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Hedgehogs

This year, the Society for the Study and Conservation of Mammals, the publisher of this journal, proclaimed the western hedgehog (*Erinaceus europaeus*) as the Mammal of the Year. At the same time, the German *Schutzgemeinschaft Deutsches Wild* and the City of Antwerp did the same thing. Thus, in several neighbouring territories, 2009 has been the Year of the Hedgehog. The hedgehog can be seen as a flagship species which attracts the attention of the general public. People often see hedgehogs in their own surroundings, especially in their gardens.

Lutra has taken the Year of the Hedgehog into account by publishing two articles on this animal in this volume. In the current issue Anouschka Hof and Paul Bright report on hedgehogs in cities. And, in the first issue of this year Toni Bunnell (Lutra 52 (1): 15-22) writes about the differences in the growth rates of young in early and late litters and between the sexes.

The study of Hof and Bright is particularly relevant for the Year of the Hedgehog. It shows that the presence of wildlife-friendly features, such as hedgehog nest-boxes and feeders attracts hedgehogs to gardens. Equally, the lack of connectivity between patches of suitable habitat caused by barriers, such as impenetrable fences, restricts hedgehog abundance. The local hedgehog population will increase if people put out the right food, provide them with shelter and allow them into their gardens by making gaps in the fence. Typically, the field data for this study were collected by volunteers, people with a love of mammals, who took part in a survey ('Living with Mammals') organised by the Mammals Trust UK.

Although the hedgehog is a well-known animal, there is not sufficient information on population trends. The 2006 national Red List of Mammals of the Netherlands (Thissen et al. 2009: Lutra 52 (1): 23-35) has listed the hedgehog as 'Data Deficient'. The Society for the Study and Conservation of Mammals suspects that the numbers have gone down since 1950, the year of reference for the Dutch Red Lists, but it has no idea of the size of the decline, whether it is around 20% or even over 50%. As in other West European countries, it seems that the hedgehog is not faring well. As a result of evidence of a significant decline in Great Britain, the hedgehog has recently been included in the UK Biodiversity Action Plan.

Lutra has a tradition of publishing articles about hedgehogs. The first issue of volume 42 was a hedgehog 'special'. Marcel Huijser was the main contributor, with three papers. In a review he concluded that the strong increase of density of the road network and the intensity of traffic was having a serious effect on hedgehog populations (Huijser 1999: Lutra 42 (1): 39-56). In another paper, jointly written with Nigel Reeve, he argued that high levels

Young hedgehog. *Photograph: Rollin Verlinde/Vilda*.

of hedgehog mortality could be traced back to a combination of anthropogenic factors (Reeve & Huijser 1999: Lutra 42 (1): 7-24). A third paper in this volume presented results of surveys carried out between 1995 and 1997 in which volunteers counted hedgehog traffic victims (Huijser et al. 1999: Lutra 42 (1): 57-58). As part of the Year of the Hedgehog, the Society for the Study and Conservation of Mammals has organised a similar count in 2009. While the data has not yet been analysed it is hoped that it can be meaningfully compared with the results obtained in the 1990s and provide insights into how hedgehogs are now being affected by road traffic. Following on from Reeve and Huijser, Toni Bunnell (2001, Lutra 44 (1): 3-14) also showed that anthropogenic factors contribute substantially to the incidence of injury and mortality of hedgehogs in all age groups and emphasised the need for measures to maintain hedgehog populations.

More recently, in 2006, Lutra published another article about hedgehogs, by the British environmental writer Hugh Warwick (2006: Lutra 49 (2): 89-102). This article precipitated a chain of events that resulted in the saving of the lives of hedgehogs from Uist in the Western Isles of Scotland. Scottish Natural Heritage (SNH) was culling hedgehogs on the island, as they considered them to be a threat to breeding birds. SNH claimed that it was pointless to transport the hedgehogs alive to the mainland, as relocated hedgehogs would not survive. Warwick showed that hedgehogs from Uist did thrive after translocation and SNH stopped the culling and started to release the hedgehogs caught on Uist elsewhere. In the first six months after its publication the article was downloaded about 2,000 times.

Warwick has since written the inspiring book ‘A Prickly Affair’. The American edition of this book is entitled ‘The Hedgehog’s Dilemma’. This title is derived from a parable of the philosopher Schopenhauer, contained in his book ‘Parerga und Paralipomena’ (1851). In this parable, a group of hedgehogs decide to huddle together to share warmth during a spell of cold weather, but they find they start hurting each other with their sharp spines and ultimately have to sacrifice warmth for comfort. The moral that Schopenhauer is seeking to convey us that people cannot become emotionally close to one another without causing significant psychological harm. He argues that one should cultivate internal warmth in order to stay at a safe distance from the dangers of close personal relationships. Warwick describes how the hedgehogs overcome the obvious obstacle to reproduction and skilfully extends the idea to explore the current state of human-animal interactions. The dilemma we face is trying to get close enough to the wild without corrupting it out of existence.

Warwick’s book argues that the hedgehog offers a unique insight into how humans can protect nature, since it is probably the only wild animal city people have a chance of getting really close to, even in a 'nose-to-nose experience'. As part of the Year of the Hedgehog, Warwick came over to the Netherlands from the UK and held a lecture on his philosophy about hedgehogs captivating his audience with his slogan 'save the hedgehog, save the world'.

Meanwhile we are happy to announce that Bastiaan Meerburg has joined the editorial board. Bastiaan completed his PhD on the 'Zoonotic Risks of Rodents in Livestock Production' at Wageningen University. He has been a member of the editorial board of the journal *Zoogdier,* also published by the Society for the Study and Conservation of Mammals, so he is already familiar with the tasks ahead. Lutra looks forward to benefiting from Bastiaan's linguistic skills and scientific knowledge.

Schopenhauer, A. 1851. Parerga und Paralipomena. Kleine philosophische Schriften. A.W. Hayn, Berlin, Germany.

Warwick, H. 2008. A Prickly Affair: My Life with Hedgehogs. Penguin, London, UK.

Warwick, H. 2008. The Hedgehog's Dilemma: A tale of obsession, nostalgia, and the world's most charming mammal. Bloomsbury, New York, USA.

A prickly affair: the spines of a hedgehog. *Photograph: Jasja Dekker*.

The winning photo of the Year of the Hedgehog photo contest 2009. *Photograph: Peter Zeeman.*

The value of green-spaces in built-up areas for western hedgehogs

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Abstract: With ongoing urbanisation an increasing number of wildlife species face rising levels of pressure due to habitat loss and fragmentation. The impact of urbanisation on species has been mainly investigated for avian life. It is however less well known how urban dwelling mammals are affected. The western hedgehog (*Erinaceus europaeus*) is closely associated with built-up areas and has recently been included in the UK Biodiversity Action Plan, as a result of evidence of significant decline in Great Britain. We studied the presence of western hedgehogs and other mammals in green-spaces in built-up areas throughout Great Britain using effort-based volunteer surveys. We used these data to investigate which factors were associated with variations in relative abundance of hedgehogs in urbanised landscapes, and to draw conclusions on which mitigation measures might benefit hedgehogs and other mammal populations. The present study suggests that the presence of wildlife friendly features, such as a hedgehog nest box and feeders, attract western hedgehogs to gardens. The presence of predators had a significant negative impact on the relative abundance of western hedgehogs in built-up areas in countryside regions. The lack of connectivity between patches of suitable habitat caused by barriers such as large water-bodies and impenetrable fences also restricted hedgehog abundance. The need for the incorporation of good environmental management, with consideration for habitat connectivity, in development planning seems to be crucial for the viability of hedgehog populations in built-up areas. Awareness amongst the public of the possibilities to increase the attractiveness of private gardens for wildlife might also increase the viability of wildlife in harsh environments.

Keywords: conservation, environmental management, *Erinaceus europaeus*, gardens, habitat fragmentation, western hedgehog, mammals, predators, urban green-spaces, volunteer survey.

Introduction

With the continued growth of the world population the expansion of urbanised areas persists. This leads to an increased pressure upon natural habitats both in rural and urban areas (Antrop 2004, Anonymous 2006, McDonald et al. 2008). Urban areas in particular are predicted to suffer an increased loss of green-spaces which is reflected by social, economic and demographic changes. Natural patches such as parks, road verges and gardens are often maintained within urban areas, and are able to support numerous populations of wildlife (Dickman 1987, Bland et al. 2004, Angold et al. 2006). Sheltered climatic conditions, extra food supplied by wildlife friendly gardeners, compost heaps and scattered organic waste provide good situations for various species in built-up environments. Several species such as the red fox (*Vulpes vulpes*) and coyote (*Canis latrans*) are known to thrive in built-up areas (Harris & Rayner 1986, Atkinson & Shackleton 1991, Gloor 2002). Nevertheless, many examples of local extinction or declining species richness due to urbanisation can be found in literature (e.g. Czech et al. 2000, Marzluff 2005). The house sparrow (*Passer domesticus*) for instance was thought to favour built-up areas, but has been declining drastically over the last few decades (Robinson et al. 2005, De Laet & Summers-Smith 2007). Species can often cope with or adapt to a certain level of stress factors such as limiting habitat availability and fragmentation. However, when values reach a threshold the viability of populations can decline and once common species might become locally extinct (Hanski et al. 1996, Fahrig 2002).

Changes in built-up landscapes can have a substantial impact on species diversity and abundance in these settings (Dickman 1987, Czech et al. 2000, Baker & Harris 2007). Increasing fragmentation, housing density and loss of habitat due to rising needs for development all have negative effects on wildlife. The impact of these changes has been well studied for several mainly avian taxa such as house sparrow (*Passer domesticus*), house martin (*Delichon urbicum*), and starling (*Sturnus vulgaris*) (Crick et al. 2002, Crick et al. 2004, De Laet & Summers-Smith 2007). It is however less well known how urban dwelling mammals such as the western hedgehog (*Erinaceus europaeus*) have been affected. Mammals face high mortality risks in built-up areas due to high road and traffic densities, high levels of predation by feral and domestic pets and other predators, high concentrations of garden pesticides causing diminishing food supplies and (secondary) poisoning, and other human related disturbances (Shore et al. 1999, Wilson et al. 1999, Huijser 2000, Frid & Dill 2002, Woods et al. 2003, Ditchkoff et al. 2006).

The western hedgehog has recently been included in the UK Biodiversity Action Plan, as a result of evidence of significant decline in Great Britain (Reeve 1994, Morris 2006). The hedgehog is closely associated with green-spaces in built-up areas such as gardens, greens and parks (Huijser 1999), and it has been suggested that built-up areas might offer refugia for hedgehogs from predators (Micol et al. 1994, Young et al. 2006). Hof and Bright (unpublished data) however, state that the relative abundance of hedgehogs in Greater London has declined considerably in the last few decades. Increasing fragmentation and further loss of green-spaces in built-up areas were thought to be the drivers behind this decline. The western hedgehog is a generalist feeder and a predator of macro-invertebrates, which are the staple diet of numerous other taxa; its decline may well signify a more general loss of environmental quality which may have important implications for environmental management. Additionally, the potential constraints faced by western hedgehogs might be even more severe for less mobile taxa that have to cope with an increasingly fragmented landscape. It is therefore important to get an understanding of the current value of green-spaces in built-up areas and to discover which particular features might enhance habitat suitability for western hedgehogs and other taxa.

The monitoring of mammals in built-up areas is subject to various constraints; problems with accessibility and visibility often arise, which makes data less valuable. Volunteer surveys have yielded valuable results in the monitoring of mammals in gardens, and provide a relatively low-cost, low time-consuming method of sampling large areas (Toms & Newson 2006, Baker & Harris 2007). Home owners were thought to spend a reasonable amount of time in or near their garden and were thought to be familiar with common and easily recognisable mammals, like the western hedgehog, red fox and badger (*Meles meles*), that may frequent their garden. We used these data in the present study to investigate the significance of habitat connectivity for hedgehogs, to investigate the impact of predators and wildlife friendly features on the presence of hedgehogs in built-up areas, and to draw conclusions on which mitigation measures in built-up areas might benefit hedgehogs and other mammal populations.

Material and Methods

The survey ‘Living with Mammals’ (LWM) has been designed by the Mammals Trust UK in conjunction with Royal Holloway Univer-

Table 1. The variables requested from the surveyors of the 'Living with Mammals' survey and used for the analyses of the dataset. * Data derived from the 'Countryside survey 2000' (Defra & NERC 2007).

Variable	Description
Arable in surrounding	Arable fields in surroundings (yes/no)
Box on site	Presence of hedgehog nest box (yes/no)
Built-up	Density of built-up area in 2000 (ha · $100km^{-2}$)*
Common in surrounding	Commons with rough grass or scrub in surroundings (yes/no)
Compost on site	Presence of compost heap (yes/no)
Concrete percentage	Percentage of concrete/gravel/pavings (logratio transformed)
Density badgers	The average number of badgers per min observation
Density foxes	The average number of red foxes per min observation
Density hedgehogs	The average number of hedgehogs per min observation
Feeder on site	Presence of pet feeder (non bird) (yes/no)
Fence	Site fenced (yes/no)
Gaps in fence	Gaps in the boundary large enough for hedgehogs (yes/no)
Garden in surrounding	Garden in surroundings (yes/no)
Grass percentage	Percentage of grass (logratio transformed)
Hedge	Hedge as site boundary (yes/no)
Open	No site boundary (yes/no)
Park in surrounding	Park/ village green/ residential square in surroundings (yes/no)
Pasture in surrounding	Pasture/ grass fields in surroundings (yes/no)
Pile on site	Presence of pile of dead wood (yes/no)
Pond in surrounding	Pond/ lake in surroundings (yes/no)
Pond on site	Presence of pond (yes/no)
Presence badgers	Presence badger (yes/no)
Presence dogs	Presence of dog (yes/no)
Presence foxes	Presence red foxes (yes/no)
Presence hedgehogs	Presence hedgehogs (yes/no)
River on site	Presence of river (yes/no)
Shed on site	Presence of shed (yes/no)
Shed percentage	Percentage of shed/ hut/ building (logratio transformed)
Shrubs percentage	Percentage of shrubs (logratio transformed)
Site	Type of site
Site age	Approximate age of site (4/33/82/157 years)
Site size	Approximate size of the site (13/38/126/300 ha)
Stream in surrounding	Stream/ river in surroundings (yes/no)
Trees percentage	Percentage of trees (logratio transformed)
Wasteland in surrounding	Wasteland/ derelict land in surroundings (yes/no)
Wild percentage	Percentage of wild untended areas (logratio transformed)
Woodland in surrounding	Woodland in surroundings (yes/no)

sity of London to record mammals in greenspaces within and around built-up environments. The survey took place in the period 2003-2006. During each of these years data were recorded throughout 13 consecutive weeks starting at the beginning of April. People were not only asked to record the mammals they saw; they were also asked to record site data such as location, habitat type, size and description of the site, boundary, and surrounding area. Additionally they were asked to state the approximate observation length each week per time of day (dawn, day, dusk, night). Table 1 summarises the basic data requested from the surveyors. Data about the density of built-up area were derived from the 'Countryside survey 2000' (Defra & NERC 2007)

Analysis of the LWM dataset was limited to the western hedgehog and its potential predators: the badger, and the red fox (Reeve 1994). The survey used the approximate observation length as an index for effort. The power of the effort depends on the activity pattern of the animal. Hedgehogs are for instance generally not active during the day, and if they are it is often due to reduced fitness (Reeve 1994, Morris 2006). The probability of sighting a western hedgehog during the day was therefore estimated at dawn, day, dusk and night (table 2), based on findings regarding their activity pattern (Reeve 1994). The effective recorder effort per time of day was calculated by using equation 1.

$$EE = \sum(SP_i \cdot AE_i) \qquad \text{Equation 1}$$

Where *EE* is the effective recorder effort, *SP* is the sighting probability for a species during each survey period *i* (dawn, day time, dusk, and night time), and *AE* is the actual effort defined as the total number of minutes spent surveying during each survey period *i*.

Four categories of the number of individuals seen were defined in the survey: 0, 1, 2 or 3+. To calculate the total number of western hedgehogs the values of the categories were summed. The category 3+ was classified as 3.

Table 2. The probability of sighting a badger, a hedgehog and a red fox in the course of the day based on equation 1 (see text).

Course of the day	badger	hedgehog	red fox
Dawn	0.25	0.10	0.30
Day	0.00	0.00	0.10
Dusk	0.25	0.20	0.30
Night	0.50	0.70	0.30

The total number of hedgehogs recorded per site over the 13-week survey period divided by the 'total effective recorder effort' represented the number of hedgehogs sighted per minute per site and was used to provide an index of relative abundance. Unfortunately it was impossible to account for potential duplication of hedgehog sightings. We made the assumption that the likelihood of seeing a western hedgehog has a positive and linear correlation with their relative density; a fixed amount of recording effort will result in seeing a fixed proportion of the population. This implies the assumption that the relative density is proportional to the factual density and that the rate of proportionality is constant (Schwarz & Seber 1999). In order to obtain an estimate of the minimum number of sites that have to be surveyed to gain confidence in the estimated relative density of hedgehogs, the mean number of hedgehogs observed per site was calculated using random sub-samples (ranging from 0-1700 with steps of 100). The mean relative density of badgers and foxes was calculated in a similar way. The probability of sighting a badger and a red fox in the course of the day was estimated as well (table 2), based on their general activity pattern (Harris & Yalden 2008). Relative abundance of badgers, red foxes, and western hedgehogs was estimated for 'built-up areas in the countryside' (henceforth called countryside) (built-up <50%; derived from the 'Countryside survey 2000' (Defra & NERC 2007)), 'urban areas' (built-up >50%), and both areas together. This gives an indication of the relative abundance of the different species in different surroundings.

To estimate the area occupied by grass, shrubs, trees, concrete, sheds and wild areas within the individual survey sites, the logratios of the five categories set on the survey sheet (0%, 1-25%, 26-50%, 51-75%, 76-100%) were taken (Aitchison 1982, Kucera & Malmgren 1998). Averages of the different categories have been taken to estimate the age and the size of the site (see table 1 for the categories). Only variables that might have an impact on the presence of western hedgehogs were included in the database (table 1). Therefore, data such as the presence of domestic cats and birdbaths were discarded. We used Pearson Chi-Square and Pearson Correlation in SPSS (for windows 14th edition, SPSS Inc., Chicago, USA) to study whether the presence of hedgehogs was significantly related to the variables. Student *t*-test and the nonparametric Kruskal-Wallis test have been used by us to study the differences in population means. We used Generalized Linear Modelling, (GLM) modelling of binomial proportions by transformation logit in the programme GenStat (for windows' 8th edition, VSN International Ltd, Lawes Agricultural Trust, Oxford, UK) to explain the variation in relative hedgehog abundance. The models were built manually using the backward stepwise method. Minimal adequate models were selected based upon the Akaike Information Criterion (Akaike 1981). The effective recorder effort was used as a weight factor to correct for differences in recorder effort. Different models were built for different environmental zones within Great Britain in order to reduce the impact of the general environment on differences in hedgehog abundance. Environmental zones were defined by the 'Countryside Information System' and formed from aggregations of the 40 base classes of the ITE land classification of Great Britain (figure 1) (Bunce et al. 1996, Defra & ADAS 2005). Models were built for the arable-dominated and the pasture-dominated lowlands in England and Wales only, due to insufficient records to build minimum adequate models for the other environmental zones.

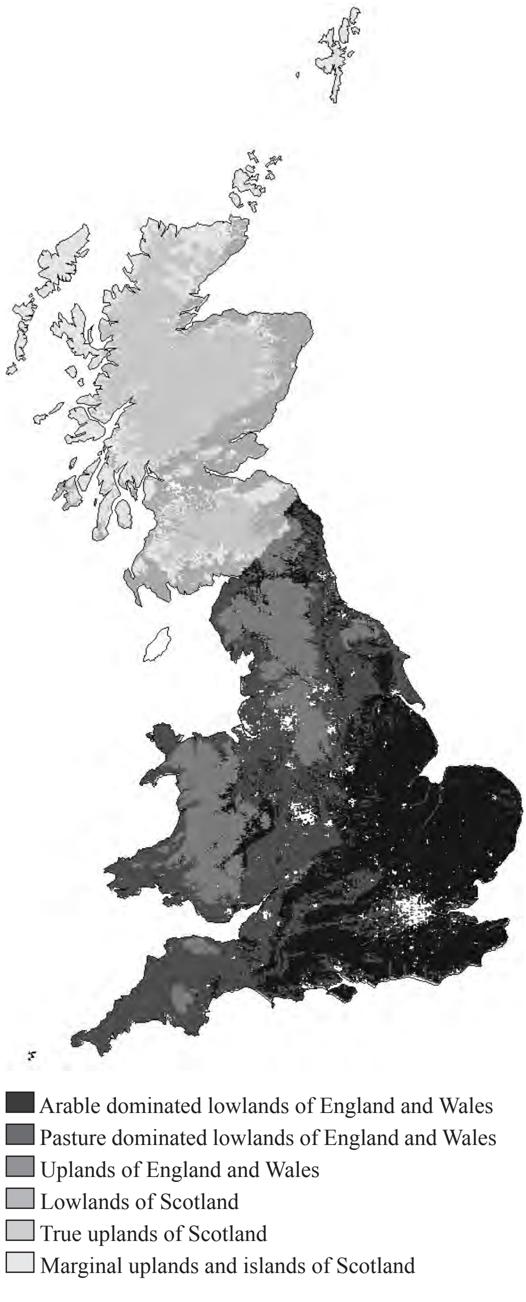

Figure 1. The environmental zones of Great Britain as defined by the Countryside Information System (Defra & NERC 2005).

Results

In total 1711 sites were surveyed. Figure 2 shows the distribution of the sites throughout Great Britain and shows on which sites badgers, red foxes and western hedgehogs have been found and on which sites they were thought absent. Figure 3 shows the mean relative abundance of badgers, red foxes and hedgehogs per region. Differences in mean relative abundance per region were significant for badgers (Kruskal-Wallis: χ^2=25.115, df=10, *P*=0.005), red foxes (Kruskal-Wallis: χ^2=84.716, df=10, *P*=0.001), and hedgehogs (Kruskal-Wallis: χ^2=39.158, df=10, *P*=0.001). Western hedgehogs were relatively more abundant in the eastern regions of England and in the West-Midlands compared to all other regions of Britain, whereas badgers were relatively more abundant in the southwestern regions of England and in Scotland. Red foxes were relatively most abundant in Greater London and in the South-East of England.

Figures 4A, B and C show the mean number of badgers, red foxes and western hedgehogs seen per minute observation in built-up areas in the countryside, urban areas, and both areas together. Although an asymptote has not been reached in every situation, a clear distinction can be seen for red foxes. The average relative abundance for red foxes was significantly lower in built-up areas in the countryside than in the urban areas (Student t-test: t=-2.106, df=1192, *P*=0.035), whilst this trend was reversed for badgers and hedgehogs. These differences however were not statistically significant.

The GLM was able to explain 42% of the variance in presence of hedgehogs in gardens

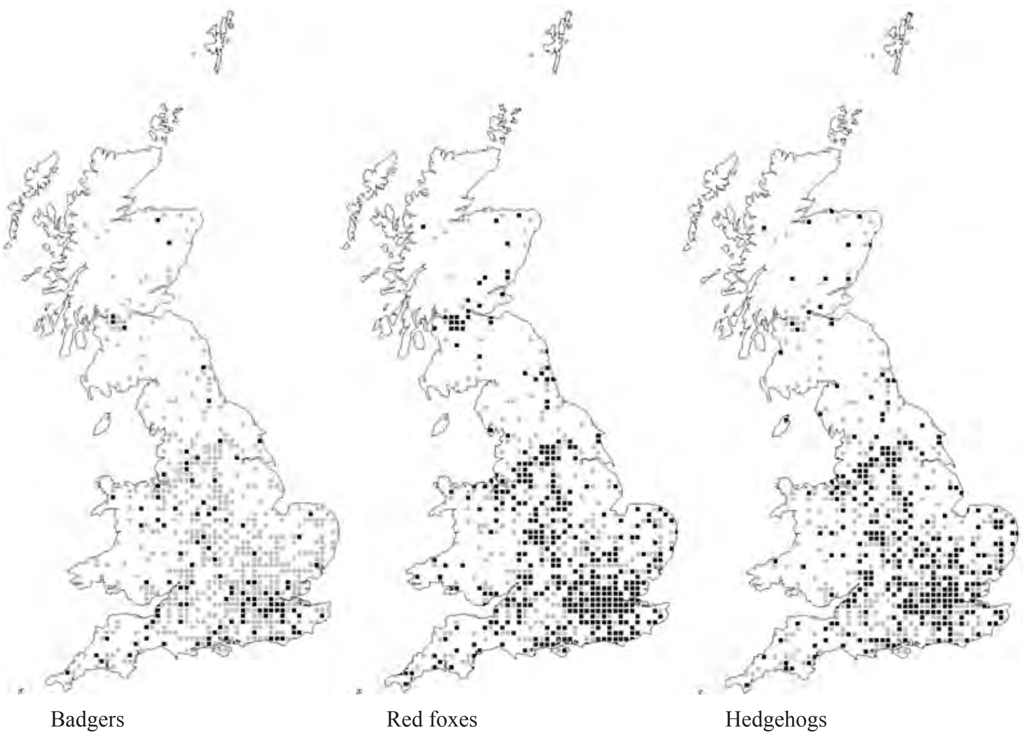

Figure 2. The locations of the participants of the LWM survey 2003-2006. Black dots show where the species has been found and grey dots show where the species has not been found. Badger: presence *n*=153, absence *n*=1558. Red fox: presence *n*=823, absence *n*=888. Western hedgehog: presence *n*=515, absence *n*=1196.

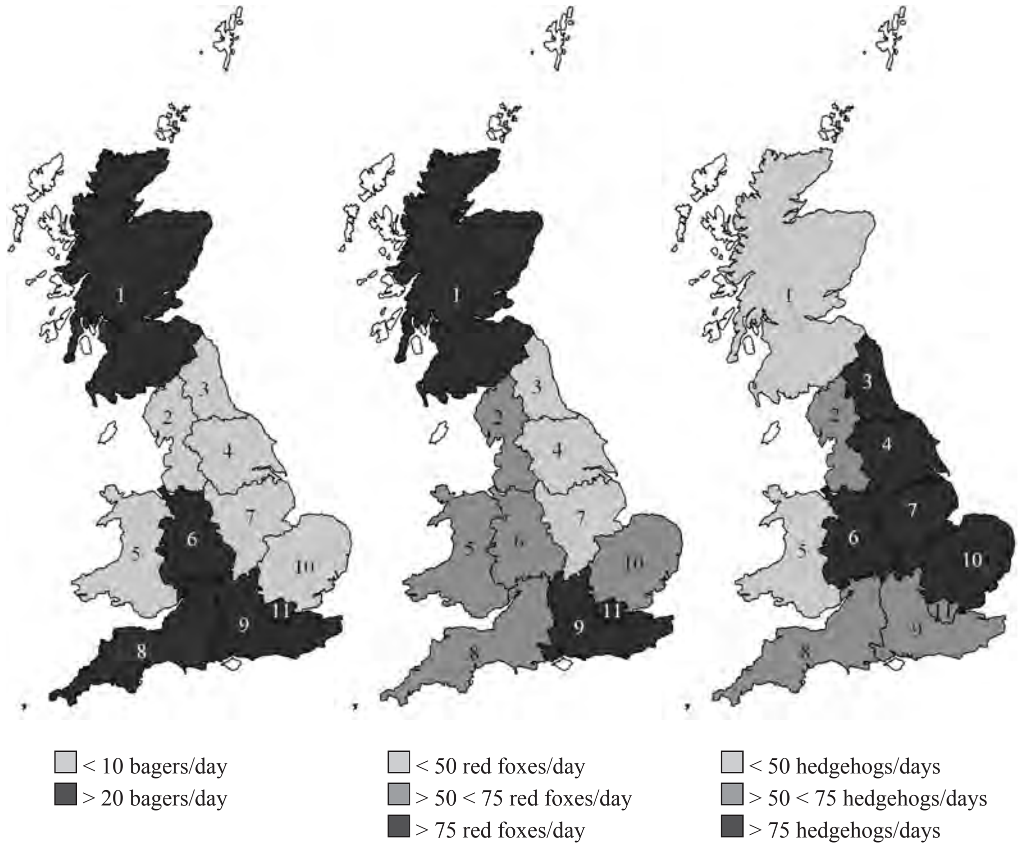

Figure 3. Mean relative abundance of badgers, red foxes and western hedgehogs seen per day of continuous observation per region of Great Britain, with 1. Scotland, 2. Northwest of England, 3. Northeast of England, 4. Yorkshire and The Humberside, 5. Wales, 6. West- Midlands, 7. East-Midlands, 8. Southwest of England, 9. Southeast of England, 10. East of England, and 11. Greater London.

in the pasture-dominated lowlands and 54% in gardens in the arable-dominated lowlands of England and Wales. Table 3 shows the summary of the models. The variable 'pasture in the surroundings' was able to explain the highest percentage of variance (21%) in the arable-dominated lowlands. The availability of a large amount of shrubs and or a pond or lake at or in the surroundings of the site and the presence of a feeder at the site, were also positively correlated with hedgehog presence. Western hedgehogs were on the other hand less often seen at sites also frequented by badgers. The presence of a hedgehog nest box had the highest explaining power (10%) in the pasture-dominated lowlands. A hedgehog nest box, feeders on site, a large percentage of grass on the site, gaps in the boundary, and a common, woodland or a park in the surrounding of the site were all positively related to hedgehog presence. In this environmental zone, hedgehogs were less often seen in gardens that had arable in the surroundings, high densities of built-up areas, or domestic dogs and/ or badgers frequenting the site. A river through the site was also negatively related to hedgehog presence.

Western hedgehogs were found on 30% of all the sites, whilst red foxes were found on 48% and badgers only on 9%. Domestic dogs (*Canis lupus familiaris*) regularly frequented 36% of the sites. The presence of badgers had

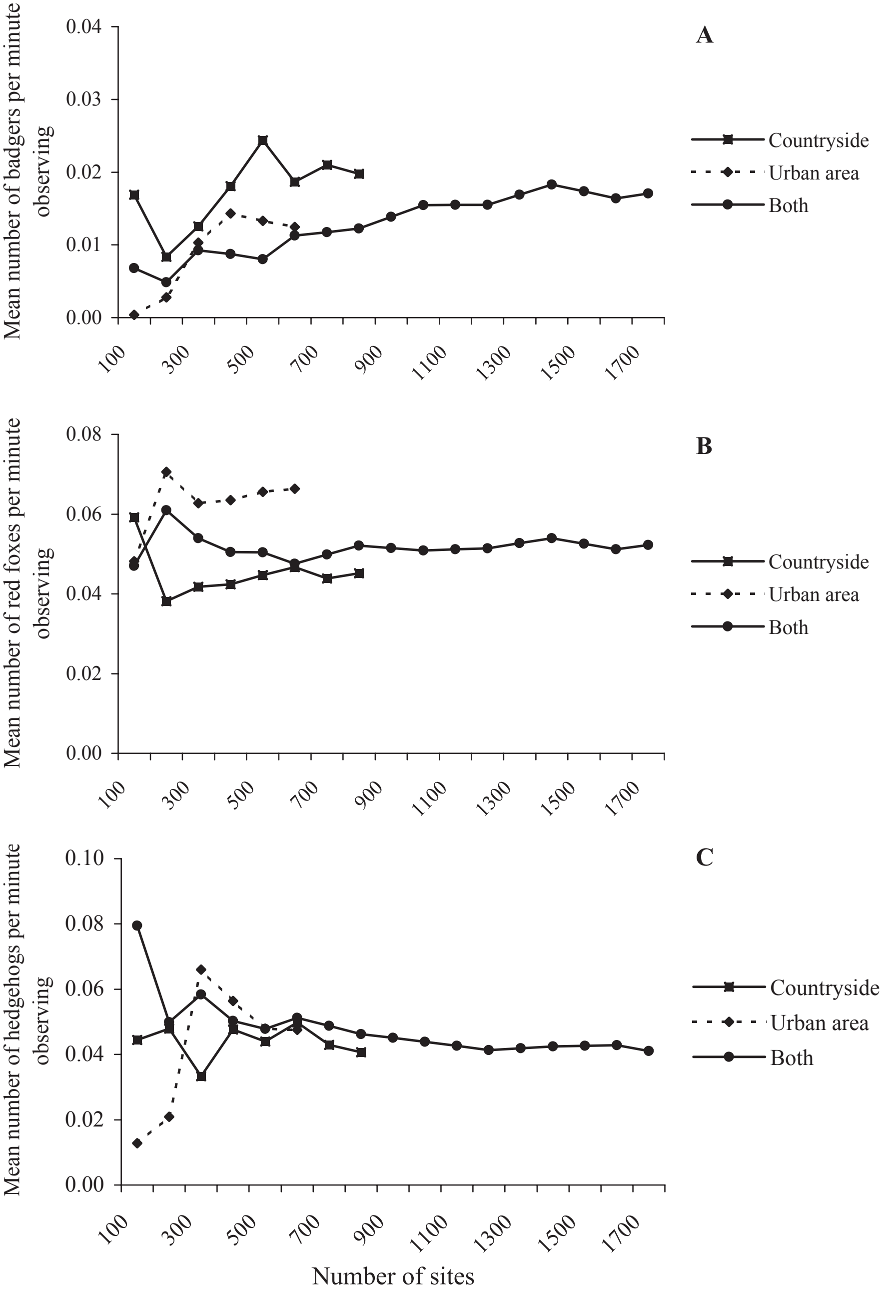

Figure 4. The average number of badgers (A), red foxes (B) and western hedgehogs (C) per minute observing versus the number of sites in the countryside, in the urban areas and in both areas, in the period 2003-2006. Standard deviations are not shown for clarity. (Average standard deviation: badger countryside = 0.110, badger urban area = 0.077, badger both areas = 0.102, red fox countryside = 0.142, red fox urban area = 0.148, red fox both areas = 0.143, hedgehog countryside = 0.151, hedgehog urban area = 0.220, hedgehog both areas = 0.210).

Table 3. Summary of the two GLMs (modelling of binomial proportions by transformation logit) for the arable and pasture-dominated lowlands of England and Wales with dependent variable 'hedgehog presence', and 'effective recorder effort' as the weighing factor.

Hedgehog presence in gardens 2003-2006	Variable	Estimate	r^2	*P*
Arable-dominated lowlands of England and Wales Explained: 42%, *n*=380, *P*<0.001	Constant	-5.370		<.001
	Feeder on site	1.699	0.037	<.001
	Pasture in surrounding	3.043	0.205	<.001
	Pond in surrounding	2.607	0.104	<.001
	Pond on site	1.986	0.076	<.001
	Presence badgers	-3.557	0.091	<.001
	Shrubs percentage	1.544	0.023	<.001
Pasture-dominated lowlands of England and Wales Explained: 54%, *n*=285, *P*<0.001	Constant	-2.498		<.001
	Arable in surrounding	-3.927	0.092	<.001
	Box on site	3.611	0.097	<.001
	Built-up	-2.282	0.059	<.001
	Common in surrounding	1.648	0.043	<.001
	Feeder on site	1.997	0.034	<.001
	Gaps in fence	3.122	0.030	<.001
	Grass percentage	1.200	0.023	<.001
	Park in surrounding	1.980	0.035	<.001
	Presence badgers	-2.816	0.027	<.001
	Presence dogs	-1.625	0.030	<.001
	River on site	-4.897	0.086	<.001
	Woodland in surrounding	1.735	0.041	<.001

a significant negative effect on the presence of hedgehogs in survey sites classified as countryside areas (Chi-square test: χ^2=4.447, df=1, *P*=0.035), but not in survey sites classified as urban areas. A similar situation arose with the presence of dogs, with a significant negative impact in the countryside (Chi-square test: χ^2=4.533, df=1, *P*=0.033), but not in the urban areas. The presence of red foxes on the other hand was not significantly related to the presence of hedgehogs. When all the potential predators, badgers, red foxes, and domestic dogs, frequented the site, there was a larger significant negative impact on the presence of hedgehogs than the negative impacts from badgers and dogs separately (Chi-square test: χ^2=7.573, df=1, *P*=0.006).

Discussion

The present study suggests that western hedgehogs are likely to be present in a higher relative abundance in the eastern regions of England and in the West Midlands than in other areas of Great Britain. In contrast, the eastern regions of England were characterized by a low relative abundance of badgers and largely as well by a low relative abundance of red foxes. It seems straightforward to suggest that a negative relation exists between the abundance of potential predators and the abundance of hedgehogs. The presence of badgers was indeed negatively correlated with the presence of hedgehogs in both the arable and the pasture-dominated lowlands of England and had a significant negative effect on the presence of hedgehogs in survey sites in countryside areas. The negative impact of badgers on hedgehogs has also been shown by other studies (Doncaster 1992, Doncaster 1994, Micol et al. 1994, Young et al. 2006). However, in urban areas this negative impact of badgers was not clear. Although the presence of hedgehogs was also negatively affected by the presence of badgers here, the relationship was not statistically significant. The fact that the density of badgers was higher in countryside areas than in urban areas might explain the different impacts upon the presence of hedgehogs between these two environments. Nonetheless, sett densities can be high in urban areas and more and more conflicts with badgers have consequently arisen in recent times (Delahay et al. 2009). Although it is known that red foxes frequently roam in gardens in urban areas (Harris 1986, Gloor 2002), they did not seem to negatively affect the presence of hedgehogs. Domestic dogs however also often wander freely in gardens, especially in more rural areas, and are known to inflict injuries upon hedgehogs and occasionally kill them (Doncaster 1994, Reeve 1994). Western hedgehogs were indeed less often seen on sites that were frequented by domestic dogs. Although no statistically significant relationship existed in urban areas, a negative impact of dogs on the presence of hedgehogs was visible in countryside areas, where the prevalence of dogs was higher in the present survey. Additional to the higher dog density in countryside areas, dog owners in these areas might more frequently have several dogs than dog owners in urban areas thus creating a higher density per km^2, which will inevitably be of greater significance to hedgehogs. The GLM for the pasture-dominated lowlands also showed a negative impact of dogs on hedgehog presence. Thus, the present study suggests that the presence of predators can indeed have a significant negative impact on the presence of hedgehogs. Increasing numbers of predators both in rural and in urban areas might lead to local extinctions of prey species (Holyoak & Lawler 1996). Predator control is frequently practised in order to protect prey species (Reynolds & Tapper 1996). Though, since both practical and ethical issues are likely to arise whilst culling one species in order to protect the other, it seems imperative to seek more effective and non-lethal methods to preserve prey species. The control of the number of pets such as dogs will undoubtedly be even more prone to difficulties. Non-invasive mitigation measures might therefore prove more time and cost efficient.

People in general like to have wildlife in their gardens and therefore often try to increase the attractiveness of their garden for wildlife. Features in gardens that were attractive to hedgehogs in the present study were a high percentage of shrubs and grass, the presence of a pond, the presence of a hedgehog nest box, and the availability of extra food sources. It is likely that some of the people decided to place a hedgehog nest box in their garden after first seeing a hedgehog there. It therefore cannot be concluded from these data that a hedgehog nest box itself will attract hedgehogs to gardens. Nevertheless a hedgehog nest box does provide shelter and a suitable nest site location which might indeed encourage hedgehogs to return to those sites that include one. Well established and dense shrubbery is also able to offer shelter and nest sites to hedgehogs (Morris 2006). Hedgehogs can often be found at food bowls put out in gardens to feed pet and feral cats or other mammals (Morris 2006). It is therefore not surprising that hedgehogs were more often seen in gardens by people that provide food for wildlife. It has also been shown by other studies that wildlife friendly features may favour the presence of other taxa (Baker & Harris 2007). Raising awareness amongst the general public and stressing the importance of wildlife friendly features in private gardens is therefore likely to benefit wildlife in general.

Many gardens are at least partly fenced

which limits the accessibility for large and medium sized mammals. Gaps in boundaries of gardens did indeed have a significant positive effect on the presence of hedgehogs in the pasture-dominated lowlands, provided they were large enough, and will enhance the connectivity between suitable habitats, thereby enlarging the area available to hedgehogs. It was therefore not surprising that the occurrence of green-spaces like parks, commons and woodlands in the surroundings of the site positively affected the presence of hedgehogs. Streams and rivers were significantly related to a low presence of hedgehogs, although hedgehogs are able to swim and are known to have crossed large water bodies (Doncaster 1992); they do seem to reduce connectivity through creating partial barriers. Connectivity between patches of habitat in fragmented landscapes by good quality dispersal routes is frequently deemed essential for the prevalence of viable populations of various taxa (Fahrig & Merriam 1985, Fahrig & Merriam 1994, Beier & Noss 1998). Green-spaces in heavily urbanised areas however are frequently not interconnected and also lack good quality dispersal routes. Ongoing urbanisation and the need for new developments will doubtlessly further decrease habitat connectivity. The viability of populations of various taxa will be jeopardized by further habitat loss and fragmentation if their critical thresholds in habitat connectivity are reached (Mönkkönen & Reunanen 1999, Fahrig 2002, Ovaskainen et al. 2002). Unfortunately the density of roads in the direct surroundings of the site could not be included in the GLM, since these data were not provided by the surveyors. However, possible impacts of roads should not be ignored. Especially large roads were infrequently crossed by hedgehogs in an experiment by Rondinini and Doncaster (2002); nevertheless work by Doncaster et al. (2001) has shown that road verges can work as movement corridors for hedgehogs and thus roads in such do not form impenetrable barriers to hedgehogs. Bergers and Nieuwenhuizen (1999) also state that the viability of hedgehog populations decreased dramatically as a result of fencing roads. Roads on the other hand can form a barrier to hedgehogs because of the risk of death caused by traffic. Large numbers of hedgehogs die every year on roads (Huijser 2000, Morris 2006), and Huijser (2000) suggests that roads and traffic may reduce hedgehog populations by up to 30% in the Netherlands.

Conclusions

The present study suggests that the presence of predators like the badger and the domestic dog can limit the number of western hedgehogs found in built-up areas in the countryside. Ongoing study might clarify the extent of this impact and identify mitigation measures. Wildlife friendly features on the other hand do increase the suitability of green-spaces in urbanised landscapes for hedgehogs. Awareness amongst the public of the possibilities to increase the attractiveness of private gardens for wildlife, and of the restrictions fences and free roaming pet dogs pose on the movements of various mammal species, might increase the viability of wildlife populations in areas where they face the threat of increasing urbanisation. Additionally, the need for the incorporation of good environmental management, with consideration for habitat connectivity, in development planning seems to be highly important for the viability of hedgehog populations and likely for other mammal species as well.

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Samenvatting

Het belang van groene gebieden in stedelijke omgeving voor egels

Een stijgend aantal dieren en planten krijgt te maken met een verhoogde mate van stress door het verlies aan en fragmentatie van habitat door verdergaande urbanisatie. De invloed van urbanisatie is met name onderzocht met betrekking tot vogels. Het is beduidend minder duidelijk wat de eventuele invloed van urbanisatie is op zoogdieren. De egel (*Erinaceus europaeus*) wordt over het algemeen nauw geassocieerd met (sub)urbane gebieden en kan, naar gedacht, relatief hoge verstoringen verwerken. De egel is echter sinds kort opgenomen in het actieplan voor biodiversiteit van het Verenigd Koninkrijk 'UK Biodiversity Action Plan', als resultaat van een significante daling in het aantal egels. De aanwezigheid van egels en andere zoogdieren in groene gebieden in (sub)urbane gebieden verspreid over Groot-Brittannië is onderzocht met de hulp van vrijwilligers. De data zijn gebruikt om te onderzoeken welke factoren variaties in relatieve dichtheden aan egels kunnen verklaren in (sub)urbane gebieden. Ook werd getracht te bepalen welke maatregelen voor egels en andere zoogdieren gunstig zouden kunnen zijn. De huidige studie suggereert dat de aanwezigheid van bijvoorbeeld speciaal uitgezet voedsel voor dieren en voldoende struikgewas, egels naar tuinen lokt. De aanwezigheid van potentiële predatoren, zoals de das en de hond, had echter een significante negatieve invloed op de aanwezigheid van egels in tuinen; met name in bebouwde gebieden op het platteland. Het gebrek aan connectiviteit tussen gebieden met een geschikt habitat, door barrières zoals rivieren en omheiningen, had ook een negatieve uitwerking op het aantal egels. Het is dan ook van groot belang dat de aandacht gevestigd wordt op de connectiviteit van habitat bij nieuwe stedelijke ontwikkelingsplannen. Besef van het belang van connectiviteit en van dier- en plantvriendelijke tuinen bij de bevolking zou het perspectief van de flora en fauna in stedelijke gebieden ook kunnen vergroten.

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Partial baldness in relation to reproduction in pond bats in the Netherlands

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Abstract: Temporary bald spots in mammals are usually related to moult. Alternatively, they may be a sign of bad health, or a side effect of hormones. Pond bats (*Myotis dasycneme*) commonly show partial baldness. Using data from more than 2,200 pond bats, captured between 2003 and 2008, we investigate the possible social, ecological and physiological factors involved in this phenomenon. A large proportion of pond bats were partly bald during a short period of the year, mainly between mid-May and the first week of August. Hair loss was observed in just a small area on the back of the bat, between the shoulder blades. These bald spots were much more common among females than males. The occurrence of baldness was temporally correlated with the nursing period of females. To test the generality of these patterns we studied animals from museum collections and photographs of roosting animals taken during the past two decades. While these data remain anecdotal, the position of the bald spots and the timing of appearance are consistent with those found in this study.

Keywords: pond bat, *Myotis dasycneme,* partial baldness, bald spot, hormones, reproduction, parasites, fungi, nutrition deficiencies, moult.

Introduction

Temporary hair loss in relation to moult is a common phenomenon in mammals. Most mammals change their coat every year and some have two different types of hair: a dense winter fur and a lighter summer fur. Most moults can be classified in one of two groups: dorsad and diffuse. Dorsad moult is a uniform sequence of replacement and diffuse moult is characterised by an irregular and blotchy pattern of replacement (Rowsemitt et al. 1975). Other causes for temporary hair loss can be bad health or a side effect of hormones that may be adaptive or selectively neutral.

Excessive loss of fur, caused by bad health, occurs frequently in many bat species (Keller 1994, Butchkoski & Hassinger 2002, Ter Hofstede et al. 2004, Pederson 2006, Wolters 2006). Fur loss can be caused by external parasites (e.g. bat flies, Streblidae and Nycteribiidae) or skin-growing fungi (dermatohpytes) or *Demodex* mites (small mites which live in hair follicles). In captivity, bats' hair loss can also be due to nutritional deficiencies, poor hygiene, improper housing, injury or low humidity (Wilson 1988).

Reproductive hormones have effects on various aspects of hair growth and moult in mammals and some of these effects may be adaptive (Fraser & Nay 1953, Johnson 1958). For example, in rabbits hormones regulate the loosening of hair from the ventrum and inner thighs. This process occurs from the day of parturition until 3-4 days into lactation. Rabbits pluck these hairs and use them for nest building (González-Mariscal et al. 2003). Hormonal change is known to have side effects on hair loss / retention. For example, humans show a change of hair structure that is related to reproduction (Ohnemus et al.

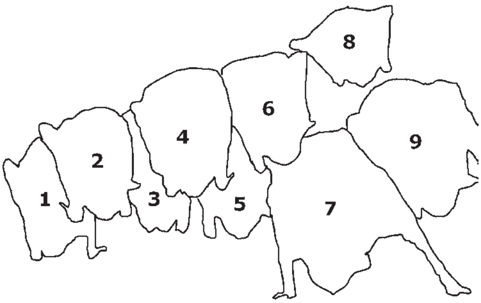


Figure 1. Photograph of roosting pond bats from the church loft in Berlikum, summer 2005. The bald spots can be seen between the shoulder blades. In each individual the bald spot is similarly shaped. Left: Most of the individuals in the photograph can be distinguished by age (juvenile and adult). Individuals with obvious bald spots are: 1 (juv), 2 (juv), 3 (juv), 4 (ad), 6 (juv), 8 (juv). Individuals which might be losing their hairs are: 7 (ad), 9 (ad). Individual 5 (ad) has no bald spot. *Photograph: Zomer Bruijn.*

2006). A change of hormone levels, especially oestrogen, during pregnancy causes hair that under normal conditions would have fallen out to be retained and new hairs to change structure. When hormone levels return to normal after child birth these retained hairs fall out and hair structure changes back to normal. Presumably, such changes have no particular function, but are a selectively neutral pleiotropic effect.

In 2002, during our first year of study on pond bats (*Myotis dasycneme*), we noticed that a large proportion of bats we captured showed bald spots during a short period of the year. The current literature contains no observations on this phenomenon but, due to its inconspicuous nature, it could have been overlooked in the past. We therefore investigated several historical records to check if the occurrence of these bald spots is a recent phenomenon.

To understand the cause or function of the bald spots (also referred to in this paper as partial baldness) we investigated all the bats we captured between 2003 and 2008 and described possible causal factors such as parasite load, body condition, sex, sexual maturity and reproductive status. By comparing descriptions of marked individuals we could

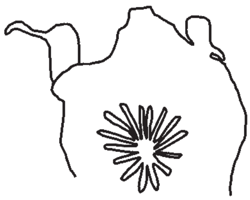


Figure 2. A pond bat captured in Reeuwijk, Zuid-Holland, August 2007. Between the shoulder blades a typical regrowth pattern can be seen, the darker hairs growing from the centre outwards. Left: Line drawing of the outline of the regrowth pattern.*Photograph: René Janssen.*

identify if individuals became partially bald in two or more successive years. We were also interested in the spatial and temporal patterns of the occurrence of these bald spots and took observations of pond bats in several Dutch provinces between April and September in each year.

Material and methods

Captures and measurements

During six years of study, between 2003 and 2008, the authors and bat volunteers captured pond bats in several locations in the Netherlands between April and September. These bats were mostly captured on their commuting routes using mistnets (Haarsma & van Alphen 2009a). In addition, pond bats were captured in spring and autumn while they were swarming in front of their hibernacula in the provinces of Gelderland, Limburg and Zuid-Holland.

Each individual was handled and described by the first named author using the Dutch protocol for the assessment of reproductive status, age and health of bats (Haarsma 2008, Haarsma & van Alphen 2009b). Sometimes, for ethical reasons (e.g. a highly pregnant female, large number of bats) handling time was shortened and some characteristics were not recorded. Standard biometric measurements were taken from every bat (forearm length and weight) as well as sex and reproductive status. Based on the fusion of phalangeal epiphyses, descriptions of male testes and epidydimes and of female abdomen and nipples, bats were classified into three maturity groups: juvenile, sexual immature animals and sexual mature animals. Females were grouped into three reproductive groups: not reproductive, nursing and pregnant. In addition the presence or absence of parasites on the wing membrane and in the fur was recorded.

The hairstyle of each bat was categorised into three groups: 1. normal (absence of bald spots), 2. visible bald spot and 3. regrowth of hair. The location of bald spots (on the back, around the umbilicus or other location) was also noted. The typical shape and location of the bald spots can be seen in figure 1. Regrowth was easy to distinguish because the under fur, which has a grey colour, grows back first, followed later by the top fur. The hairs typically regrow from the centre outwards (figure 2). To investigate the factors influencing the phenomenon of partial baldness, we clustered the hairstyles into two groups: absence of bald spots (normal hairstyle) and presence of bald spots (visible bald spot and individuals with regrowth).

Approximately 75% of the population were marked with a ring and fitted with a transponder. We avoided marking the entire population, because of the risk of damage or injuries from the marking methods. By recapturing marked individuals, we could monitor how quickly hairs regrew and whether individuals showed partial baldness in successive trapping sessions.

Investigation of historical records

All the pond bats within the collection of the National Museum of Natural History (Naturalis) were investigated for signs of bald spots. These included 19 dried stuffed specimens (8 females and 11 males) and 87 specimens preserved in alcohol (21 males and 57 females captured in winter, 7 males and 2 females captured in summer). All of these had been collected in the Netherlands between 1917 and 2002. The hairstyle of each animal was recorded.

Mr. Z. Bruijn investigated his collection of photos of roosting pond bats from church lofts in Berlikum and Tjerkwerd (in the province of Friesland). These were taken annually between 1999 and 2006, with an initial photo session from the early 1990s. Although these pictures were not taken for this purpose, the bald spots can be distinguished in the photos as pond bats always hang with their bellies against objects and their backs visible (figure 1).

Statistical analysis

Binary logistic regression was used to compare the binary dependent variable (presence/absence of bald spots) with categorical independent variables such as sex, province, parasite load, sexual maturity and reproductive status of females. As a measure for body condition index we took the unstandardised residual of the linear relation between forearm length and body weight (Kaňuch et al. 2005, Vázquez-Morón et al. 2008). A Kruskal Wallis test for independent samples was used to compare the frequency of bald spots over the five research years. Statistical analyses were carried out using SPSS V15.

Results

Historical records

None of the specimens from the Naturalis collection showed signs of partial baldness, with the exception of one stuffed animal from Russia, collected on 16 August 1989 in Nizhni Chir (RNHM reg. no 37172). The size and coloration of the nipples indicate this was a lactating female. Between her shoulder

Table 1. The presence (+) and absence (-) of partial baldness on photos, slides and videos taken from the churches of Tjerkwerd and Berlikum.Years in which no photos were taken are marked with a ?.

Year	Tjerkwerd	Berlikum
Early 1990s	+	+
1999	+	?
2000	+	+
2001	-	?
2002	?	?
2003	+	?
2004	+	?
2005	?	+

blades the typical regrowth pattern of the partial baldness described in this article could be distinguished (figure 3).

Examination of the historical photographs from Berlikum and Tjerkwerd showed that the phenomenon was present in the early 1990s (table 1). Between 1999 and 2005 in all years, except 2002, pond bats with bald spots were present in one or both of the churches. The photos were not taken systematically so no other conclusions could be drawn from these pictures.

Animals captured between 2003 and 2008

Between 2003 and 2008 we captured and described 627 male and 1592 female pond bats (531 and 1233 individuals respectively). Of these animals a total of 404 males (76.1%) and 927 females (75.2%) were individually marked. For the analyses in this paper all 2219 descriptions of individual bats were used.

Sex, sexual maturity, parasites and body condition

Almost all observed bald spots were located on the back of the bat, between the shoulder blades (the three exceptions were located around the navel and the nipples). The presence or absence of partial baldness was scored for all the captured bats (figure 4). Partial baldness was more common in female pond bats than in males (table 2, P=0.000). Partial baldness was related to sexual maturity (table 2, P=0.000). 27.9% of the females from the sampled population showed signs of partial baldness. Partial baldness was not evenly distributed between the female maturity groups: it was found in 44.1% of the juveniles, 2.9% of the sexual immature individuals and 36.3% of those that were sexual matures. The male population also showed shows signs of partial baldness (15.4%), but the juvenile age group was the only group with a relative high frequency of bald spots (41.1%). The other maturity groups had a low percentage of individuals with bald spots: sexual immature males (3.2%) and sexual mature ones (1.9%).

Although the majority (88.7%) of pond bats captured for this study had at least some parasites, no relation between the number of parasites and partial baldness was found (table 2, P=0.810). The presence of bald spots was also not related to the body condition index (table 2, P=0.401).

Table 2. Results of binary logistic regression between the dependent variable ‘partial baldness’ (presence/absence of bald spots) and several categorical independent variables. Significant relations with the dependent variable are marked with an asterisk.

	Wald statistic	df	Significance
Sexual maturity	77.57	2	0.000*
Sex	88.18	1	0.000*
Body condition	0.652	1	0.401
Parasite load	0.3016	1	0.810
Province	50.00	8	0.000*
Reproductive status of females	144.96	2	0.000*

Figure 3. Female pond bat from Russia, collected on the 16th August 1989 (RNMH reg nr 37172). Between the shoulder blades a hair regrowth pattern can be distinguished. This pattern is only observed in animals which previously showed bald spots. *Photograph: Hein van Grouw.*

Spatial patterns
Approximately three quarters of the total sample of pond bats used in this research were captured in Zuid-Holland. The majority of the remainder were captured in the provinces of Overijssel, Friesland, Utrecht and Noord-Holland (table 3). The occurrence of bald spots in pond bats was more common in some provinces than in others (table 2, P=0.000). The highest percentage of individuals with bald spots was found in Utrecht (50.6% females and 18.5% males).

Temporal patterns
In all the research years (2003-2008) the timing of partial baldness occurred in a similar manner (table 4). The first bald spots were noticed around mid-May (week 19). During week 24 (second week of June) the highest number of individuals showed signs of partial baldness, and the last individuals with bald spots were observed around week 32 (first week of August). The first signs of regrowth were found in the second week of June (week 24). During week 29 (mid-July) the highest number of individuals showed signs of regrowth. By the beginning of August (week 35) no more signs of partial baldness or regrowth were found.

Female reproductive status
Females with a swollen abdomen, which was taken as a sign of pregnancy, were captured from mid-April (week 15) onwards, with peak densities in week 20 (mid-May) (figure 5). The graph shows a dip in week 19 as we tried to avoid capturing pregnant females. Swollen mammae and bald areas around the mammae, which were taken as a sign of nursing, were observed from the second week of May (week 19), with a peak in week 25 (mid-June).

The peak in partial baldness correlated with the peak in nursing (figure 5). The occurrence of bald spots in adults females was sig-

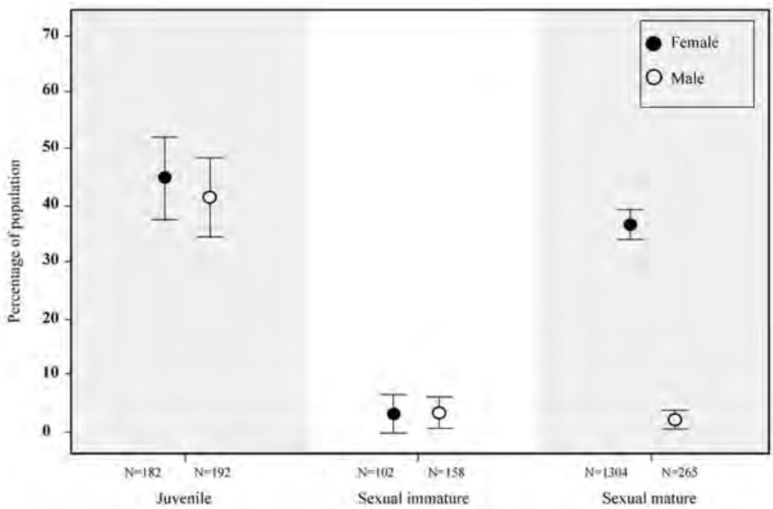


Figure 4. Percentage of the population with signs of partial baldness for three maturity groups (juvenile, sexual immature and sexual mature). The males and females are represented by open and shaded circles, respectively. The error bars show the 95% confidence interval for the mean.

Table 3. The number of individuals captured on commuting routes in different provinces and the percentage of this sample showing signs of partial baldness.

	Females		Males	
Province	*n*	%	*n*	%
Friesland	119	47.1	46	10.8
Overijssel	149	14.1	13	7.7
Flevoland	17	29.4	14	7.1
Utrecht	89	50.6	27	18.5
Noord-Holland	93	16.2	46	13.0
Zuid-Holland	1098	37.8	400	17.7
Gelderland	16	0	39	0
Limburg	11	0	39	0
Zeeland	0	0	3	0
Total	1592		627	

Table 4. The first, peak and last observation of partial baldness and regrowth between 2003 and 2008 (expressed as week number).

	Partial baldness			Regrowth		
Year	First observation	Peak	Last observation	First observation	Peak	Last observation
2003	22	24	32	24	28	31
2004	19	25	30	25	29	33
2005	20	24	30	24	29	31
2006	21	24	30	24	29	34
2007	21	25	31	25	28	33
2008	19	24	29	25	29	29

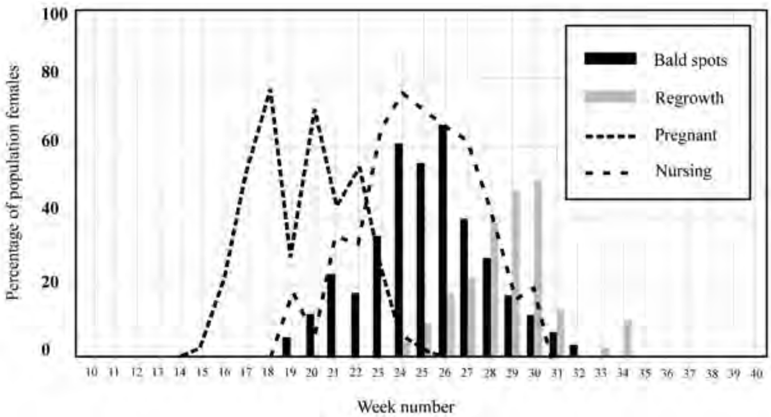


Figure 5. Percentage of the female population showing bald spots or the typical dark hairs which indicate regrowth of a former bald spot per week. The figure also shows the timing of reproductive status of females: pregnant and nursing are indicated as a percentage of the population.

nificantly correlated to reproductive status of females (table 2, *P*=0.000).

The pattern described in figure 5 occurred in all the years of the study period. There was some variation in the timing of the first and last observations (table 4). In 2004 and 2008 the first signs of bald spots were observed in week 19, which is one week earlier than average. The pattern of regrowth that year corresponded with previous years. In 2006 the last signs of regrowth were observed in week 34, which is one week later than average. The difference between the years was not significant (χ^2=4, df=5, *P*=0.406).

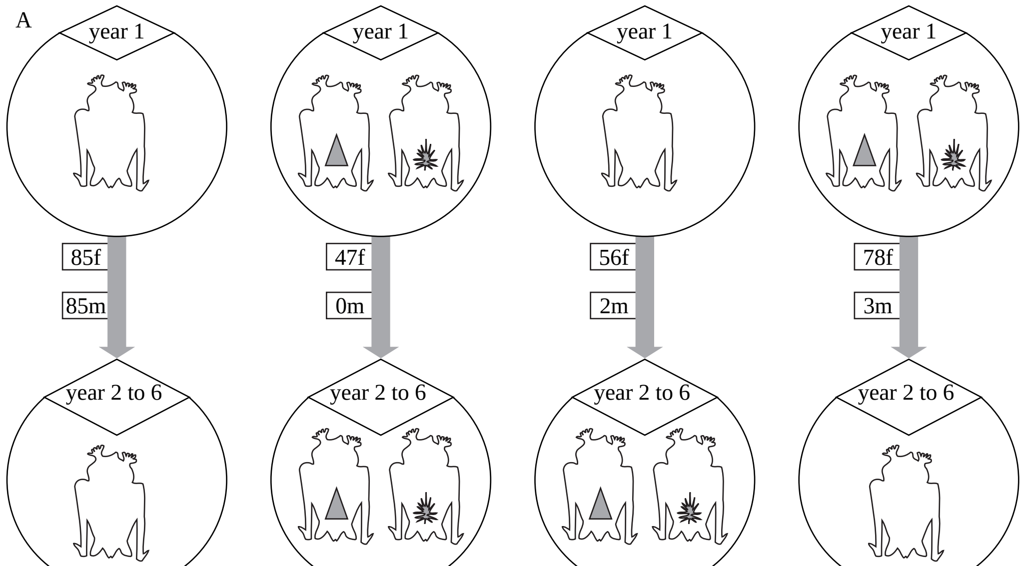
298 individuals (216 females, 82 males) were captured, described and assessed for the presence or absence of bald spots more than once. Several individuals were recaptured in the same season, some in different years, others were recaptured in both. In total we used 137 recapture sightings (99 females and 38 males) of pond bats captured within one season (figure 6B) and 356 recapture sightings (266 females and 90 males) of bats captured in two different years (figure 6A). Some bats were observed with the same hairstyle (normal, bald spots present or regrowth), some had different hairstyles. Partial baldness is a recurrent, rather than a one-off, characteristic (at least among females): 17.7% of the recaptured females that once had bald spots, were observed with partial baldness the next year and 29.3% of these females were recaptured without showing signs of bald spots. None of the males, on the other hand, became partially bald in two successive years. 94.5% of the males did not show any bald spots over the years.

We observed 53 individuals (49 females and 4 males) that lost and regrew their hair during one summer season. 44.4% of the recaptured females and 86.8% of the recaptured males were observed more than twice during one season without bald spots.

Partial baldness was not observed during hibernation, according to annual observations of approximately 300 pond bats in hibernacula in several parts of the Netherlands (A.-J. Haarsma, unpublished results). During the pond bat swarming season (between week 33 and week 37, Janssen et al. 2008) no pond bats with bald spots were captured.

Conclusion

The results show that partial baldness in pond bats is not a recent phenomenon. Historical evidence of this was found from both the Naturalis specimens and the photographic



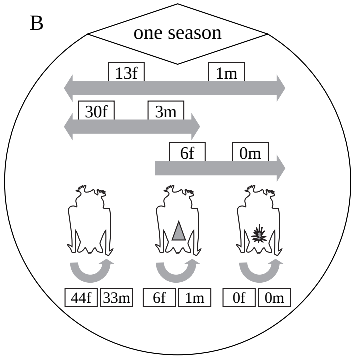


Figure 6. An overview of observations of pond bats recorded in two different years (A) or twice or more within one year (B). Three different hairstyles are schematically presented: bald spots absent ( ), bald spots present ( ) and regrowth ( ). The number of observations for each arrow are given for males (m) and females (f). Over the years, pond bats may develop bald spots or bald spots may disappear, or bats with bald spots may develop regrowth. A particular hair condition (not bald, bald or regrowth) may also remain unchanged.

archive of Z. Bruijn. The photographs from Tjerkwerd and Berlikum indicated that the phenomenon has existed in the Netherlands at least since the early 1990s. Based on geographic evidence from Russia, we hypothesise the phenomenon also occurs in other European counties. Recently, during a fieldtrip in northern Germany with local bat workers, we witnessed evidence for this hypothesis: in this part of Germany bald spots have frequently been observed since 2004 (A. Seebens & F. Gloza-Rausch, personal communication).

Partial baldness is found across the Netherlands. Bald spots were observed among bats captured in the provinces of Noord-Holland, Zuid-Holland, Friesland, Overijssel and Utrecht. In spring and autumn partial baldness did not occur in areas without maternity roosts, such as the provinces of Gelderland and Limburg.

Bald spots in pond bats always occurred in the same part of the body, between the shoulder blades. The results show that partial baldness in pond bats can be an annually recurrent phenomenon, occurring mostly in juveniles and females, and that it is linked with reproduction in females. The onset of partial baldness in female pond bats was around mid-May and hair regrowth started around mid-June. Partial baldness was not observed in hibernating bats, indicating this regrowth is completed at least before winter and that partial baldness is not found the whole year round. We conclude that partial baldness in pond bats is not a sign of bad health and is not related to body condition.

Discussion

Our results do not provide a decisive answer about the functional factors that influence partial baldness in pond bats. Here we give an overview of hypothetical causes. These can be classified into three groups: bad health, a neutral (non-adaptive) side effect of hormones, and an adaptive side effect related to reproduction.

Bad health

Several external factors may be responsible for hair loss in pond bats: external parasites (e.g. bat flies), skin-growing fungi, *Demodex* mites, nutritional deficiencies, poor hygiene, improper housing, injury, low humidity and moult. The fact that bald spots are restricted to a small area on the back of the bats may be explained by their grooming behaviour. Bats are able to clean their bodies very thoroughly, except for a small area on their backs, which is difficult to reach. So, while they can get rid of parasites, skin growing fungi and *Demodex* mites from most of their body, it is possible that part of their back remains infected and becomes bald. The results of this study, however strongly suggest that baldness is not a sign of bad health. We found no relation between body condition or parasite load and partial baldness. Furthermore, bad health would not account for the sex difference in the incidence of partial baldness and the occurrence of bald spots could not be predicted to be site-specific or restricted to a particular time of year.

A neutral (non-adaptive) side effect of hormones

The temporal pattern in adult females seems indicative of a hormonal effect. Both male and female juveniles develop bald spots in their early stages of life. We hypothesise that offspring of balding females acquire these hormones through their mother's milk and this leads them to develop bald spots themselves. There could be several hormones involved, possibly including reproductive hormones like oestrogen and aggression-inducing hormones (testosterone). During a short period of the year pond bats, especially those with young, need to be very aggressive because of high competition for food. During this research we did not notice any signs of aggressiveness among pond bats in summer. Signs of aggressiveness are found regularly in male pond bats during the mating season when bite marks in the ears and wings are visible (A.-J. Haarsma, personal observation). While this indicates aggression towards each other, it does not indicate partial baldness.

A second hypothetical neutral side effect is linked to the behaviour of animals in the roost. In the second week of May the number of individuals in the maternity roost increases, due to the birth of young. Individuals tend to form clusters (figure 1) and many sit on top of each other. This behaviour could result in physical damage, especially when the nails of the thumbs lay on the backs of other individuals. However, it seems very unlikely that this would result in similarly shaped bald spots and that it would only affect reproducing individuals (not all individuals reproduce each year: about 30% of the sexual mature females within a roost do not reproduce in any particular year; A.-J. Haarsma, unpublished data).

Adaptive side effect related to reproduction

The reproductive success of pond bats depends on a female bat's ability to produce milk.

Good milk production ensures that a female can wean her single young faster, giving the young more time to prepare for hibernation. Researchers discovered that energy export during lactation is limited by the ability of mothers to dissipate body heat (the heat dissipation limit hypothesis, Król & Speakman 2003). The mothers need to lose the additional heat produced in processing food and producing milk. In support of this hypothesis nest building mammals select nests based on their insulative value, not only to reduce heat loss in cold conditions but also to dissipate heat during warm periods (Guillemette et al. 2009). Pond bats do not often move between different roosts and are not able to change the construction of their roost. Temperatures within a maternity roost remain relatively stable (Voûte 1972). Partial baldness may therefore be an adaptation to enhance milk production.

Another hypothetical explanation for partial baldness in pond bats is that it is a trade-off, where resources needed for the maintenance of hairs are allocated to other functions, such as lactation or acquiring brown tissue. There are, however, no studies to support this hypothesis. Pond bats are a migrating species, travelling between 70 and 350 kilometres each year between summer and winter roosts (Haarsma 2009). It is possible that changing the most important body hairs first gives animals that leave the maternity roost relatively early in the year (the reproductive females) a head start during the moult, which would otherwise take place during migration.

The third hypothetical explanation for partial baldness in pond bats is associated with olfactory communication. Many species of bats secrete substances, for reasons such as mate recognition, territory marking, offspring recognition and sexual selection. Scent glands are located on different parts of a bat's body, including the face, ears, neck, chest, shoulders and genital area. Scent glands in bats can be very inconspicuous and only visible during a short period of each year (Nassar et al. 2008). Although the bald spots did not excrete an odour perceivable by humans, they might have an olfactory function.

Further studies

Further studies are required to assess whether partial baldness in this species has an adaptive function. In this respect, comparative studies with other bat species would be useful. Species that are naturally partial bald, such as the Neotropical bat *Pteronotus davyi*, would be of special interest. This species is permanently hairless on its back, which is caused by the dorsal side of the wing membranes meeting in the middle of the back (Bonaccorso et al. 1992). Experiments in a laboratory setting are needed to distinguish between the different hypotheses: for example, by temporally preventing bats from cleaning themselves with their tongues and hind feet. Equally, reproductive hormones could be administered to captive, non pregnant females. If bald spots really are an effect of hormones, such manipulation should induce baldness. The temperature in maternity roosts might also be of influence and gathering data about temperature fluctuations in roosts, such as church lofts might lead to new insights into this hypothesis.

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Samenvatting

Het voorkomen van kale plekken in relatie tot reproductie bij de meervleermuis

Kale plekken in de vacht van zoogdieren worden meestal veroorzaakt door rui. In sommige gevallen kunnen kale plekken veroorzaakt worden door ziekte of een bij-effect zijn van hormonen. Meervleermuizen (*Myotis dasycneme*) vertonen vaak opvallende kale plekken op de rug. Aan de hand van data van meer dan 2200 gevangen meervleermuizen tussen 2003 en 2008 hebben we de mogelijke sociale, ecologische en fysiologische oorzaken achter dit fenomeen onderzocht. Het merendeel van de gevangen meervleermuizen vertoonde kale plekken in een korte periode van het jaar, meestal tussen midden mei en de eerste week van augustus. De kale plekken bevonden zich in een duidelijk afgebakend gebied op de rug van de vleermuizen, tussen de schouderbladen. Vrouwtjes vertoonden vaker kale plekken dan mannetjes. De aanwezigheid van kale plekken is duidelijk gerelateerd aan de zoogperiode van vrouwtjes. We hebben onderzocht hoe recent het door ons waargenomen patroon is. Hiervoor hebben we onze patronen vergeleken met de Naturalis-museumcollectie en met archieffoto's van rustende meervleermuizen op kerkzolders. Ondanks het feit dat vroegere waarnemingen van kale plekken alleen door toeval verzameld zijn, is de positie van de kale plek en het patroon van verschijnen door het jaar heen, gelijk aan de resultaten van huidige onderzoek.

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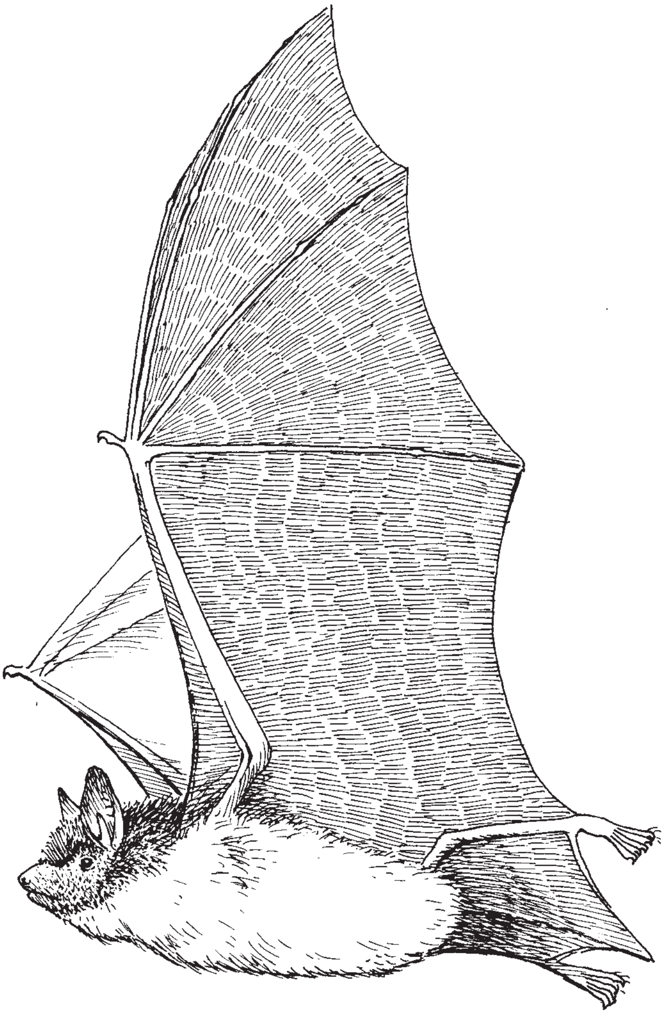

Chin-spot as an indicator of age in pond bats

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Abstract: In field studies of animal populations, it is often useful to be able to assess the age of an individual. In this paper we investigate the use of chin-spots as an indicator of age in pond bats (*Myotis dasycneme*). During six years of research, from 2002 to 2008, we captured more than 2,500 pond bats. To test whether the chin-spot can be used, we gathered data on chin-spot colour and other indicators of age, such as dental wear, degree of fusion of phalangeal epiphyses and reproductive status. We tested the correlation between chin-spot colour and these indicators of age. We also studied the transformation of these characteristics during bats' life course and therefore between different age classes. We found significant correlations between the colour of the chin-spot and other known age indicators. The results showed a significant relation between colour and the number of days between the first and the last capture. The longer the period between two capture events, the larger the change in colour of the chin-spot. Animals of a known age, captured as juveniles, showed a transformation in coloration from deep purple (class 5) to light-coloured (class 1) over an average time period of two to four years. Most of the juvenile pond bats had a chin-spot coloration in class '4' or '5', most sexual immature animals in class '3' and most mature animals in class '1'. We conclude that the colour of the chin-spot is a reliable predictor of the age class of pond bats.

Keywords: pond bats, determination of age, chin-spot, dental wear, fusion of phalangeal epiphyses, reproductive status, life-history trait, mark-recapture.

Introduction

Researchers capturing bats for scientific purposes often record the individual characteristics of each bat, such as standard biometric measurements, gender, reproductive status and age. Although age is an important property of an animal, year-round suitable methods for estimating age are rare. In a study on Daubenton's bats (*Myotis daubentonii)*, Richardson (1994) found the chin-spot to be a reliable characteristic for estimating age. The author defined chin-spots as: ".... a jet black, often shiny, sharply defined area of skin covering the centre of the lower lip for about 1 mm and tapering, slightly down to the chin. It contrasts markedly with the pink and pale brown skin of the rest of the lower face." Richardson (1994) concluded that animals with a dark chin-spot are juveniles or sub-adults and animals with a light-coloured chin-spot are always adults.

There are several advantages of using the chin-spot as opposed to other age indicators, such as the fusion of the phalangeal epiphyses, dental wear or reproductive status: 1. in autumn, when commonly used characteristics for estimating age become vague, it is possible to use the chin-spot to distinguish between age classes (Rivers et al. 2005). 2. This method does not require any handling of animals during hibernation when seeking to determine their age (Kokurewicz & Speakman 2006). This is especially useful when studying hibernating animals that are sensitive to disturbance.

Until now the chin-spot has only been used as an age indicator for Daubenton's bats. Pond bats (*Myotis dasycneme)* are morphologically very similar to Daubenton's bats. Like Daubenton's bats, some pond bats show a chin-spot and this characteristic could be a practical method to distinguish between age classes. For this reason, we gathered data on chin-spot colour and other indicators of age during an extensive monitoring study on pond bats (Haarsma 2009). We were especially interested in the changes of chin-spot colour during the course of life of a bat and the correlation of these changes with other age indicators.

Materials and methods

Chacteristics used

Protocol

In the Netherlands there is a protocol for assessing the reproductive status, age and health of bats (Haarsma et al. 2009). The purpose of this protocol is to ensure the comparability of datasets between bat researchers. The protocol standard uses five classes to describe each characteristic. In order to simplify comparisons between characteristics, all the characteristics are classed from '1' – extra small (XS)/ absent/ light-coloured to '5'- extra large (XL)/ present/ dark. A manual provides photos and descriptions to identify each class (Haarsma 2008). This allows researchers to make more or less standardised interpretations about age and reproductive status.

During six years of study, between 2002 and 2008, we worked with bat volunteers, capturing pond bats. Each individual was handled and described by the first author using a pilot version of the protocol. (The characteristics discussed in this paper remained unchanged between the pilot and final versions of the protocol). Most of the captured pond bats were individually marked with a ring, a transponder or both. At each recapture of marked individuals, a new description was made which covered the following characteristics: dentition wear, age-class based on interphalangeal fusion and the various aspects of reproductive status. Sometimes, for ethical reasons (e.g. highly pregnant female or a large number of bats) handling time was shortened and some characteristics were skipped.

Dental wear

The dentition of bats is diphyodont. After losing a complete set of deciduous teeth, permanent teeth have fully emerged by the time they are weaned (Fenton 1970). In the course of a lifetime, the tooth surface becomes abraded from repeated mastication (Anthony 1988, Evans 2006). The canines in particular lose their pointed appearance. With age, sometimes dark lines of tartar or dental plaque formed along the edges of the molars. Various investigators have tried to establish a link between different age categories and progressive stages of wear in canines and/or molars (Twente 1955, Sluiter 1961, Phillips et al. 1982). They found a considerable overlap between animals judged to belong to different age groups and the amount of dental wear. Hence they concluded that dental wear may be used as a broad indicator of age in bats, but not a valid characteristic for assigning bats to absolute age groups. Although the accuracy of dental wear in determining age class is still much debated, it is widely used by researchers as it is a relatively visible characteristic. The Dutch bat protocol (Haarsma et al. 2009) uses a combination of dental wear and dental plaque as an indicator, which is scored on a scale from class '1' (no dental wear or plaque) to '5' (heavy dental wear and all molars with plaque).

Interphalangeal fusion

Patterns of closure of the cartilage in finger bones can be used to asses the juvenile status of bats (Felten 1973, Brunet & Austad 2004). Mammals are born with soft cartilage epiphysial plates. At the start of the first autumn after birth these phalangeal epiphyses start to fuse (Elangovan et al. 2002). The fusion of the epiphyses in the bones of the fingers of a bat can be seen by using a torch to illuminate the wing membrane and fingers under the wing. The cartilaginous zones appear lighter than the ossified parts. Some investigators have been able to identify young (of that year) during the winter by the shape of their joints (Davis & Hitchcock 1965). During our research we determined the absence (class '1') or presence (class '5') of fusion in each animal captured. Epiphyseal growth plates which were almost closed were scored as class '3'. We could only use this characteristic during a limited time period (until the end of September), until fusion is complete.

Reproductive status
In most bat species juveniles have different pelage colours than adults (Anthony 1988). Pond bat juveniles are greyish brown and their bellies are greyer than those of adults. There are other distinctive characteristics that also indicate a juvenile status: 1. shorter and softer pelage hairs 2. fluffy grey down on the inside of the thighs and 3. a short dark nose. These characteristics are always accompanied by transparent phalangeal epiphyses and therefore not recorded separately, although we did use them as a reminder to look at the phalangeal epiphyses. During this research we also noticed that juveniles have a shorter, more rounded face, which elongates with aging. The pigmentation of the nose and face of juveniles is dark, older individuals have a lighter face and nose (A.-J. Haarsma, unpublished results). Very old individuals have pink spots, apparently without pigment, especially around their nostrils. Although easily recognisable in age extremes (very young or very old), we found no reliable criteria to describe change in pigmentation of nose and face for each age class; therefore, this characteristic was not used.

Sexual maturity is sometimes used to asses the age classes of bats (Kunz 1973, Encarnação et al. 2006). The onset of sexual development in juveniles is in their first or second autumn. In male bats this can be seen by an increase in the size of the testes and, later the distension of the epidydimus becomes visible through the perianal skin (Entwistle et al. 1998, Encarnação 2004). Before their first spermatogenesis the sheath around both testes and the tip of the epidydimus is dark and heavily pigmented. At the end of the spermatogenesis the epidydimus swells; leading the sheath to become stretched and the pigmentation to become more diffuse. In female bats, the first external signs of sexual development are visible after the first winter in which they mated, as they become pregnant and start to lactate. The distension of the lower abdomen caused by the developing foetus cannot be recognised until late in the pregnancy. Towards the end of pregnancy (in pond bats: week 26; A.-J. Haarsma, unpublished results) and during lactation the nipples become enlarged. The mammary gland can be seen underneath the skin as a yellow disc (Haarsma 2008). During lactation, most females lose most of the hairs in the immediate vicinity of their nipples as a result of repeated suckling by their young. Later the nipples become keratinised, presumably through continued distension and suckling or chewing of the young. After lactation the nipples retain their keratinised, enlarged appearance and this is a sign of parity. During this research we used descriptions of male testes and epidydimes and of female abdomen and nipples, following the protocol for assessing the reproductive status, age and health of bats (Haarsma 2008).

Chin-spot
Classification of the chin-spot was done by visual inspection using a headlamp, with extra-bright LED lights (Black Diamond Zenix IQ and Princton Tec Apex). For a complete inspection of the chin-spot the mouth of the bat had to be slightly opened. The colour of the chin-spot was compared with the colour of the transition zone between the palate and the bottom side of the nose (minimum colour) and the colour of the nose (maximum colour) (see figure 1). For each animal the chin-spot was designated to one of five coloration classes (figure 2):

1. Light-coloured chin-spot that was the same colour as the transition zone between palate and the bottom side of the nose.
2. Barely visible chin-spot, with few pigmented

spots, sometimes only around the edge of the chin.
3. Intermediate chin-spot, which has about 50% or diffuse pigmentation.
4. Visible chin-spot, where more than half of the chin-spot has pigmentation and has an overall purple colour.
5. Completely purple. The chin-spot is densely pigmented with an overall deep purple colour.

We assume the first pond bats are born in the end of week 19 (around the 13th of May) (A.-J. Haarsma, unpublished results). In this week the first female animals without distended bellies and with swollen mammae and bald areas around the mammae, which were taken as a sign of nursing, were observed. The last pregnant female was observed in week 25 (between 18 and 24 June), the week in which the last juveniles will be born. On average pond bats are born in week 22. In the rest of this analysis week 22 will be assigned to as week 0 (or day 0) of the life of a bat. Only recaptured bats that were classified as a juvenile at their first capture, have a known age. This age is based on the number of days between the first and subsequent captures and the estimated day 0 of their lives.

Statistical analyses

Statistical analyses were carried out using SPSS V15. Spearman's rank correlation coefficient was used to test the relation between the ordinal dependent variable 'chin-spot colour' (five categories) and the independent variables 'dental wear', 'fusion phalangeal epiphyses' and 'minimum age' (in years). The relation between change in colour and sexual mature/ sexual immature animals was calculated using binary logistic regression, with sexual maturity as the dependent variable.

Results

Average colour of the chin-spot

We captured and described 787 male (606 individuals) and 1735 female (1321 individuals)

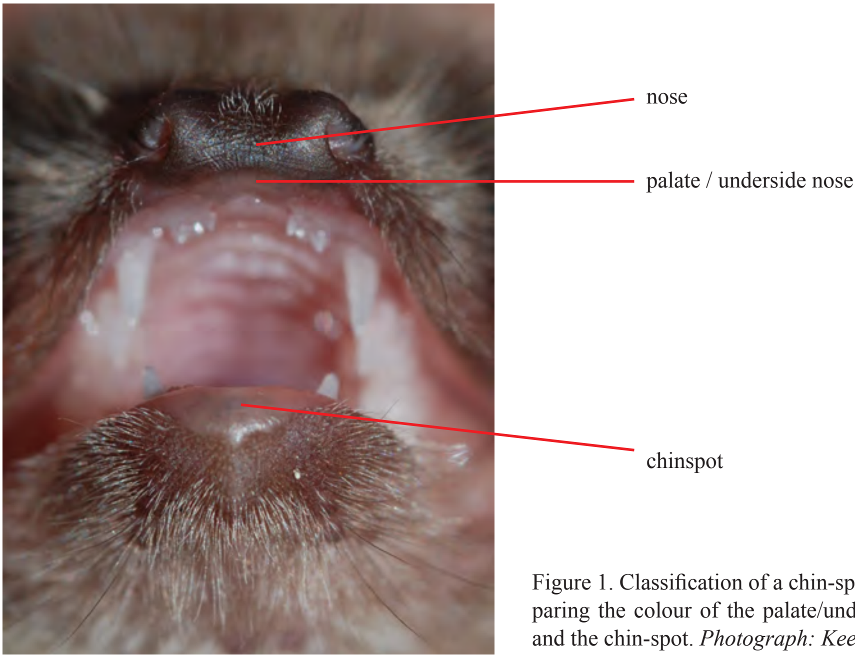
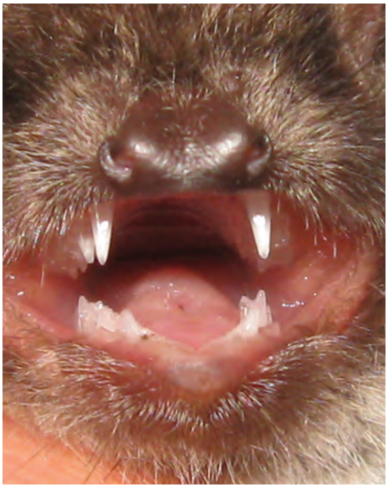


Figure 1. Classification of a chin-spot is done by comparing the colour of the palate/underside of the nose and the chin-spot. *Photograph: Kees van Bochove*.

1.

2.



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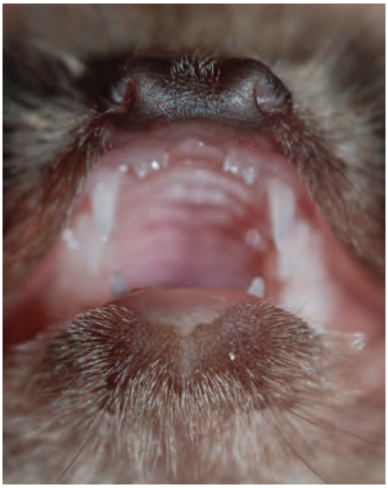

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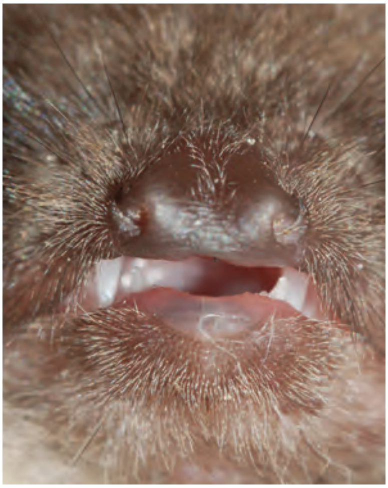

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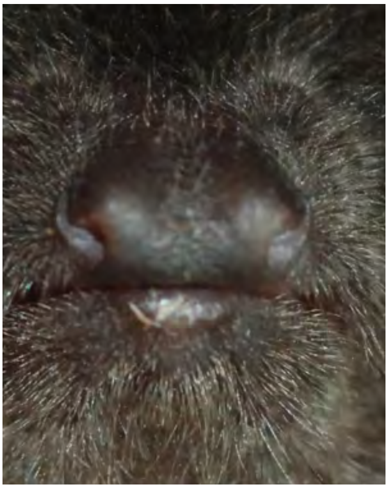

Figure 2. Photos representing the five coloration classes of the chin-spot. *Photographs: Kees van Bochove (1, 3, 4 and 5) and A.-J. Haarsma (2).*

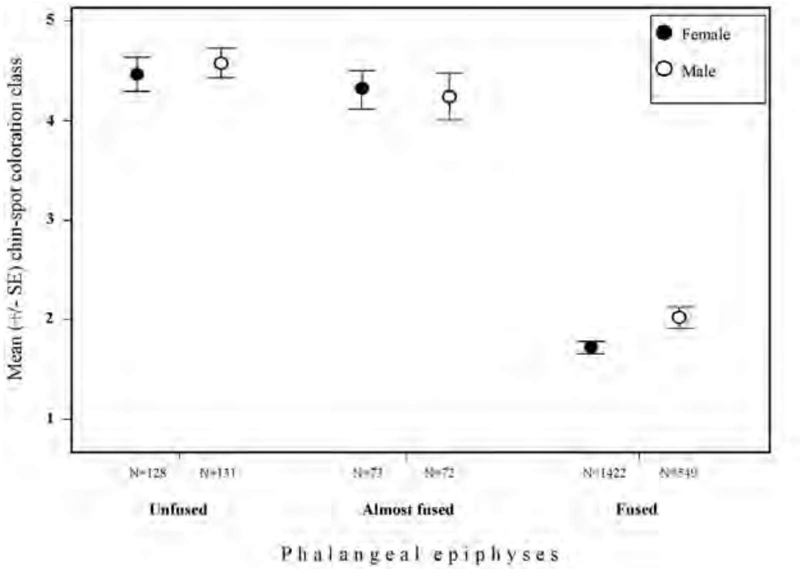

Figure 3. Mean (+/ SE) chin-spot coloration class (class '1'= light-coloured to class '5'= dark purple) plotted against the fusion of the phalangeal epiphyses. For each fusion category sample sizes are given for both females and males.

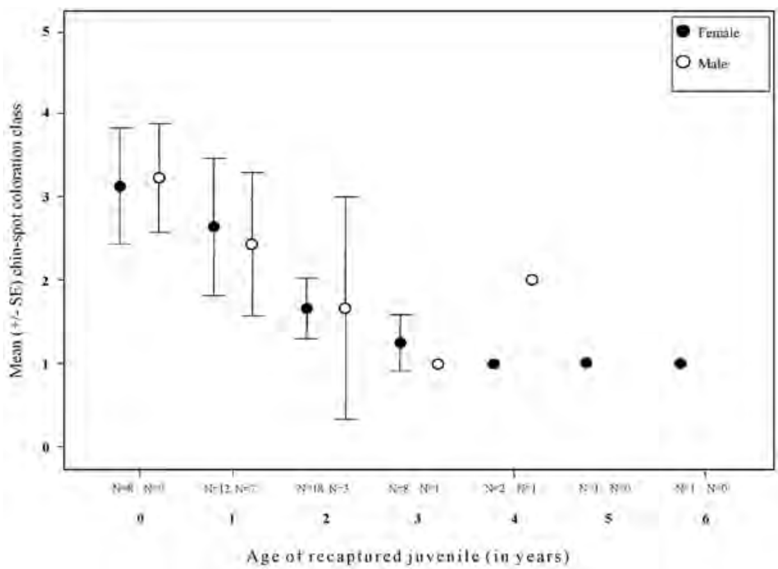

Figure 4. Mean (+/- SE) chin-spot coloration class (class '1'= light to class '5'= dark purple) plotted against calculated age (in years) of recaptured bats, classified as juvenile at first capture. For each year sample sizes are given for both females and males.

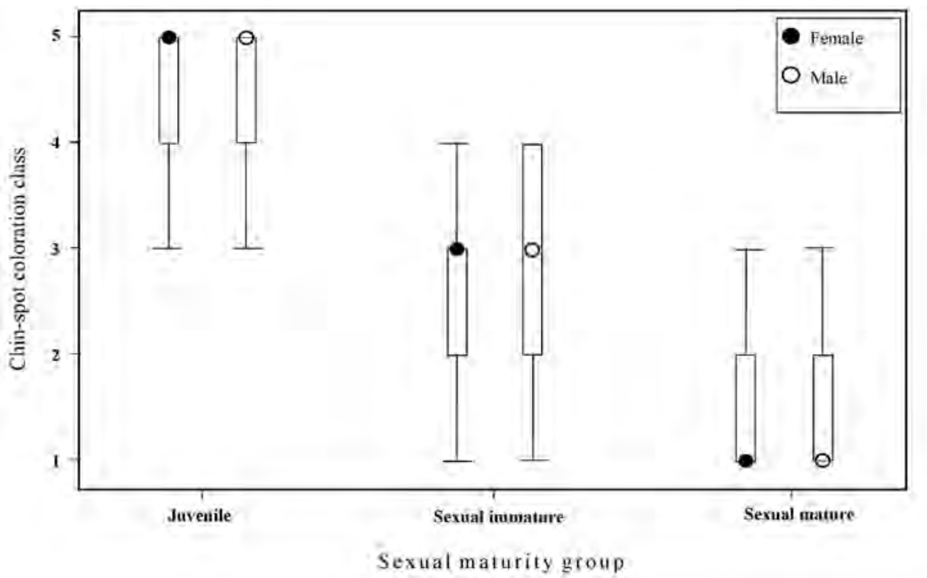

Figure 5. Box plot of the chin-spot coloration class with sexual maturity groups (juvenile, sexual immature and sexual mature). Shown as median, middle 50% and top/bottom 25% of the scores. The results are given for both males and females.

pond bats. We individually marked 501 of the males (82 %) and 1014 of the females (76%). By assessing the fusion of the phalangeal epiphyses we could classify 201 females and 203 males as juveniles. Animals with unfused phalangeal epiphyses generally had a darker chin-spot (class 4 or 5) than animals with fused phalangeal epiphyses (figure 3). We found a significant relation between the fusion of phalangeal epiphyses and the colour of the chin-spot (Spearman's rho = 0.644, n=2110, P=0.000), i.e. a dark chin-spot is associated with unfused phalangeal epiphyses.

Change in the colour of recaptured juveniles

The difference between chin-spot coloration and the fusion of phalangeal epiphyses implies that chin-spot coloration changes during the life of a pond bat. Recaptured bats (those which were classified as juvenile at first capture) hold the key to understanding the speed of transformation of chin-spot colour. This can be done by correlating the age of these bats with changes in chin-spot colour. Although we marked a total of 180 juveniles, we recaptured only 40 of these individuals (27 females and 13 males). We do not know if this was because of a high dispersal rate, low survival of juveniles or fatalities due to marking.

The transformation of the chin-spot of juveniles from dark to light is gradual (figure 4). After two years the first individuals were observed with a class '1' chin-spot. At three years of age the transformation was complete for most individuals. After the age of four no changes in chin-spot coloration class were observed, although a low sample size (n=5) means we can draw no conclusions from this. The relation between a change in pigmentation and the number of years between capture and recapture was significant for both females and males (Spearman's rho for females = 0.600, P=0.000, n=49; Spearman's rho for males = 0.552, P=0.005, n=21).

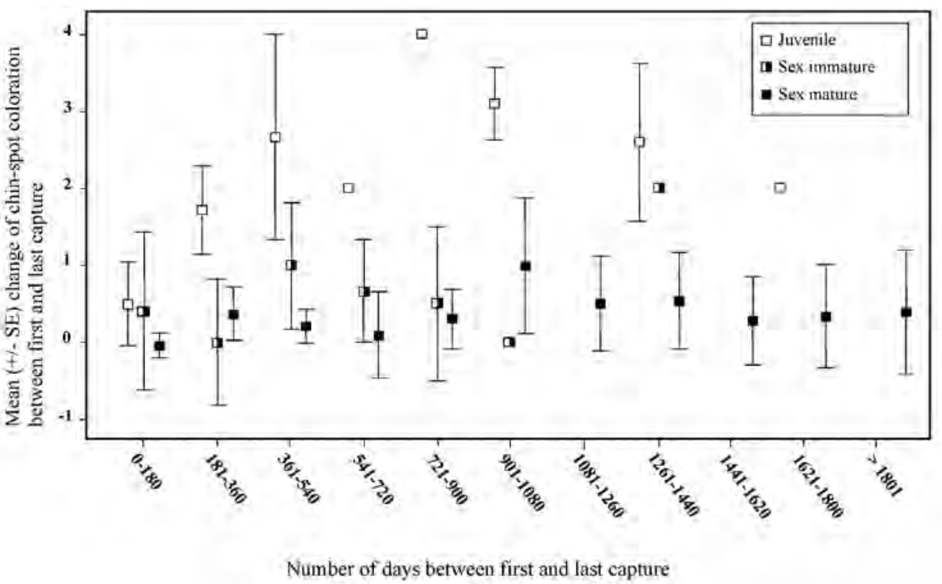

Figure 6. Mean (+/- SE) change between two chin-spot colours plotted against the number of days between the first and the last capture. Animals are grouped according to their sexual maturity during the first catch (juvenile, sexual immature and sexual mature). The largest possible change (four steps) is from a dark chin-spot (class '5') to a light chin-spot (class '1').

Chin-spot in relation to other age indicators

Dental wear

We scored dental wear in 973 female and 428 male pond bats. Dental wear classes '4' and '5' were clustered, because of the low sample size. There was a significant negative correlation between dental wear and chin-spot colour (Spearman's rho = -0.369, *P*=0.000, *n*=1401), i.e. lighter-coloured chin-spots were associated with an increased dental wear. The same result was found when the sexes were analysed separately (Spearman's rho for females = -0.324, *P*=0.000, *n*=973; Spearman's rho for males = -0.398, *P*=0.000, *n*=428,).

Reproductive status

We scored the colour of the chin-spot of 1148 sexually mature females and 278 sexually mature males and for 294 sexually immature females and 366 sexually immature males. A lighter-coloured chin-spot indicated sexual maturity (Wald statistic = 585.54, -2 Log likelihood = 1606.29, df=1, *P*=0.000). The same result was found when the sexes were analysed separately (females: Wald statistic = 327.75, -2 Log likelihood = 888.70, df=1, *P*=0.000; males: Wald statistic= 151.71, -2 Log likelihood = 546.09, df=1, *P*=0.000). Most of the juveniles had a chin-spot with a class '5' coloration, most sexual immature animals had one with class '3'and mature animals had a class '1' chin-spot (figure 5).

Reliability of characteristic

For chin-spot to be a reliable indicator of age the transformation from dark to light must be unidirectional. Furthermore, two independent observations on the same individual must have either the same value or (if the two observations are made over a longer time period) a value that only changes in one direction. To check the reliability of the chin-spot (and the usage of the 5 classes) we compared coloration classes of the chin-spot between the first and last captures (figure 6). In total, the chin-spot was scored twice or more for 208 animals (150 females, 58 males). The maximum change in colour can be four steps, from dark (class '5') to light-coloured (class '1'). The transformation from a dark to a lighter chin-spot was made by 78 animals; the change in colour was the largest for juveniles (between 1 and 4 steps) and sexual immature animals (on average between 0 and 2 steps). 119 individuals, mostly sexual mature animals, obtained the same score at both captures. In 11 individuals (9 females, 2 males) a darker chin-spot was recorded on the second capture.

Conclusions and discussion

The colour of the chin-spot can be used to assess the age class of pond bats. We found significant correlations between the colour of the chin-spot and the other known indicators of age: dental wear, fusion of phalangeal epiphyses and reproductive status. Dark chin-spots corresponded with light dental wear, unfused phalangeal epiphyses and sexual immaturity. By contrast, a light-coloured chin-spot corresponded with intermediate/heavy dental wear, fused phalangeal epiphyses and sexual maturity. The results show a significant relation between the change in colour and the number of days between the first and the last capture. The longer the period between the two capture events, the larger the change in the colour of the chin-spot.

None of the characteristics, dental wear, fusion of phalangeal epiphyses and reproductive status, completely explained the variability of the chin-spot colour. The average coefficients of determination (R^2) for males and females were 14.7%, 41.4% and 36.3% respectively. The chin-spot colour itself is a reliable characteristic, but there is still some overlap between chin-spot coloration classes and the calculated age classes (in years). Therefore we recommend using a combination of characteristics for an accurate age assessment.

For the animals captured as juveniles we observed that the chin-spot coloration transformed from class '5'(deep purple) to class '1' (light-coloured) over between two and four years. After their third winter, almost all the pond bats had a class '1' chin-spot. Most of the pond bats between 0 and 90 days of age (juveniles, with unfused or almost fused phalangeal epiphyses) had a chin-spot with a coloration between class '4'and '5', sexual immature animals class '3' and mature animals class '1'.

The size of pond bats and the combination with other facial characteristics provides sufficient distinction between the five used chin-spot colours to make an accurate age class assessment. Although manual assessment might easily lead to large errors, the results show the opposite. Of the 208 recaptured animals, only 11 individuals were observed with a darker chin-spot on the second capture. Presumably these transformations in colour were based on observer error. To simplify the assessment of chin-spot colour, we advise using only the coloration classes '1', '3' and '5'.

During the production of the manual for the assessment of reproductive status, age and health of bats (Haarsma 2008) experienced bat workers were asked to judge the coloration class of chin-spots shown on a total of 35 pictures of several species of bats. All their judgements were similar, although sometimes there were variations between judgements which did not exceed more than one class. These results confirm that the assessment of chin-spots can be performed accurately by a wide group of users. We advise that bat researchers adopting this technique acquaint themselves with the classification of chin-spot colour by practicing with pictures of chin-spots of several species. Pictures should be displayed with a beamer on a large screen, as a computer screen has too much reflection. We believe that the chin-spot is also applicable as an age indicator for other *Myotis* species. During other studies, in the

Netherlands as well as in France, Germany, Poland and Romania, the first author has seen *Myotis myotis*, *M. nattereri* and *M. bechsteinii* with both dark and light chin-spots.

Acknowledgements: This study came out of a joint project between the Institute of Biology, Leiden University and the Society for the Study and Conservation of Mammals (Zoogdiervereniging), both working together with volunteers from local mammal groups. The research is part of Anne-Jifke Haarsma's study project at the Animal Ecology Group, Leiden University, which is headed by Jacques van Alphen. We are grateful to all the bat workers and other volunteers who helped on this project, without their help we could not have succeeded in gathering all the data on pond bats in the Netherlands. We also thank Kees van Bochove for taking photos and Ken Kraaijeveld and Peter-Jan Keizer for reading the manuscript.

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Samenvatting

Kinvlek als leeftijd-indicator voor de meervleermuis

Tijdens ecologisch veldonderzoek is het vaak nuttig om de leeftijd van een dier te kunnen bepalen. Bij de watervleermuis (*Myotis daubentonii*) kan de verkleuring van de kinvlek gebruikt worden om de leeftijd van het individu te bepalen. In dit artikel onderzoeken we in hoeverre de verkleuring van de kinvlek ook toepasbaar is voor leeftijdsbepaling bij meervleermuizen (*Myotis dasyneme*). Tijdens zes jaar veldonderzoek, uitgevoerd van 2002 tot 2008, hebben we meer dan 2500 meervleermuizen gevangen. Om de bruikbaarheid van de kinvlek als leeftijd-indicator te bepalen hebben we naast informatie over kinvlekkleur ook informatie over andere leeftijdvariabelen, zoals tandslijtage, vergroeiing van kraakbeenschijven en reproductieve status verzameld. We hebben significante correlaties gevonden tussen de kleur van de kinvlek en andere bekende methoden om leeftijd te bepalen. De resultaten laten een positieve relatie zien tussen de mate van verandering in kleur van de kinvlek en het aantal dagen tussen de eerste en de laatste vangst. De kinvlek van dieren die als juveniel zijn gevangen verbleekte gemiddeld binnen een periode van twee tot vier jaar van kleurklasse ‘5’ (donkerpaars) naar kleurklasse ‘1’ (licht). De kinvlek van juveniele meervleermuizen bevindt zich doorgaans in kleurklasse ‘4’ tot ‘5’, die van de meeste onvolwassen dieren in klasse ‘3’, en die van de meeste sexueel volwassen dieren in klasse ‘1’. We concluderen dat de kleur van de kinvlek een betrouwbaar kenmerk is om de leeftijd van een meervleermuis te bepalen

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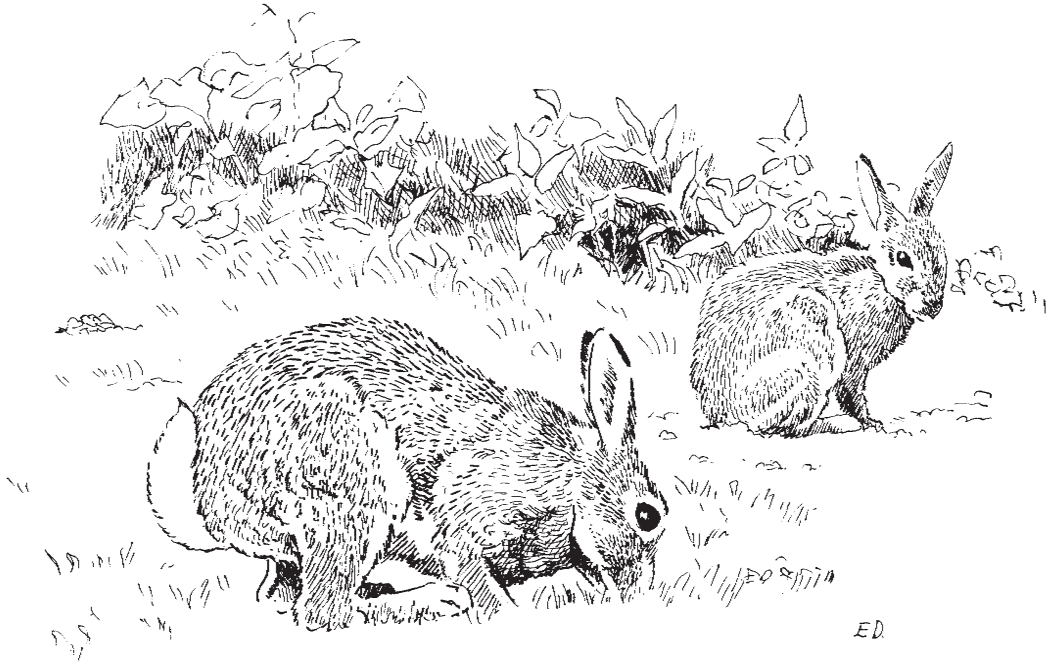

The translocation of rabbits in a sand dune habitat: survival, dispersal and predation in relation to food quality and the use of burrows

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Abstract: A decrease in a local rabbit (*Oryctolagus cuniculus*) population can be offset by translocation and restocking the area with rabbits from other areas. However, such translocation programmes tend to suffer from a low survival rate - possibly due to stress and lack of cover. As part of a project, that sought to evaluate the potential of translocating rabbits in Dutch coastal dune areas, we were able to compare the movements of resident rabbits with those of translocated rabbits. This was the first such experiment in the Netherlands. Mortality during the translocation process was minimised by reducing stress during the trapping, handling and transportation. However, following the rabbits' release there was a high mortality from fox predation in the first week. We tested for other factors that could influence the outcome of the experiment such as the quality of food in the new habitat and immunity to RHD. Most of the translocated rabbits left the artificial burrows for unused natural burrows during the first night. They continued to use several burrows throughout the study. We conclude that this should not be interpreted as a lack of settling, but as a behaviour which is adapted to sandy dunes: rabbits will naturally use more than one burrow where sufficient burrows are available.

Keywords: *Oryctolagus cuniculus*, rabbit, restocking, settling, food quality, burrows, coastal sand dunes.

Introduction

Rabbits (*Oryctolagus cuniculus*) play an important role as small herbivores in European coastal dune ecosystems. They can be considered as a key species or an 'ecosystem engineer' because their activities affect the diversity of flora and fauna in dunes (Bakker 2003, Delibes-Mateos et al. 2008). Through grazing and digging, they also facilitate their own pecies: when they are present in a high density they keep the vegetation in open, early successional stages which provides them with food of a high quality (Bakker et al. 2005, Dekker 2007).

After their introduction in the 13th century, rabbits became very common in the Dutch coastal dune areas. Their predators were severely hunted and people supported the populations by providing them with extra food in the winter and constructing artificial burrows (Swaen 1948). This all changed after 1953 when infectious diseases, originating from abroad, formed a serious threat. Myxomatosis was deliberately introduced into France to control the large rabbit population and from there the disease spread rapidly throughout the rest of Europe, causing a huge decline of the wild rabbit population in the Netherlands. Most wild rabbits in Europe have now obtained some immunity to myxomatosis, but the disease still pushes down rabbit numbers (Trout et al. 1992). Since 1990 a new disease, Rabbit Haemorrhagic Disease (RHD) is reducing rabbit numbers. In the Netherlands, RHD caused a decrease in rabbit numbers of up to 90% between 1990 and 2003 (Drees & van Manen 2005, Van de Bildt et al. 2006). While the origins of RHD are still debated (Forrester et al. 2006), it is known to be an introduced virus which had an epizootic effect on Dutch wild rabbits.

The present situation

Since 2003, rabbit numbers have been rising again on a national scale (see: www.cbs.nl), but in some areas there has been no recovery. We think that a recovery is prevented by a combination of persisting RHD, a decline in the suitability of habitats, and predation by red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) and that the combined effect of these three factors explains why the population at some locations is not recovering.

The effect of these factors differs between high and low densities of rabbits; RHD becomes endemic at high rabbit numbers (Henning et al. 2006). In such cases the rabbits depend upon their acquired resistance to RHD, carried in the immunoglobulins which their bodies produced during previous infections. At low population densities RHD comes and goes and more rabbits in the population lack resistance.

The same applies to habitat suitability. At high numbers rabbits can maintain a habitat that is highly suitable for them. At low numbers there is a decrease in vegetation quality and shelter. Vegetation growth leads to the vegetation becoming less digestible and having a lower protein content (Dekker 2007). The collapse of no longer used burrows makes the habitat less safe as it reduces shelter possibilities. Contrary to popular belief, rabbits do not readily dig new burrow systems. Only pregnant females expand their burrows or make new ones (Lockley 1974, Cowan 1991).

The effect of predation also differs with prey density. When rabbit numbers are high, the population size is limited by food availability in winter and peak numbers are suppressed by predation (Wallage-Drees & Croin Michielsen 1989). However, once rabbit numbers fall below a certain level predation can strongly limit the population size (Newsome et al. 1989, Trout & Tittensor 1989). The red fox is most important rabbit predator in Dutch coastal areas. Red foxes reappeared in Dutch coastal areas in 1968 and the major part of their diet consists of rabbits (Mulder 2005).

Translocation and restocking

Translocation, in which wild animals are trapped at one location and released at another, is one possible management tool to facilitate the recovery of rabbit populations. Translocation is widely used in wildlife management and conservation biology to induce population recovery (Griffith et al. 1989, Letty et al. 2008). In Spain, the translocation and restocking of rabbits is done mainly to provide prey species for threatened predators: the Iberian lynx *(Lynx pardinus)*, the Spanish imperial eagle (*Aquila adalberti)* and Bonelli's eagle (*Hieraaetus fasciatus*). In France, it is done to create hunting opportunities (Letty et al. 2002, Moreno et al. 2004, Letty et al. 2008). In the present study we describe the first experimental translocation of rabbits in the Netherlands.

When translocating rabbits one needs to pay special attention to several points: the stress during and after the translocation and the dangers to animals that are released in an unknown environment.

Being trapped, handled, and transported is a stressful event for rabbits (Calvete et al. 2005). Letty et al. (2003) measured the effects of catching and handling on the survival of rabbits. He did this by handling and transporting rabbits before releasing them back to their own regions of origin. This did not result in extra mortality. So, if these aspects of translocation and / or restocking are done carefully, mortality from such causes can be avoided.

After translocation it is important to maximise survival and minimise dispersal at the new site. This involves minimising social stress. Letty et al. (2008) mention social behaviour as a key influence on restocking success. Von Holst et al. (1999) found a relation between social rank, stress and survival. Social stress is caused by conflicts with the local rabbits and between translocated rabbits of the same sex. A rabbit population is typically composed of several neighbouring social groups in which both sexes are involved in separate social hierarchies. The females compete for burrows, the males for the females (Cowan 1991). When there are local rabbits present, the new rabbits have to compete with them for burrows and females. Moreno et al. (2004) found a better survival rate among rabbits that were released in low population density areas. We choose to conduct the experiment in wintertime, when rabbits settle more quickly (3.7 days) (Moreno et al. 2004), probably because their levels of aggression and territoriality are lower (Von Holst 1998).

Moreno et al. (2004) practiced what is known as the 'hard release': just releasing the rabbits and leaving them to find a site to settle into. The maximum dispersion distance was 1000 m, in unfavourable (dry) areas. Letty et al. (2000, 2008) tested 'soft release' with artificial burrows and acclimatization pens of 100 m^2 to condition the rabbits to their new environment. The acclimatization pens improved the survival of the females. The survival of the males was not improved, probably because the fencing left the males no chance of escaping from other male rabbits. The fences were one m high, so did not exclude red foxes. In another experiment Letty et al. (2008) measured the distances that the rabbits moved from the artificial release burrow systems. Some rabbits dispersed long distances in the first days, but most settled within 300 metres of the artificial burrows. These researchers made artificial warrens consisting of a huge pile of stumps, soil and boughs, which are commonly used in France.

Most studies report a high mortality by predation in the first days after release. Fences are only partly successful in keeping red foxes out. Providing sufficient cover is important for decreasing mortality by predation after translocation (Calvete & Estrada 2004).

This study

The purpose of this study was to evaluate the potential of rabbit translocation as a management technique for Dutch nature managers. We had the opportunity to experimentally translocate a population of rabbits into a Dutch coastal dune area, where the populations had been depleted by RHD. This was the first time such an experiment had been conducted in the Netherlands, so we drew on the knowledge and experience of such operations collected by overseas colleagues. This led us to design a study in which we created artificial burrows, and used radio tracking, marking and direct observations to study the individual survival of introduced rabbits and their use of burrows.

Methods

Research opportunity

In the winter of 2005-2006 an opportunity arose to carry out this experimental relocation project. For nautical reasons, a small sandy island in the 'Noordzeekanaal' near the docks of IJmuiden, called 'Middensluiseiland', had to be removed. This 5.6 ha island was home to a rabbit population of about 100 individuals. The authority in charge of the island - 'Rijkswaterstaat' (part of the Ministry of Transport and Water Management) - wanted to humanely remove the rabbits, before removing the island. Natuurmonumenten, the management authority of a nearby coastal dune reserve 'Zwanenwater', was interested in releasing the rabbits there, because the density of rabbits in this area was very low and this was having detrimental effects on biodiversity (E. Menkveld, personal communication).

Study areas

Source area: Middensluiseiland, IJmuiden
Middensluiseiland was formerly a dune area in the municipality of IJmuiden, which became isolated when the Noordzeekanaal was enlarged. The vegetation was eutrophous, due to a large breeding colony of gulls (*Larus fuscus* and *Larus argentatus*). In 2004, the rabbit population on the island became infected with RHD (Cottaar 2005), but the population recovered and in October 2005 the present authors assessed the population size to be approximately 100 individuals. Rabbit burrows were widespread over the whole area. Natural predators of rabbits, such as goshawk (*Accipiter gentilis*), buzzard (*Buteo buteo*) and red fox were also present (Cottaar 2005, Cottaar 2006).

The vegetation contained mainly dicotyledons and very few grasses. The main plant species were *Cerastium arvense, Rubus caesius, Medicago arabica, Myosotis ramosissima, Plantago lanceolata, Festuca rubra, Cirsium vulgare, Anthriscus caucalis, Glechoma hederacea, Jacobaea vulgaris, Anchusa officinalis* and bushes of *Sambucus nigra* and *Hippophaë rhamnoides* (Keizer 2000).

Target area: Zwanenwater, Callantsoog
Zwanenwater is a protected coastal dune area near the village of Callantsoog. It is a nature reserve of 604 hectares, owned by the conservation organization Natuurmonumenten since 1973. Despite fluctuations in rabbit densities over the years, the general trend since the 1980s has been a steady decrease.

The release site was selected: a three hectare dune valley in the outer dunes. We estimated the number of rabbits in the dune valley in December 2005 to be no more than three. We counted 54 rabbit burrows on the slopes, most of which seemed old and unused.

The vegetation consisted mainly of dense and tall grass (*Ammophila arenaria* with *Calamagrostis epigejos)* and some bushes of *Sambucus nigra*, *Salix repens* and *Rubus caesius,* and some rabbit-grazed, very short, vegetation patches on the lower slopes. Tall vegetation provides relatively low quality forage for rabbits. To counter this, the valley was mown on the 8th of November, 2005. Seedlings of *Urtica dioica* and *Cirsium arvense* appeared within the mown area in February. The short vegetation on the rabbit grazed patches consisted mainly of *Carex arenaria, Luzula campestris, Trifolium micranthum, Viola curtisii, Cirsium vulgare* and *Jacobaea vulgaris*.

We didn't expect the rabbits to start digging their own burrows until the beginning of the breeding season. To provide shelter in the interim period, 16 artificial burrows were provided in the bottom of the valley. These consisted of plastic pipes with a diameter of 16 cm stuck into a pile of hay. Every artificial burrow had two or four pipe entrances.

In Zwanenwater red fox numbers are controlled by night shooting to protect the breeding colony of spoonbills (*Platalea leucorodia).*

Food quality

To assess the food quality at the two sites we determined the crude protein of the vegetation. We followed Rödel (2005) and discriminated between grass stems and leaves (aerial vegetation) and ground-level sprouts and roots (ground shoots). This distinction is important as Rödel (2005) showed that, over the course of the winter, rabbits increasingly switch to ground-level plant parts as their source of food, in order to satisfy their needs for nitrogen. Animals feeding on sprouts and roots are assumed to co-ingest comparatively higher amounts of sand. Rödel (2005) used the sand content of fresh faeces as an indicator of the content of sand within the diet and as a proxy on reliance on ground-level sprouts and roots.

Vegetation samples were taken at both sites on 11 January and 28 February 2006. On 4 April 2006 additional samples were taken at the Zwanenwater site. Twelve sites were randomly chosen in IJmuiden. In Zwanenwater four samples were taken in each of three vegetation types: Tall Grass (TG), Mown Grass (MG) and Short Patches (SP). At all these sample sites a 20 x 20 cm^2 plot of aerial vegetation was clipped and ground-level sprouts and roots were collected by taking a 2 cm thick piece of turf (also 20 x 20 cm^2). The sprouts and roots were separated from the soil by washing with water. In both aerial and turf samples the dead plant parts and mosses were discarded. The food quality was assessed by measuring the nitrogen content of the vegetation samples using the Kjeldahl-method (Deys 1961).

To estimate the amount of foraging on ground-level sprouts and roots by the rabbits, the sand percentage of ten fresh pellets from each vegetation type was determined, following Rödel (2005). The pellets were collected on the same days the vegetation was sampled. The dried faecal samples were weighed and then burned at 85 °C. The only solid remains after this procedure were small balls of silicon oxide, which were weighed.

Translocation management

Catching and handling

The rabbits on Middensluiseiland were caught in wooden life traps or in nets after chasing them out of the burrows with muzzled ferrets. The wooden life traps were made following the design of the Department of Animal Physiology, Bayreuth University, Germany. Using heart-telemetry, this group found these traps to be more rabbit-friendly as trapped rabbits are not able to see people approaching when they are inside the trap (H. Rödel, personal communication). The traps were prebaited for about two weeks before every trapping period with Lucerne hay. The caught rabbits were transported in dark bags to reduce stress. All the rabbits were weighed, sexed and marked. Marking was done by placing reflective numbered metal ear tags and by colouring the rabbits' tails with sheep marking wax.

Twelve radio-collars were used, starting on 13 February, to track the fate of individuals. With this method we could locate both live and dead rabbits underground. When a radio-collared rabbit was found dead, the collars were cleaned and re-used. The rabbits were released in the translocation area at a maximum of three hours after capture.

The radio-collars weighed 32 grams, ca 2% of the mean body weight. We could not detect that radio-collars, which were far below the commonly accepted maximum weight of 5% of body weight, had any effect on the rabbits. Letty et al. (2008) previously used radio-tags with a weight of 30 grams and found no adverse effects on behaviour. Radio collared rabbits were tracked daily to determine burrow use and to check if they were still alive. The survival rate is expressed as the percentage of initially released radio-collared rabbits not found dead. In March the traps were moved to the target valley at Zwanenwater where we caught two autochthonous rabbits, which were both fitted with a radio-collar.

RHD status

A blood sample was taken from 17 rabbits caught in the source area, to measure for immunity against the RHD-Virus. The serum samples were analyzed by M.Van de Bildt of the Dutch Wildlife Health Centre (DWHC), based at the Department of Virology, Erasmus Medical Centre in Rotterdam. A RHDV antibody ELISA kit (Kalon Biological Ltd, Guildford, Great Britain) was used to measure optical density, which represents the amount of RHDV antibody present in a sample. Antibodies were considered to be present at an optical density of 0.7499 or more.

Release method
The rabbits were released into the artificial burrows. Rabbits that seemed to be socially related (i.e. those that were trapped close to one another) were released into the same burrow. After placing the rabbits in the artificial burrows, the entrances of the burrows were stopped with a tuft of grass in order to avoid panicked escape-runs by the released rabbits, at least for a while.

For predator control we relied on the night shooting programme.

Monitoring after translocation

Leaving or entering the burrow
Infrared movement detectors (TrailMaster 1500, Goodson & Associates Inc., USA) were placed near to every entrance to the artificial burrows These movement detectors consist of a beamer and a receiver. An infrared beam is constantly sent from the beamer to the receiver. Every time the infrared beam is interrupted the date and time of that interruption are logged by the receiver. Care was taken to remove tall grass, so only rabbit movements were registered. These data were used to determine the use of the artificial burrows and to check the times at which the rabbits left these burrows after release.

Habitat use
The amount of faecal pellets in a plot is a good indicator of the foraging time spent at that plot (Bakker et al. 2005). Rabbits' preference for foraging in different vegetation types was estimated by counting and removing all pellets in 30 circular plots of four m^2, ten in each of three vegetation types (tall grass, mown grass and short patches) once every 14 days between 5 January and 26 April 2006. There were no latrines in the plots.

Survival and burrow use
Survival of the translocated rabbits was monitored by observations and by tracking radio-collared animals. The release valley and its surroundings were checked daily for signs of dead rabbits such as carcasses, body parts, ear tags or tufts of hair. In cases of death the cause was determined by examining the carcass.

The project was approved by the Committee on Animal Experimentation, RUG, number 4472A, as required by the Dutch Act for Animal Experiments.

Results

Translocation

Fifty-eight rabbits were caught in the source area, 40 with traps and 18 by ferreting. When the rabbits were weighed it was found that the body weight of the females was normally distributed and that there were seven exceptionally heavy males (figure 1). The weights were within the range of values found in another study of a Dutch coastal dune area (Wallage-Drees 1989). Most rabbits were caught individually in a trap, but in four cases two rabbits were caught together in one trap. In one of these cases, where two male rabbits had

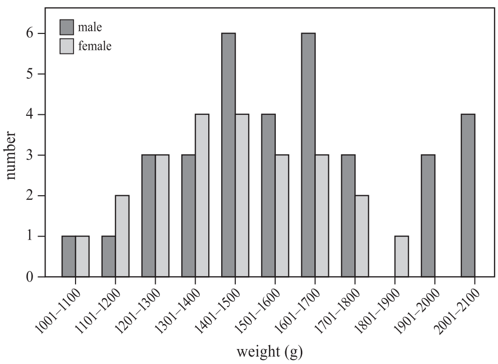

Figure 1. The distribution of bodyweight of translocated rabbits divided into classes per gender.

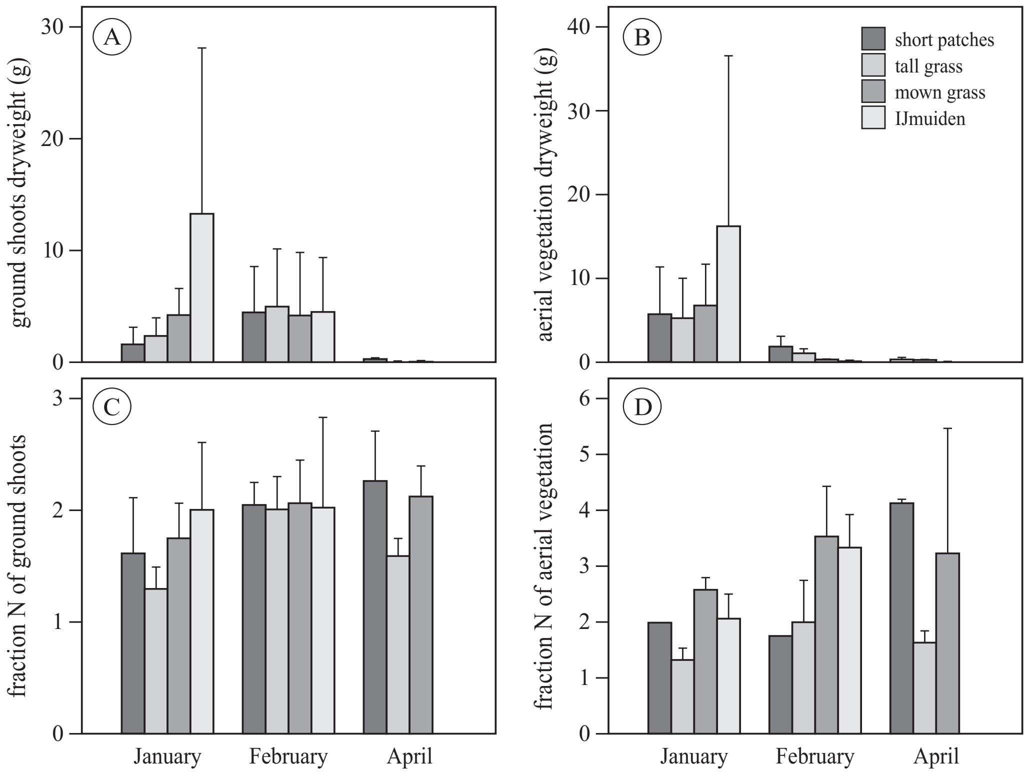

Figure 2. Food quality parameters for winter and spring 2006: biomass of ground-level sprouts and roots per month (A), biomass of the aerial vegetation per month (B), nitrogen content in ground-lying shoots and roots (C) and nitrogen content in aerial vegetation (D). The food quality is given for three vegetation structures at the translocation site: short patches, tall grass and mown grass and for the original site.

entered one trap, one was found dead when the trap was inspected.

The mean ambient temperature during the project was (averaged daily mean for the Netherlands): December: 4.0 °C; January: 1.5 °C; February: 2.9 °C; March: 3.9 °C; and April: 9.0 °C. The winter of 2005-2006 was considered as an average winter, although March was colder than average.

RHD-status

We found that 41% (*n*=17) of the rabbits on IJmuiden had antibodies for RHDV, which is in line with the observation that there had been a reduction of the population in 2004 (Cottaar 2005).

Habitat use and food quality

Using faecal pellet density as a proxy for foraging time in the translocation area, we found that the rabbits spent 74% of their foraging time on the short patches, 16% on the mown grass and 10% on the tall grass. This preference remained stable over the winter and early spring.

Quantity and quality of the vegetation

The quantity of food on offer decreased during the winter, especially in IJmuiden, the site where the rabbits came from. The quantity was lowest at the start of spring, in April: 7.5 $kg.ha^{-1}$. In winter (February) the ground shoots offered more food than the aerial vegetation ($F_{1,46}$=18.58, P<0.01) (figures 2A and 2B).

The quality of the food in the target area, as estimated by nitrogen content, did not decrease during the winter ($F_{1,22}$=3.75, P=0.06) (figures 2C and 2D). On the short patches, the nitrogen content was higher at the beginning of April than it was in the winter ($F_{1,12}$ =5.9133; P=0.04). (figure 2C and D).

Sand level of the pellets

In the Zwanenwater there was an increase in percentage of sand in the pellets from January to April in all vegetation types. The sand percentage was much higher than in the samples from IJmuiden than those from Zwanenwater (figure 3).

Survival

On the day of translocation, 19 rabbits were radio collared. Two rabbits that were translocated without a collar were later fitted with one, after they were recaptured in the dune slack where they were introduced. Two autochthonous rabbits were also caught and fitted with a collar. This yielded a total of 21 translocated rabbits and two resident rabbits that could be tracked.

Unfortunately, 13 of the 21 radio collared, translocated, rabbits died within one week and another four in the following month (see figure 4). The other four radio collared rabbits survived for 70, 143, 190 and 239 days, respectively. All the 17 collared rabbits found dead within the first month were killed by red fox. Remnants of nine of these were found on the surface, and the other eight were buried underground (i.e. cached). Five of these corpses were intact, in the other cases only the head was buried. Corpses found above the ground were mostly almost complete eaten with only the radio collar and / or ear tags remaining. Of the 36 uncollared animals that were found dead, we once identified buzzard as the predator and twice a goshawk.

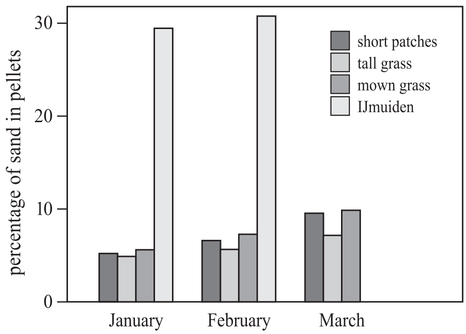

Figure 3. Percentage of sand in faecal pellets collected in different vegetation types between January and March.

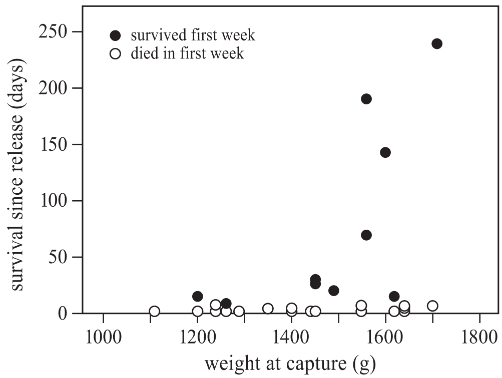

Figure 4. Correlation between bodyweight at capture and survival time of translocated rabbits.

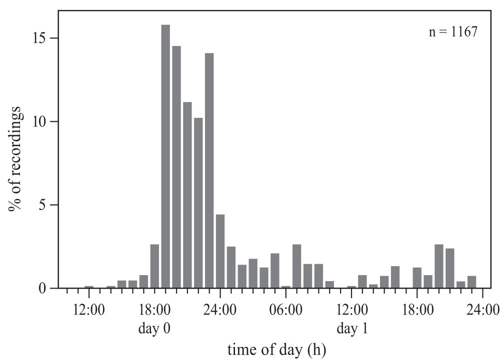

Figure 5. Activity of the translocated rabbits: recorded as the number times the rabbits left and (re)entered the artificial burrow entrances after translocation. Every time a rabbit passed the entrance of an artificial burrow was counted. The data is presented as the number of records per hour expressed as a percentage of the total number of records (n=1167).

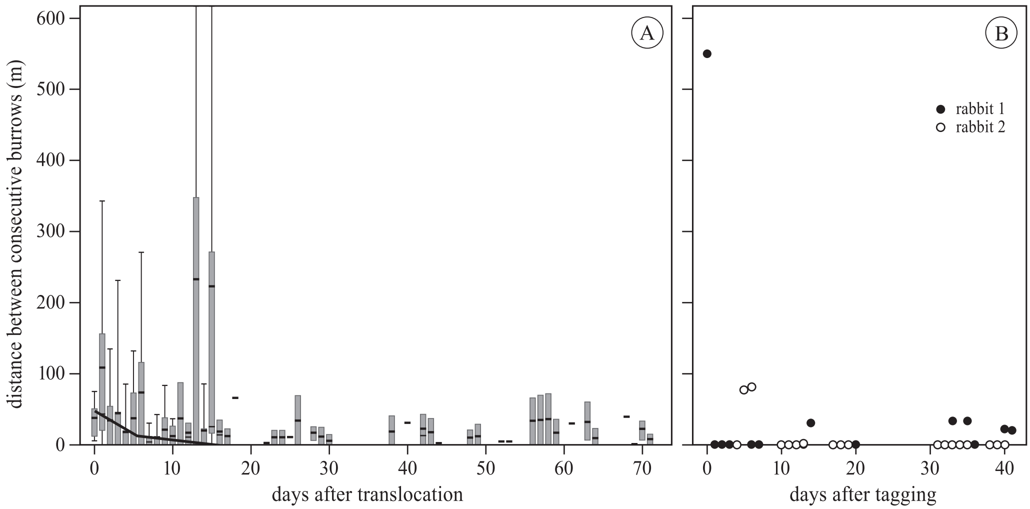

Figure 6. The distance moved by collared translocated rabbits between burrows on consecutive days, beginning on the day of release (A). The line represents the relation between the distance between burrows and day after release, fitted using generalised linear modelling. The movement of two resident radio collared rabbits is recorded from the day they were caught and radio-fitted (B).

There was no difference in survival rate of males and females after one week of translocation ($\chi^2_{n=21,\ df=1}$=0.29, *P*=0.864) or after one month ($\chi^2_{n=21,\ df=1}$=0.011, *P*=0.916).

Analysis of covariance showed that effect of weight (at capture) significantly influenced the survival period (mortality in the first week versus longer survival; $F_{1,23\ (interaction)}$=12.10, *P*=0,002). Animals with a larger body mass that made it through the first week, survived longer. By contrast, in the week following translocation, the survival time was independent of the body mass of the animals (see figure 4).

Use of the artificial burrows and dispersal

The rabbits were released at Zwanenwater in the daytime. Movement detector data showed that the first activity after release took place around 6 pm, i.e. around sunset. Activity (leaving and entering the burrows) during the first night after release was concentrated between 6 pm and 11 pm. After 11 pm activities around the burrows stayed at a low level and no other peaks in activity were recorded (figure 5). So most rabbits left the artificial burrows on the first night and did not return.

We have additional information about the radio-collared rabbits. Eighteen of the 19 radio-collared rabbits were released inside an artificial burrow. One escaped before we could place it in the burrow. One rabbit went to a different artificial burrow where it stayed for four days, until it was predated by a red fox. The other 17 rabbits all vacated their artificial burrow on the first or second night and moved to old rabbit burrows on the slopes of the valley, within 150 metres of the release point. The one rabbit that escaped at release adopted a natural burrow at approximately 400 metres from the release point.

After moving to a natural burrow, the translocated rabbits kept changing burrows. We wanted to compare the time before translocated rabbits could be considered ‘settled’ and so we plotted their daily dispersal distances (figure 6). Contrary to our expectations the translocated animals did not settle, although the dispersal distances seem to decrease after day 18 (figure 6A). All males and females used several burrows.

To better understand this behaviour we also monitored the two resident rabbits that were caught in the valley. They also used several burrows, although there was a significant difference between resident and translocated animals in the distance moved between burrows on consecutive days (W=450, P=0.002).

There were large individual differences in distance moved, but no systematic difference in relocation behaviour between those animals that were predated within one week and those animals that survived longer (W=3084, P=0.09). The longest distance between burrows used in subsequent nights was 1025 meters. This rabbit (a male) did not return to the release valley.

Discussion and conclusions

Food quality in source and target area

Most rabbits caught on Middensluiseiland had a weight that fell within the 'normal' range, although a few heavier males were outside this range. Males continue to put on weight every year, while females lose weight during each breeding season (Twigg et al. 2000).

The present study shows that the quantity of available vegetation became very low at the end of the winter. This coincides with an increase in the uptake of ground-level shoots and roots, as revealed by the increase in the percentage of sand in the rabbits' faeces (cf. Rödel 2005). The quantity of available biomass in February was lowest in the more open and ruderal vegetation in IJmuiden, where dicotyledons dominate. Here there were few grasses, but much *Jacobaea vulgaris* and *Anchusa officinalis.* These plants have thick roots that contain nutrients (van der Meijden et al. 2000) and may form a valuable element in the diet when above ground food becomes scarce. We often saw these roots in the 'rabbit scrapes' that probably were made to get at the root crowns of the rosettes of *Jacobaea vulgaris*.

A decrease in food quantity or quality can be a problem, leading to longer foraging times (Dekker 2007) or weight loss. In this case the quantity and quality of the standing crop of the target area Zwanenwater was sufficient (7.5 $kg.ha^{-1}$ in March), because the cover of grasses stays high in March (Wallage-Drees 1983).

The measurements of food quality were undertaken to evaluate the suitability of the habitat of the target area. We concluded that the target area had a sufficient quantity and quality of food which was better than that available in the source area.

Survival

Fox control in the area was not as efficient as we expected. Consequently the survival rate of the translocated rabbits was low; only 19% of the rabbits were still alive one month after translocation. In nearly all cases, death was caused by predation by the red fox. Red foxes display "surplus killing": if they can catch more prey than needed at that moment, they cache it. The high number of buried rabbits in this experiment was an indication that the translocated rabbits were caught by red foxes. High mortality by predation has also been found by other authors where no night-shooting was applied or fences were not erected (Calvete et al. 1997, Calvete & Estrada 2004). Fencing reduces the loss due to fox predation, but does not prevent it completely (Calvete & Estrada 2004).

In this study the mortality was highest during the first two days. Other studies also show mortality to be highest in the first two to nine days after release (Calvete et al. 1997, Letty et al. 2002, Calvete & Estrada 2004, Moreno et al. 2004). Our approach showed a slightly lower mortality rate compared to traditional releases (Calvete et al. 1997: > 97% for the first ten days; in Letty et al. 2008: 50% in the first two days), but a higher one compared to cases where the artificial burrows were fenced, when predators in the release area were controlled (Calvete & Estrada 2004) or when pens or tranquilizing during transport was used (Letty et al. 2000).

In accordance with Letty et al. (2002), we found a positive relation between bodyweight and survival time after the first week. Heavier rabbits may have a better survival rate because they are older and could be more experienced in avoiding predators. Alternatively, it might be because they have a higher social rank which makes it easier for them to conquer the best (i.e. safest) burrows.

Mobility: dispersal and daily movements

All the rabbits (except one) were released inside an artificial burrow. Movement detectors showed that rabbit activity was concentrated between 6 and 11 pm, with a peak at around 6 pm. In general, the peak period of activity for rabbits is between 3 and 6 am (Nuboer et al. 1983, Wallage-Drees 1989). This peak did not show in our results as most of the rabbits had moved to other burrows, mostly unused natural ones on the slopes of the valley.

Finding a natural burrow

According to Cowan (1991) burrows are an essential resource for rabbits. Since rabbits do not dig burrows in winter (Lockley 1974) it was essential to have burrows present in the area of release. The translocated rabbits that moved out of the artificial burrows all stayed within 150 meters from the place of release on the first night. It seems that the use of artificial burrows in combination with the presence of old, unused, rabbit holes, helped to limit dispersion at release. Translocation experiments in other areas with low burrow availability resulted in a much larger dispersion distances (Calvete et al. 1997: 435 ± 440 meters; Calvete & Estrada 2004: 441 ± 161 meters; Moreno et al. 2004: 220 ± 120 meters).

Daily movements

Moreno et al. (2004) and Letty et al. (2002) consider ‘settling’ as an important measure of the success of restocking (or translocating). Moreno et al. (2004) found that, on average, rabbits need 8.3 days to settle, regardless of sex or season. Letty et al. (2002) found that rabbits moved less distance each day after their release, and hardly moved at all after day 18. Our results did not reveal the same behaviour.

After leaving the artificial burrows, the translocated rabbits searched for natural burrows which, although they looked old, might not have been fully abandoned (as three resident rabbits were seen in the valley). The present study shows the presence of (natural) burrows in the area of release is beneficial: they provide shelter for the translocated animals and are readily adopted.

The translocated rabbits (males and female) did not stay in one burrow but regularly switched between burrows. The usage of more than one burrow is part of the normal rabbit behaviour in sand dunes where there a large number of burrows are available (Cowan & Garson 1985, Kolb 1991). Comparable behaviour has been described for a natural low density population (Gibb et al. 1978). In our study the resident rabbits moved as often as the translocated rabbits, although they moved shorter distances.

Conclusions for conservation

Food and cover are the main elements that determine the suitability of habitat for rabbits and these are essential for successful translocation programmes. The release of rabbits in artificial burrows can help to keep dispersal distance low, but the optimal situation is a surplus of (natural) burrows for the rabbits to choose from. The presence of empty natural burrows limits dispersal and aids survival.

The present study showed that it is possible to avoid mortality by stress from handling and transport when translocating rabbits. Other measures are required to avoid high mortality due to predation after release in a new area, i.e. selecting areas with natural burrows, a high level of vegetative cover and providing fencing around the burrows. However, we argue that mortality in the first week after release can probably not be totally avoided, and it should be taken into consideration when deciding whether or not to adopt the translocation or reintroduction of rabbits as a conservation tool.

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Samenvatting

Verplaatsen van konijnen in de duinen: overleving, verspreiding en predatie in relatie tot voedselkwaliteit en het gebruik van holen

Het gecontroleerd en legaal uitzetten van konijnen (*Oryctolagus cuniculus*) wordt in Nederland niet toegepast. Toch zou het een nuttig hulpmiddel kunnen zijn voor het herstel

van de konijnenstand in situaties waar herstel uitblijft en de biodiversiteit van een natuurterrein achteruitgaat. In een experiment hebben we ervaring opgedaan met het uitzetten. Door het zenderen van konijnen kon de overleving en het gebruik van burchten worden bepaald. Daarbij konden we het gedrag van de uitgezette dieren vergelijken met een tweetal lokale, gezenderde konijnen. In de eerste week na het uitzetten was er hoge sterfte door predatie door de vos. De voedselkwaliteit was voldoende en de uitgezette dieren hadden enige immuniteit tegen RHD (VHS). De meeste konijnen verlieten de kunstburchten al de eerste nacht en verhuisden naar ongebruikte en gedeeltelijk ingestorte oude holen. De uitgezette konijnen trokken minder ver weg (hadden een kortere dispersieafstand) dan in andere onderzoeken. Ze bleken meerdere burchten te blijven gebruiken. Dat lijkt op 'natuurlijk' gedrag in kustduinen: als er meerdere burchten beschikbaar zijn maken konijnen optimaal gebruik van dat aanbod. Het uitzetten van konijnen kan dus gerealiseerd worden, mits het verlies door predatie voor lief wordt genomen. De beschikbaarheid van meerdere (kunst)burchten, waardoor wordt tegengegaan dat de dieren de uitzetlocatie verlaten en gaan zwerven, kan dan de overleving helpen verhogen.

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Barbed wire hair traps as a tool for remotely collecting hair samples from beavers (*Castor* sp.)

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Abstract: The recolonisation of much of Europe by the Eurasian beaver (*Castor fiber*) entails new management, conservation and research challenges. DNA analysis can function as a powerful method in this respect. We conducted a trial to determine the effectiveness of barbed wire hair traps for remotely plucking hair from free-ranging beavers. At all sites it was possible to rapidly obtain hair samples containing guard hairs with follicles. Barbed wire hair traps can thus be employed as a cost effective way of collecting DNA from beavers without subjecting them to the stress of capture and handling.

Keywords: barbed wire, beaver, *Castor* sp., DNA, genetic monitoring, hair, non-invasive.

Introduction

Eurasian beavers (*Castor fiber*) have staged a remarkable comeback since the late 19th century following reintroductions to and natural recolonisation of most of their former geographical range (Halley & Rosell 2002). This has also led to a desire to better understand the underlying biological processes that influence population growth, e.g. colony composition, dispersal patterns, inbreeding, and to a necessity to address various management or conservation issues, e.g. population monitoring, hybridisation of subspecies, or possible presence of American beaver (*Castor canadensis*).

Individuals, sexes and both beaver species are virtually indistinguishable behaviourally and morphologically in the field (Rosell et al. 2005). Therefore, studies aiming at individual, sex or species identification usually have to resort to capture in order to look at more subtle clues such as anal gland secretion colour (Rosell & Sun 1999) or to collect material for subsequent genetic analyses (i.e. tissue, blood, hair) (Crawford et al. 2008). However, live-trapping is often expensive, time consuming or impractical. It can also cause considerable stress or even harm to the animals (Rosell & Hovde 2001). Ideally, genetic material could be collected without resorting to trapping. Recently glue or barbed wire hair traps have been successfully used to remotely pluck hair from terrestrial mammals (e.g. Frantz et al. 2004). In terms of semi-aquatic mammals remote hair capture has only been applied to the North American river otter (*Lontra canadensis*) (Depue & Ben-David 2007), but never to beavers.

Here we report on the results of a trial conducted to assess the feasibility of barbed wire hair trapping as a simple, cost effective and non-invasive way of remotely collecting hair samples from free-ranging beavers, which could be used for DNA analysis.

Materials and methods

The study was carried out in Luxembourg, which is currently being recolonised by beavers from the neighbouring regions of Belgium, France and Germany. Between 26th February and 4th April, 2008 we set up hair

Photo 1. Barbed wire hair trap (trap ID = *erp1*) suspended between two willow (*Salix* sp.) stems next to a river in Luxembourg. *Photograph: J. Herr.*

traps at all four beaver sites then known in Luxembourg. The sites were situated on the rivers Sûre (site and trap codes: *erp*, *ste*, *was*) and Clerve (site and trap code: *dra*) and had only been colonised recently with beaver activity having first been discovered between February 2006 and October 2007. None of the available information from crepuscular observations, reports or photographs indicated the presence of more than a single beaver per site.

Hair traps consisted of ordinary barbed wire (2-strand wire, four point barbs, 15 cm between barbs). We placed the traps (n = 7) on the shore (1-2 m from the water's edge), in proximity to obvious fresh beaver activity such as cut trees, feeding beds or visible trails. Due to difficulties of giving metal stakes a firm hold in the muddy ground we chose to attach the wire to the stems of woody vegetation instead. The wire was suspended 20-25 cm above ground (photo 1). Beavers were lured to the traps with apples (2-3 per site; cut in half and rubbed against tree stems to enhance the smell), a commercially available beaver scent lure (Ground Castor, Wildlife Control Supplies, East Granby, CT, USA) or a combination of both. The apples were attached to vegetation 40 cm above ground to prevent muskrats (*Ondatra zibethicus*) from taking them. Where, due to dense vegetation, beavers could reach the bait from one side only, the trap consisted of a single strand of barbed wire suspended between two trees. Where the bait could be reached from several sides a barbed wire enclosure was formed around the bait or lure by suspending the wire around three or more woody stems (Woods et al. 1999, Frantz et al. 2004). Consequently the length of the wire (and thus the number of barbs) varied from trap to trap.

Traps were checked and hairs collected at one- or two-day intervals, except during flooding events when trapping was suspended (no baiting, no trap-checking). A 'control day' was

Photo 2. Beaver hair sample containing guard hairs and underfur hairs (trap ID = *was1*, control day: 3 – see table 1). *Photograph: J. Herr.*

defined as any day on which a trap was checked. A 'sample day' was defined as a control day on which at least one sample was collected from a given trap. A 'sample' was defined as all the hairs (underfur and guard hairs) that were collected from a single barb (Scheppers et al. 2007). Thus a single trap could yield several samples on one sample day. Each sample was removed with tweezers and stored separately in a paper envelope. Beaver guard hairs could be easily identified based on colour and morphology, which was characterised by a conspicuous narrowing of the hair diameter in the middle portion of the hair (Keller 1983).

Results

Twenty-seven beaver hair samples (photo 2) were collected on 31 control days, translating into a hair-trapping success of 0.87 samples per control day. When only considering samples with ≥4 guard hairs, trapping success was 0.26 samples per control day. At each one of the four sites we obtained at least one sample with ≥10 guard hairs (table 1). Based on hair morphology, only one hair sample could be assigned to a non-target species (badger, *Meles meles*). The first sample was usually already obtained one or two days after a trap had initially been set or after trapping was resumed following a flooding event (table 1). Trap *was3* was dismantled without having provided a sample because traps *was1* and *was2* had by then already yielded good samples for that site. All samples contained underfur, but only 19 of 27 samples (70.4%) contained at least one guard hair with a visible follicle (table 1).

Discussion

We have shown here for the first time that it is possible to remotely pluck hairs from beavers. This method could provide a harmless and cost-effective alternative to the use of either live-trapping, collection of roadkill or destructive sampling. In North America, destructive sampling may be acceptable or, from a nuisance management perspective, even desirable (e.g. Crawford et al. 2008). However, it is clearly unacceptable for Eurasian beavers which are strictly protected within the European Union. Research on other wildlife has demonstrated that questions on group size, kinship and mating strategies can indeed be addressed by using DNA from remotely plucked hair (e.g. Scheppers et al. 2007).

Few studies have used hair (from dead or live-trapped individuals) as a source of DNA for genetic analyses in beavers (Kühn et al. 2000, Kühn et al. 2002, Ducroz et al. 2005, Durka et al. 2005). Kühn et al. (2000, 2002) used between five and 20 guard hairs per beaver to extract DNA for successful gender and species discrimination. No such information was available from the other studies. We managed to collect, from each site, one or more samples for which the number of guard hairs was situated within the range indicated by Kühn et al. (2000, 2002). In Norway a standard of only four guard hairs per beaver has been used for genotyping purposes (F. Rosell & M. Sabo, personal communication). However, studies on other species have shown that DNA from a single guard hair may be sufficient and in some cases necessary for carrying out complex genetic analyses such as genetic

Table 1. Hair trapping summary data for seven barbed wire hair traps at four active beaver sites in Luxembourg.

Trap ID	Trap control day [a]						Total (*n*)		
	1	2	3	4	5	6	Sample days [b]	Samples	Guard hairs
erp1	1(0) [c]	0 [d]	3(2,2,0)	1(35)	0	0	3	5	39
erp2	-	1(4)	0	0	0	- [f]	1	1	4
dra1	2(3,1)	6(17,5,4,1,0,0)	0	0	-	-	2	8	31
was1	0 ‖ [e]	0	2(45,3)	0	-	-	1	2	48
was2	0 ‖	1(2)	0	-	-	-	1	1	2
was3	0	0	0	-	-	-	0	0	0
ste1	0 ‖	0	0	3(1,0,0)	6(10,2,1,1,0,0)	1(8)	3	10	23
Total:							11	27	147

[a] day on which the hair trap was checked
[b] control days on which a sample was collected
[c] x(y,z): x = # of samples, y and z = # of guard hairs per sample
[d] no sample collected
[e] double vertical line: several days interruption due to flooding of the trap
[f] no control of trap

profiling based on microsatellites (Scheppers et al. 2007).

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Samenvatting

Prikkeldraad-haarvallen als instrument voor de collectie van haarmonsters van bevers (*Castor* sp.)

De rekolonisatie van een groot deel van Europa door de bever (*Castor fiber*) brengt nieuwe uitdagingen met zich op het terrein van beheer, bescherming en onderzoek. DNA-analyse kan hierbij een belangrijke hulp vormen. We hebben een proef uitgevoerd om de effectiviteit vast te stellen van prikkeldraad-haarvallen voor het verzamelen van haar van vrijlevende bevers. Op alle onderzoeklocaties zijn snel haarmonsters van haren met haarfollikels verkregen. Het gebruik van prikkeldraad-haarvallen kan daarom gezien worden als een kostenefficiënte manier voor het verzamelen van DNA van bevers zonder deze te onderwerpen aan stress als gevolg van het vangen van de dieren.

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