it was around 1910. On 1 May 2014, after an exceptionally mild winter, the number had increased to around 2390 (see the annual reports on this on the website of Staatsbosbeheer (Dutch Forestry Commission): <http://www.staatsbosbeheer.nl/Nieuws%20en%20achtergronden/Themas/Oostvaardersplassen/Feiten%20en%20cijfers.aspx>

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