

LUTRA

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Contents *Inhoud*

Editorial / Redactioneel

1 Food markets

Contributed Papers / Artikelen

- 3 **Distribution of the badger (*Meles meles* L.) in the Netherlands, changes between 1995 and 2001**
Geert C.M. van Moll
- 35 **Home range of the badger (*Meles meles*) in a heterogeneous landscape in Denmark**
Morten Elmeros, Aksel Bo Madsen & Allan Prang
- 45 **Habitat selection by female otters with small cubs in freshwater habitats in northeast Spain**
Jordi Ruiz-Olmo, Antoni Batet, Juan Jiménez & Diego Martinez
- 57 **Het voorkomen van de gewone baardvleermuis (*Myotis mystacinus*) en Brandts vleermuis (*Myotis brandtii*) in Nederland**
Kees Mostert, Kamiel Spoelstra & Jan Piet Bekker



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Food markets

The discovery of new mammal species still continues. To date about 5000 species from this taxonomic group have been described worldwide, but some scientists predict that, based on the frequency with which new species are found, the number of mammal species will increase to about 8000. Although most discoveries are of small animals, like rodents, bats, monkeys, tenrecs and lemurs, large mammals are still also added to the list. Like the black-faced mangabey (*Lophocebus kipunji*), recently discovered in the highlands of Tanzania, that reaches almost one metre in height and weighs up to 16 kilograms. And what to say about the discovery of a new bovid species – the Vu Quang ox (*Pseudoryx nghetinhensis*) – as well as two muntjac species – the giant muntjac (*Megamuntiacus vuquangensis*) and the Truong Son muntjac (*Megamuntiacus vuquangensis*) – in the forests of Vietnam in the 1990s. And only last year a giant peccary, not yet officially named, was discovered in the Amazonian rainforests of Brazil.

It may be the dream of every zoologist to discover a mammal species that has not been known to science before. While describing new invertebrate species seems relatively easy – just spray a single tree in a tropical rainforest with detergent (only shaking is perhaps a still better option...) and a variety of new species will literally rain down – the discovery of new mammal species is often associated with adventurous expeditions deep into pristine habitats. But this is not necessarily a precondition for success. As shown in

the last decades, many new mammal species have been simply ‘discovered’ during visits to local food markets. Marmosets in Brazil (e.g. *Callithrix humilis*, *Callithrix manicorensis* and *Callithrix acariensis*), the Panay cloudrat (*Crateromys heaneyi*) on the Philippines, and the Laotian rock rat (*Laonastes aenigmamus*) in Laos: they have all been found at local markets where hunters offered their catch. The discovery of the latter must have been an especially thrilling experience, because this was not only a new species but also a so far undiscovered mammalian family. The last report of a new family of mammals had been in 1974, when the Kitt’s hog-nosed bat (*Craseonycteris thonglongyai*) – the only known genus and species of the Craseonycteridae-family – was found along the Khwae Noi River (“River Kwai”) in western Thailand.

Perhaps less spectacular, but nevertheless adding species to the list of mammals, is the discovery of new species through studying already described species in more detail. The development of genetic techniques has made large a contribution to the discovery of new species. Analysis of genetic material of elephants, for example, revealed that, not one but, two species exist on the African continent: *Loxodonta africana*, which roams the savannas, and the forest-dwelling *Loxodonta cyclotis*. The latter had long been seen as a subspecies of the savanna-elephant, but based on DNA-analysis it was concluded that the two species must have split off from each other about

2.5 million years ago. Similar cases exist on other continents, even in Europe: it is only a few decades ago (1970) that the whiskered bat (*Myotis mystacinus*) and Brandt's bat (*Myotis brandtii*) were split. Not surprising, our knowledge of the distribution and ecology of these species is still fragmented (as shown by Mostert et al. in this issue). Furthermore, it was not until 1997 that a distinction was made, based on DNA studies, between the common pipistrelle (*Pipistrellus pipistrellus*) and the Soprano pipistrelle (*Pipistrellus pygmaeus*).

But genetics is not the only helpful tool for distinguishing species. In other cases new species or subspecies have been recognised as a result of ecological research. Research into the migration patterns of fin whales (*Balaenoptera physalis*) off the coast of Italy showed that the animals did not pass the Gibraltar Straits, as had long been assumed. There was no exchange between the Mediterranean population of fin whales and fin whale populations in the Atlantic. DNA-analyses confirmed that there was no genetic kinship between fin whales on either side of the Gibraltar Straits. Eventually, the Italian fin whale was recognised as a different subspecies.

Although not adding new species to science, the rediscovery of species that were believed to be extinct is also highly important, as is the discovery of species at places they have not been found before. In 1988 it was assumed that the rhinoceros species (*Rhinoceros sondaicus annamiticus*) in Vietnam, a subspecies of the Javan rhinoceros, was extirpated. Due to reports of local inhabitants, however, doubts were rising. Remote camera systems were set up, and in 1999 the species was photographed in one of the remote corners of a national park in the south of the country. Currently the estimate is that eight specimens of this species survived.

The search for mammals will continue. Not only because of the urge to complete the list of what species exist, but also to acquire more knowledge about where species occur and how populations develop, as illustrated by the comprehensive study on distribution patterns of badgers in the Netherlands by Van Moll in this issue. But remember: high-tech genetic analyses, long-term ecological research or sophisticated remote camera systems are not necessarily needed to discover a new mammal species... just visit the local food market during your next holiday!

Distribution of the badger (*Meles meles* L.) in the Netherlands, changes between 1995 and 2001

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Abstract: In 2000-2001 a national distribution survey of the badger (*Meles meles*) was undertaken. The survey was to contribute to the interim evaluation of the badger protection plan of the Ministry of Agriculture, Nature Management and Fisheries of the Netherlands. The execution of this protection plan started in 1984. The outcomes of this survey are presented in this article. The following aspects are described: (1) the historic development in the distribution, (2) the occupation rate of suitable badger habitat, (3) the development of settlement types, (4) the merger of subpopulations, (5) the continuity of occupation, (6) the output of translocations, and (7) the number of disappeared setts and the disturbances registered. In addition, a comparison is made with the results from the surveys of 1960, 1970, 1980, 1990 and 1995. The collected data originated mainly from fieldwork. For every 1-km square, the more than incidental use of badger setts was recorded. Earlier research (1995) on the habitat of the badger qualified 15% of the research area (about 25,000 km²) as suitable. In 2001, badgers occupy about 25% of the suitable habitats available to them. The northern and eastern parts of the study area had a relatively low occupation-rate, i.e. 4 to 5 times lower than the rate for the middle and south, where the three largest populations are located. The increase of distribution in the north and east, however, was twice as much as in the middle and the south. In the Netherlands 4,400 badger setts have been recorded since 1960. During the survey more than 2,500 locations (57%) were visited. In the period 1995-2001, the distribution area of the badger increased with almost 30%. The distribution area of the nine splinter populations even increased by 48%. A decrease of 17% was recorded for the 25 dispersed populations. The average distance between the core populations existing from 1980 onwards decreased from 28 to 21 kilometres. For the period 1995-2001, in the regions of Gelderland-Veluwe and Zuid-Limburg the 18% increase in distribution area remained below the national average (29%). The large population in Gelderland-Veluwe even hardly grew (1%). The much smaller population in the Reest valley, at the border of the provinces of Drenthe and of Overijssel, did not grow at all. In the region of Gelderland-Achterhoek, the growth was minimal if the contribution from translocations is excluded. The continuity in occupation increased. Since 1960, of the 1-km squares remained occupied in the following year of survey ($n=2,536$). 1,402 1-km squares were at least occupied once by badgers. Of these, 257 were new in 2001, whereas 253 1-km squares remained vacant after initial occupation. Continuous occupation since 1960 occurred in 115 1-km squares. The remaining 892 1-km squares were occupied more than once, but not continuously. The three main distribution areas, Gelderland-Veluwe, Maasvallei and Zuid-Limburg, showed an increase of occupied 1-km squares of 36%. This is well above the national average of 29%. These large populations cover 84% of the badger distribution in the Netherlands. The increase must be credited almost entirely to the growth of the Meuse valley population. In the period 1990-1995, the increase of 1-km squares occupied by the three largest populations was 4% below the national average, i.e. 12%. In this period, the growth is concentrated in Zuid-Limburg. In the period 1987-2001, the translocation of badgers contributed at least 4% (37 km²) to the total distribution of 2001. In this period, 210 badgers were translocated from enclosed release sites at 26 locations in seven provinces. At least 202 setts disappeared between 1995 and 2001, representing about 8% of the locations visited. One in five was occupied in 1995. The amount of destroyed setts decreased with almost 40% in comparison with the period of 1990-1995.

Keywords: badger, *Meles meles*, distribution, Netherlands, survey, translocations, disturbances, habitat, occupation, Species Protection Plan.

Introduction

In 1984, the Ministry of Agriculture and Fisheries of the Netherlands issued the species protection plan concerning the badger (*Meles meles*) (Ministerie van Landbouw en Visserij 1984). For the first time in the Netherlands, a clear and verifiable perspective was outlined for one of the larger mammal species for a period of 15 years. Within the framework of this plan, several aims for each five-year period were defined. For the period up to 1990, the aim was: "stopping the decline of the number of badgers and the start up of translocation activities". For the period 1990-1995: "increase of the existing population in number and in distribution area as well as the merging of subpopulations". For 1995-2000, the last period: "the growing together of subpopulations into one continuous distribution, reaching an optimal density and effectiveness of a maximal protection". Such medium term planning with a pronounced spatial strategy demanded evaluation. One of the ways of supporting the badger protection plan and its evaluation has been the organisation of a distribution survey every five years. For the first time this was carried out in 1990 (Wiertz 1991). The distribution survey was again repeated in 1995 and 2000-2001 (van Moll 1999, van Moll 2002).

The distribution survey in 2001 served the evaluation of the following goals: 1. The growth in the distribution of the existing population. 2. The merging of subpopulations. 3. The merging into one continuous distribution. Against this background, the purpose of the survey in 2000-2001 was the description of the development of the badger distribution in the Netherlands. This was done on the basis of data, collected mainly in the field, on the occupational status of badger setts. The 2001-survey provided answers to seven questions: 1. What is the development (nation wide and regionally) of the badger distribution based on a comparison of data from the 2001-survey with earlier distribution surveys? 2. What is the (proportional) relation between the badger distribution of 2001 and the available suitable habitat? 3. What is the development of the dif-

ferent settlement types, i.e. core populations, splinter populations and dispersed populations? 4. To what extent are subpopulations merging and to what extent is the distribution developing towards a continuous distribution? 5. What is the degree of continuity in the occupation of 1-km squares and what is the consistence of the distribution of 2001 respecting the duration of this continuity? 6. What is the contribution of translocation activities in the past (from 1987 onwards) to the distribution in 2001? 7. What is the influence of sett disturbances and the disappearing of setts since 1995 on the distribution in 2001?

Methods

Research area

The research area covered the Netherlands and the border region of Germany and Belgium in cases where 1-km squares of Dutch territory exceed over the border. The research area covered 24,945 km². The research area was subdivided in sixteen regions (figure 1). This subdivision was the same as used in the study on the badger distribution in 1995 (van Moll 1999). The provinces of Zeeland and of Zuid-Holland, the low parts between the rivers Nederrijn and Waal, the low parts of Land van Maas en Waal, the province of Noord-Holland west of the Amsterdam-Rijnkanaal and the Wadden islands were not included. In the past, the badger occurred only incidentally and infrequently in these areas. The province of Flevoland was also excluded from the survey, although in the year 2000 a disturbed sett in a sand depot was found here.

Survey of setts

Between January 2000 and March 2001, (potential) sett locations were visited in selected 1-km squares. As soon as a sett location showed evidence of more than incidental use (i.e. habitation) by badgers, the 1-km square was recorded as "occupied". When visiting all known or reported sett

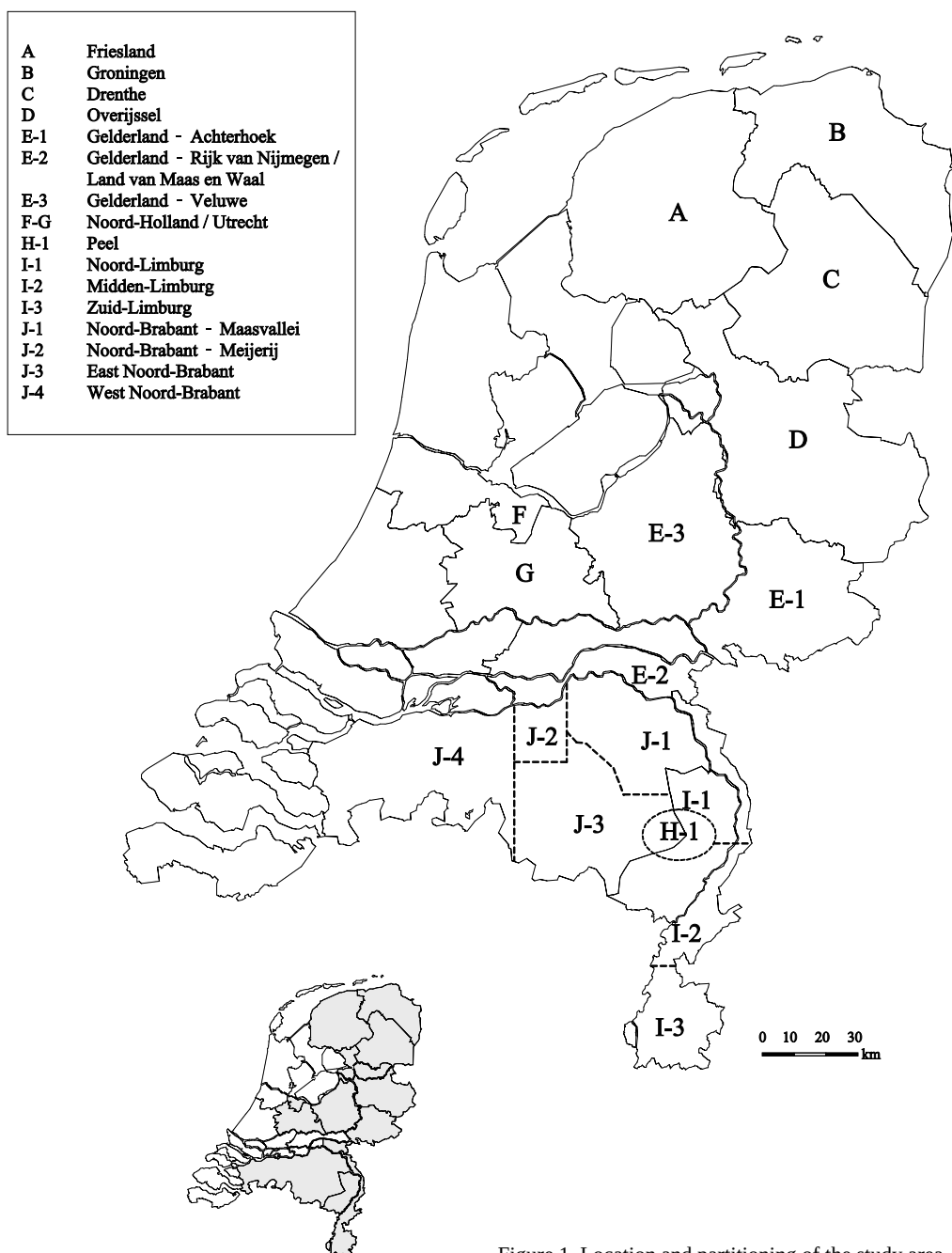


Figure 1. Location and partitioning of the study area.

locations within a 1-km square without any result or when suspected presence of occupied setts in squares with no history of occupation could not be established, the 1-km square was recorded as

“not occupied”. The inventory was based on 1-km squares. In the Netherlands a density of more than one “main sett” is usually not found. A “main sett” being defined as a sett used for

(nearly) continuous occupation and/or reproduction on a regular basis. Exceptions are only found in biotopes with a relative high carrying capacity, e.g. in certain parts of Zuid-Limburg.

Several sources have been used to determine which 1-km squares qualified for research and which sett locations should be visited within these 1-km squares. First of all, these sources were the national surveys of badger setts, the so-called "dassencensi". These were conducted in 1960, 1970, 1980, 1990 and 1995 (van Wijngaarden & van den Peppel 1960, van Wijngaarden & van den Peppel 1964a (see also: van Wijngaarden & van den Peppel 1964b), Wiertz & Vink 1983 (see also: Wiertz & Vink 1986), Wiertz 1990, van Moll 1999). The survey information was supplemented by national and regional sett data from the years 1995-2000 (source: Das & Boom, unpublished data) as well as field observations by third parties. Amongst others, these were sett data from the nature reserve areas of Natuurmonumenten (de Vries 2000), Staatsbosbeheer (H. Vink, unpublished data) and the royal estate "Het Loo" (J.H. Kuper, unpublished data). Finally, national mortality data, originating from the 'Rijksinstituut voor Natuurbeheer' (RIN) (for the year 1990) and Das & Boom (for the period 1991-2000), was used also. The (unpublished) mortality data was used in particular to determine 1-km squares to be researched in which no sett locations were known.

The status that could be assigned to a sett location itself on the basis of a field visit was: *Inhabited*: the sett location shows more than incidental use by badgers (regular habitation and/or reproduction). *Uninhabited*: the sett location shows no or at the most incidental use of a location by badgers. *Not found*: the sett location is not found.

During the survey, all characteristics in the field indicating a more than incidental use of the setts by badgers were considered, such as: digging, bedding or nest material, tracks, playing grounds, latrines, footprints, scratch marks and hairs. The presence, freshness and nature of these signs, the size and condition of the sett as well as information from third parties have formed the basis for the conclusion on the status

of a sett. The status that was granted to a sett in 2000-2001 can be considered as a summary of the visits to the sett location concerned. Setts situated in arable lands, which are to be ploughed later in the year, and small(er) setts or single holes used as temporary hide out, such as "emergency setts", were excluded from the survey. These types of sett involve only temporary or incidental use. Four field researchers have carried out the inventory. This guaranteed the consistency of sett interpretations.

Occupation of suitable habitats

Per region, the number of occupied 1-km squares was compared with the amount of suitable habitats. The data concerning suitable habitats originated from a study by Das & Boom (Dirkmaat 1996). It was partly published in the distribution research of 1995 (van Moll 1999). In this study, based on (historical) topographic material, the habitat suitable for the badger was determined per 1-km square. This was done for the years 1900 and 1995. No distinction was made between degrees of suitability. The suitability of habitats was determined based on ten criteria: 1. Cover and vegetation (land use that produces cover). 2. Adjacent food area. 3. Groundwater level. 4. Presence of sufficient surface to provide for a viable population. 5. Possibility of contact with other (actual or potential) viable populations. 6. Traffic intensity (type of road). 7. Origin and presence of relief. 8. Historical distribution data. 9. Distance to built-up areas. 10. Carrying capacity of the habitats (including land use and soil type).

The number of occupied 1-km squares was compared with the amount of available suitable habitats. The comparison carried out was numeric in character. No spatial comparison of distinct 1-km squares was undertaken. Also, for each region, the occupation of suitable habitats in 2001 was compared with the figures from 1995.

Development of settlement types

A general distinction was made between core populations, splinter populations and dispersed

populations as settlement types. This was done in respect to the aims of the badger protection plan, i.e. the development of subpopulations and the realisation of one continuous distribution. The classification in settlement types stands apart from the geographical subdivision in regions. It was meant to reflect the developments of populations through time. The classification was based on expert opinion regarding the development of subpopulations in the Netherlands in the past 40 years. In addition, the unpublished mortality data over the period 1990-2000 contributed to this.

A core population contains a minimum of nine 1-km squares separated by no more than five kilometres. Core populations are considered to be viable and produce an outflow of badgers annually. The success of this outflow will be influenced greatly by the mortality during migration (e.g. traffic mortality) and the safety of the receiving habitats. Three of the core populations stood out from the others because of their size (>100 occupied 1-km squares). These large populations are located in the Veluwe-region, the Meuse river valley ('Maasvallei'), and in the region of Zuid-Limburg. The population of the Maasvallei comprises the region of Noord-Limburg, Noord-Brabant-Maasvallei and Gelderland-Rijk van Nijmegen.

A splinter population occupies three to eight 1-km squares separated by no more than five kilometres. The survival of a splinter population is uncertain and these populations usually have a (strongly) changing distribution. Splinter populations produce (almost) no outflow of badgers.

A dispersed population occupies one or two 1-km squares at no more than five kilometres apart. Dispersed populations are mostly new settlements outside existing distribution areas or isolated settlements repeatedly occupied. They can arise also as a relict of once larger subpopulations. The survival of a dispersed population in the long run is most uncertain.

The classification into these three settlement types makes a qualitative judgement of distribution patterns possible. This means more qualitative than one purely based on numbers of 1-km

squares within the, inevitably artificial, delimitation of regions. In addition, it provides an insight in the degree of fragmentation of a given distribution. When stipulating the development of the subpopulations, the data from the research of 2000-2001 was compared with the results of 1995 (van Moll 1999). The development of the subpopulations was described also within the historical context of the developments as from 1960.

Development towards a continuous distribution

To determine the development towards a continuous distribution, for each year of survey the average distance between core populations was calculated. This measurement was carried out for the survey years 1960, 1970, 1980, 1990 and 2000-2001. To calculate the average, the distance between each core population and the nearest neighbouring core population was determined. The number of core populations minus 1 was divided by the sum of these distances.

Because no development towards a continuous distribution can be expected in the area between the populations north and south of the main rivers in the central parts of the Netherlands (Nederrijn and Meuse), a distinction was made between the core populations at the north and at the south of these rivers. These populations are separated by the geomorphology of the area, which makes it unsuitable for badger habitation. An exchange of badgers between populations on either side is considered to be very rare. Because of their small size, splinter and dispersed populations were not included in the calculation. These populations were not expected to produce a frequent outflow of badgers. The reproduction within these settlement types was expected to benefit mainly the survival of the population itself.

Continuity of occupation

The continuity of occupation of 1-km squares was analysed by means of their occupational sta-

tus in the different years of survey (1960, 1970, 1980, 1990, 1995 and 2000-2001). Also, the spatial distribution of these 1-km squares was taken into account. In this way a qualitative comparison as well as an appraisal of the occupation in terms of high(er) or low(er) continuity of occupation was possible at both a national and a regional level. For those purposes the occupation of 1-km squares occupied at least once since 1960 was subdivided in the following (occupational) categories: *Reoccupied*: 1-km squares occupied only once in the period 1960-1990 and re-occupied in 2001. *Continuous*: 1-km squares with a 'continuous' occupation since these were occupied for the first time up to 2000-2001. For determining the share of continuously occupied 1-km squares in relation to the total of the distribution of a certain year of survey, the continuously occupied 1-km squares were compared. This comparison included only the occupied 1-km squares of the previous year of survey. This meant that new 1-km squares were not considered. *New*: 1-km squares occupied for the first time in 2000-2001. *Alternate*: 1-km squares that were more than once occupied in history and were at least once unoccupied. Also, 1-km squares that were occupied in two or more successive years of survey and were not occupied since then belonged to this category. *Vacant after first occupation*: 1-km squares only once occupied, but not new. These 1-km squares were occupied only once in the years of survey between 1960 and 1995 and remained unoccupied since then. *Abandoned*: Continuously occupied 1-km squares no longer occupied in 2001. The 1-km squares that were for the first time occupied in 1995 but not occupied in 2001 were excluded from this category. Since these only have one occupation year, so there was hardly any continuity to speak of.

A distinction was made between continuity of occupation in a narrow sense and a wider sense. Continuity in a narrow sense was defined as the strictly continuous occupation as from the first moment of occupation. It indicates the stability of occupation. Continuity in the wider sense takes the fluctuations of occupa-

tion into account. It indicated the changes in occupation. In this way, the continuity of occupation that occurred in several, but not necessary in all years of survey was included also in the appraisal of the continuity of occupation. To obtain this more detailed picture, the actual number of times of occupation in two successive years of survey was compared with the number of times that this could have taken place. In formula:

$$\frac{A}{A+B}$$

where A = number of times the occupation occurred in two successive years of survey, i.e. continuities, and B = number of times an occupation was followed by non-occupation, i.e. discontinuities.

Based on occupation data the percentage of occupation for a certain period could be determined. This percentage described the permanent share of occupied 1-km squares in the latest year of survey of a chosen period in relation to the beginning of this period. It was calculated by dividing the number of the continuities with the number of discontinuities in the first year of survey multiplied with 100.

Translocations

To determine the contribution made by translocations to the distribution of the badger in the Netherlands, national data on translocation projects and population enforcement projects was used (Das & Boom 2001b). The data goes back to the year 1987. Only translocations of badgers were considered where enclosures were used. As from the moment of translocation and opening of the enclosure, the developments on site of the enclosure as well as the developments in the surroundings were monitored closely. The parties involved registered all cases of sett-occupation. From this data, the minimum contribution to the badger distribution in 2001 was determined. This was expressed in the number of extra-occupied 1-km squares.

Sett disturbances and disappeared setts

To gather data on sett disturbances and disappeared setts national records from 1996 up to 2000 were used (Das & Boom, unpublished data). Also, during the survey of 2000-2001 for each sett visited the disturbance was registered. Only disturbances of sett locations of a local nature were recorded. Disturbances originating from or with a background of landscape planning were not included, falling out of the scope of this research and requiring dedicated desk research. The following forms of disturbance were distinguished: 1. *Agriculture*: disturbance related to agricultural management, i.e. the practise of farming, such as: ploughing, use of machinery, blocking, dumping, clearing, digging and levelling. 2. *Forestry*: disturbance that related to forest management: levelling, use of machinery, cutting (deforestation, thinning etc.). 3. *Blocked*: sett entrances were closed altogether or were barred with material without a clear relation to any kind of management. 4. *Dogs*: the sett was disturbed, dug-out or destroyed by dogs. 5. *Hunting*: all disturbance which related to the practice of hunting such as: digging out, foxes on a badger sett, placing hide-outs on or nearby the sett. 6. *Nature management*: all disturbance that related to the management of nature reserves, such as: heathland management, cutting back coppice. 7. *Recreation*: all disturbances linked to recreation or pass time, such as: trekking, golf and hut-construction (mostly undertaken by children) and camping(activities). 8. *Poaching*: illegal killing of badgers, illegal digging out parts of the badger sett. 9. *Digging*: the sett was partly (chamber) or entirely dug out by people, there was no clear context (e.g. hunting, poaching). 10. *Cattle*: the sett was trampled on or caved in due to cattle. 11. *Other*: all remaining forms of disturbance, such as: construction of garden houses, paths or private roads, construction activities, cultivation, deposit of living bait, camping in the wild, filming activities, drilling. 12. *Sever-al*: the disturbances were of mixed kind falling in two or more of the categories mentioned above.

Badger setts that were no longer found in 2000-2001 were registered as such. A distinc-

tion was made between 'expired' and 'destroyed' sett locations. Expired sett locations were no longer recognizable as such or were already unsuitable a long period for badger habitation and no clear cause for this could be given or found. Destroyed sett locations disappeared recently or were no longer suitable for habitation without a clear cause.

Results

Development in the distribution

Since 1960 in total 4,435 sett locations were recorded within the research area. During the survey of 2000-2001, 2,507 (57%) of these were examined. The number of examined 1-km squares was 1,708. The number of occupied 1-km squares in 2000-2001 increased to 948 (figure 2). In 2000-2001, 257 1-km squares were occupied for the first time since 1960.

Table 1 gives an overview of the number of occupied 1-km squares as from 1960. In the period 1960-1970, the number of occupied 1-km squares increased. For the period 1970-1980, the occupation decreased. In 1980 the lowest point in the national distribution was reached. In the period 1980-1990 the distribution area increased by 252 1-km squares. In the period 1990-2001, the distribution showed a further increase of 49%. For the period 1990-2001, the increase occurred mainly in the second half of that period. The average annual increase was more than 40 1-km squares. In the period 1995-2001, the distribution decreased in none of the regions (table 2). Between 1995 and 2001, the increase of distribution in the regions of Gelderland-Veluwe, Midden-Limburg and Zuid-Limburg remained below the national average. The population in Gelderland-Veluwe showed a growth less than 1%. This also applies to the population in the valley of the river Reest ('Reestdal'), located on the border of the provinces of Drenthe and Overijssel. The increase of occupied 1-km squares in the remaining parts of these two provinces, however, was still respectively 82% and 78%.



Figure 2. Distribution of square kilometres with occupied badger setts in the Netherlands in 2000-2001.

For all other regions, the increase in occupied 1-km squares was above the national average. A large proportional increase occurred in Noord-Brabant-Meierij, Noord-Brabant-Maasvallei and in the Peel-region. In absolute figures, the increase in Noord-Brabant-Meierij and the Peel was moderate, however, both populations developed into a core population. The three largest populations (Gelderland-Veluwe, Maasvallei and Zuid-Limburg) grew 36%. This was an in-

crease well above the national average. In the period 1995-2001, the increase concentrated in the Maasvallei, especially in the region of Noord-Brabant-Maasvallei. In the previous period (1990-1995), an increase in distribution occurred particularly in Zuid-Limburg (24%). The growth in the other two large populations, Gelderland-Veluwe (11%) and Noord-Brabant-Maasvallei, with connected populations (2.5%) remained below average at that time (van Moll 1999).

Table 1. Number of occupied 1-km squares per survey year and changes in badger occupation in the Netherlands.

	1960	1970	1980	1990	1995	2001
Occupied km ²	382	424	383	635	736	948
In-/decrease		11%	-10%	66%	16%	29%

Table 2. Development in the distribution of the badger in the Netherlands since 1960 per region.

Region	Number of square kilometres						Increase / Decrease		
	1960	1970	1980	1990	1995	2001	1990-1995	1995-2001	1990-2001
Friesland	4	19	18	28	33	45	18%	36%	61%
Groningen	4	2	0	0	0	0	—	—	—
Drenthe	3	5	4	18	22	40	22%	82%	122%
Overijssel	13	10	9	13	18	32	38%	78%	146%
Gelderland - Achterhoek	10	9	1	8	9	14	13%	56%	75%
Gelderland - Rijk van Nijmegen/Land van Maas en Waal	32	22	21	31	28	36	-10%	29%	16%
Gelderland - Veluwe	21	98	95	211	234	236	11%	1%	12%
Noord-Holland/Utrecht	5	6	1	7	8	12	14%	50%	71%
Noord-Brabant - Maasvallei	54	55	58	80	77	136	-4%	77%	70%
Noord-Brabant - West	8	6	0	0	0	2	—	—	—
Noord-Brabant Meierij	8	4	0	4	8	14	100%	75%	250%
Peel	1	2	4	4	6	9	50%	50%	125%
Noord-Brabant - Oost	3	4	0	0	1	3	—	200%	—
Noord-Limburg	34	30	27	44	51	81	16%	59%	84%
Midden-Limburg	41	17	15	28	44	56	57%	27%	200%
Zuid-Limburg	141	135	130	159	197	232	24%	18%	46%
Total	382	424	383	635	736	948	16%	29%	49%

Occupation of suitable habitat

Suitable badger habitats in the Netherlands roughly can be subdivided in two parts, i.e. the area situated north of the river Nederrijn and the area south of the river Waal. The area between these two rivers has no history of continuous badger habitation of interest (figure 3).

Around 1900, north of the Nederrijn an almost unbroken stretch of suitable habitats was located in the area going east to west from Gelderland-Achterhoek up to the Gooi-area in the province of Utrecht. Another continuous stretch was going south to north from the Montferland-area in Gelderland-Achterhoek as far as the river Boorne in Friesland. The border area of Drenthe and Overijssel south of the Reestdal and the forestry area of Staphorst contained few suitable habitats around 1900. There was only a narrow strip of suitable habitats present near Balkbrug and in the area Slagharen-Gramsbergen (Dirkmaat 1996). In 1900, the badger (already) lived isolated in a number of areas. North of the river

Nederrijn, these island populations were found amongst others near Twijzelerheide, in Gaasterland, in the valley of the river Tjonger in Friesland, in the eastern part of Groningen and in the Land van Vollenhove in Overijssel.

In 1900, south of the river Waal, a nearly continuous band of suitable habitats was found - going from south to north - in Zuid-Limburg up to and including the region of Gelderland-Rijk van Nijmegen/Land van Maas en Waal. From here going east to west, suitable habitats were found up to Bergen op Zoom, in a less condensed form (figure 3). Much less suitable habitat was available on the border area of Noord-Brabant-Maasvallei and Noord-Limburg. This was except for the north of the border area due to the nutrient-rich clay sediments in the valley of the river Meuse. Many habitats along the river Meuse suitable in 1900 became unsuitable now. Due to, amongst others, building activities and large-scale extractions (sand and gravel) many habitats along the river Meuse and large parts of Noord-Brabant became unsuitable for badgers.

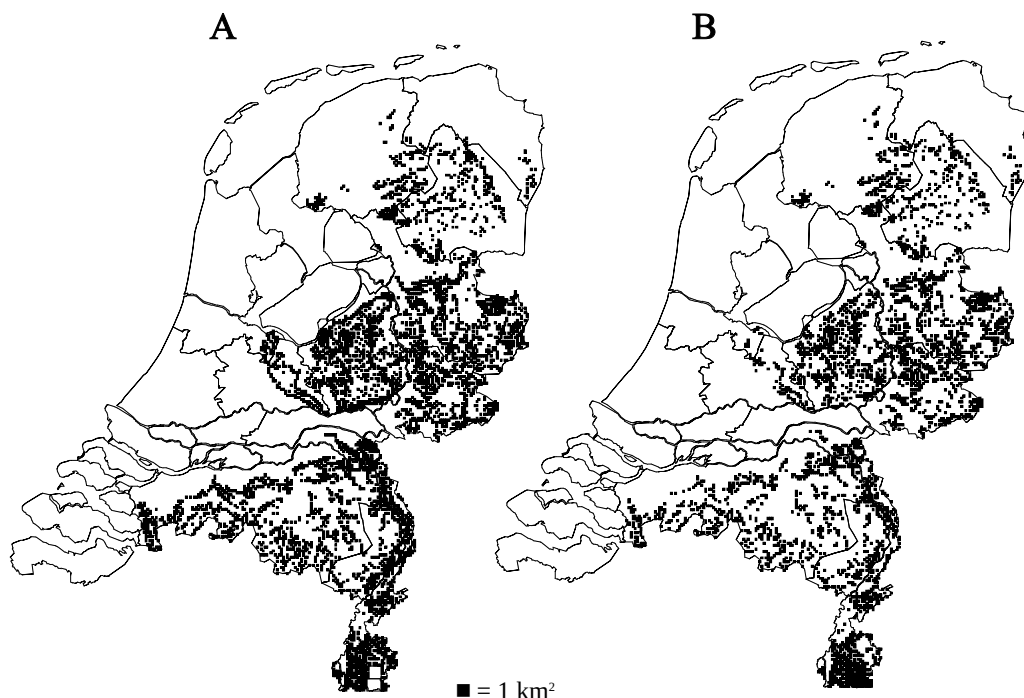


Figure 3. Suitable badger habitat in (A) 1900 and (B) 1995.

In 2001, a quarter of the suitable habitat area in the Netherlands was occupied (table 3). This was an increase of 6% in comparison with the year of survey 1995. Proportionally Groningen, Overijssel, Gelderland-Achterhoek, Gelderland-Veluwe, West Noord-Brabant and East Noord-Brabant lagged behind considerably. Other regions lagging behind were Noord-Holland/Utrecht and Midden-Limburg. More than average occupation of suitable habitats was determined for nine regions: Friesland, Drenthe, Gelderland-Rijk van Nijmegen/Land van Maas and Waal, Gelderland-Veluwe, Noord-Brabant-Meierij, Peel, Noord-Brabant-Maasvallei, Noord-Limburg and Zuid-Limburg. Gelderland-Veluwe was, despite a small increase in distribution since 1995, one of the best-occupied regions in 2001. Also Gelderland-Rijk van Nijmegen/Land van Maas en Waal, Noord-Brabant-Meierij, Noord-Brabant-Maasvallei, Peel, Noord-Limburg and Zuid-Limburg are to be considered as best occupied (table 3). These regions

with the exception of Gelderland-Veluwe also showed a considerable increase of 10% or more.

In 2001, the occupation of the five regions taken together (Friesland, Drenthe, Groningen, Overijssel and Gelderland-Achterhoek) in the north and east of the Netherlands stayed far behind that of the remaining regions. The habitats suitable for badgers in these regions were more than 40% of the 3,838 km² present but they contain only 14% of the distribution of 2001. This fraction occupied as much as 8% of the suitable habitats available. This is in great contrast to the middle and south of the Netherlands that contained almost 60% of the total of suitable habitats. Here 86% of the distribution of 2001 was found and as much as 37% of the suitable habitats available was occupied. It must be noted here that in the period 1990-2001 the increase in distribution in the north and east was twice as high as in the middle and south of the Netherlands, respectively 96% and 44%.

Table 3. Suitable badger habitat in 1995 and occupied square kilometres of suitable habitat in 1995 and 2001 per region.

Region	Area	Suitable habitat		Occupied in 1995		Occupied in 2001		Increase in occupation 1995-2001
	(km ²)	(km ²)	(%)	(km ²)	(%)	(km ²)	(%)	(%)
Groningen	2400	38	2%	0	0%	0	0%	0%
Friesland	3300	167	5%	33	20%	45	27%	7%
Drenthe	2700	249	9%	22	9%	40	16%	7%
Overijssel	3400	760	22%	18	2%	32	4%	2%
Gelderland – Achterhoek	1600	411	26%	9	2%	14	3%	1%
Gelderland – Rijk v. Nijmegen / Land v. Maas en Waal								
	450	63	14%	28	44%	36	57%	13%
Gelderland – Veluwe	2200	586	27%	234	40%	236	40%	0%
Noord-Holland / Utrecht	1650	100	6%	8	8%	12	12%	4%
Peel	35	4	11%	6	150%	9	225%	75%
Noord-Brabant - Maasvallei	840	193	23%	77	40%	136	70%	31%
Noord-Brabant Meierij	225	34	15%	8	24%	14	41%	18%
Noord-Brabant - Oost	1600	215	13%	1	0%	3	1%	1%
Noord-Brabant - West	2300	269	12%	0	0%	2	1%	1%
Noord-Limburg	670	158	24%	51	32%	81	51%	19%
Midden-Limburg	950	232	24%	44	19%	56	24%	5%
Zuid-Limburg	625	359	57%	197	55%	232	65%	10%
Total	24945	3838	15%	736	19%	948	25%	6%

Development of settlement types

In 2001, the badger distribution counted 11 core populations, 9 splinter populations and 25 dispersed populations (figure 4).

Core populations

In the period between 1995 and 2001, the core populations grew with 30% (1990-1995: 13%). Since 1960, the share of core populations increased. In the last two decades, more than 90% of all occupied 1-km squares were located within a core population (table 4).

The core populations Gaasterland, Midden-Drenthe, Reestdal, Gelderland-Veluwe, Noord-Brabant-Maasvallei, Midden-Limburg and Zuid-Limburg were already in 1995 characterised as such. Apart from these, four splinter populations developed into a core population: Tjongervallei in Friesland, Hollandsche Rading in Noord-Holland/Utrecht, Noord-Brabant-Meierij and Peel.

One splinter population (Belfeld) merged with the core population of the Maasvallei.

Splinter populations

In the period 1995-2001, three splinter populations remained, St. Nicolaasga (Friesland), Montferland (Gelderland-Achterhoek) and Land van Maas en Waal, six were new and four developed into cores. New splinter populations are: Wijster in Drenthe, Salland, Vechtdal Dalfsen and Vechtdal Ommen in Overijssel, Vorden and Winterswijk in Gelderland-Achterhoek. In the period 1995-2001, the growth percentage of splinter populations (48%) was well above the national average (29%; table 4). In the period before (1990-1995), the occupation as represented by splinter-populations hardly increased.

Dispersed populations

In the period 1995-2001, the number of dispersed populations remained the same. In 2001,

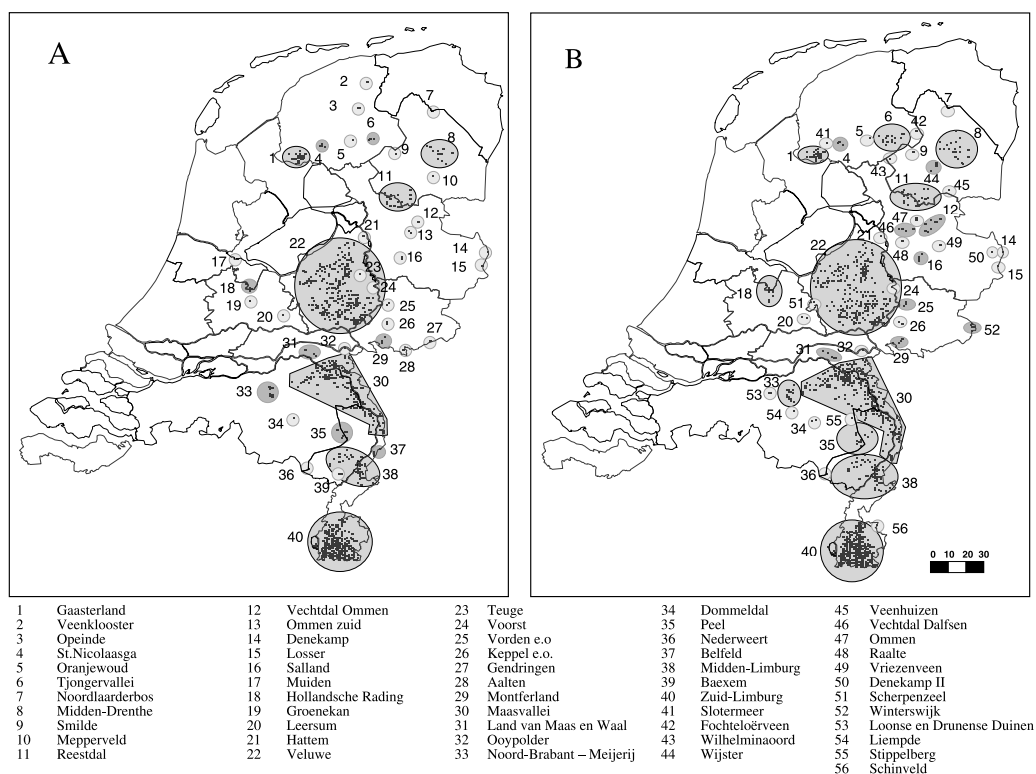


Figure 4. Settlement types in (A) 1995 and (B) 2001: core populations (dark grey with black border), splinter populations (dark grey with grey border), dispersed populations (light grey with grey border).

dispersed populations covered 17% less 1-km squares as in 1995. Twelve dispersed populations remained as such. Thirteen dispersed populations came into existence, seven others disappeared. Two dispersed populations became part of a core population: Groenekan (Noord-Holland/Utrecht) and Baexem (Midden /Limburg). Four dispersed populations developed into a splinter population: Salland together with Vecht nearby Ommen in Overijssel and Vorden in Gelderland-Achterhoek. Since 1960, the number of dispersed populations only increased in the period 1990-1995, in which it almost doubled (table 4).

Development towards a continuous distribution

In 2001, the average distance between core populations was 21 km. This average decreased by

25% since 1980 (table 5). A difference between the north and south of the Netherlands should be noted. Since 1980 south of the main rivers, the average distance between core populations decreased. This was largely due to the development of the population in Noord-Brabant-Maasvallei. In the northern part of the Netherlands, however, up to 1990, the average distance between core populations increased slightly. This was due to the development of a peripheral core population in the central part of Drenthe in 1990. After 1990, the average distance decreased. This can be explained by the development of a core population in the Tjongervallei (Friesland) filling the gap between Gaasterland and the core population in the central part of Drenthe.

Since 1980, the total number of badger settlements increased (table 4). The degree of fragmentation reached a high in the period 1990-1995.

Table 4. Spread and development of the various settlement types and number of settlements per settlement type in the period 1960-2001.

Year of survey		Settlement type			Total	Δ Core	Δ Splinter	Δ Dispersed
		Core (≥ 9 km ²)	Splinter (3-8 km ²)	Dispersed (<3 km ²)				
1960	km ²	300	39	43	382			
	% of total	79	10	11	100			
	<i>n</i>	3	8	38	49			
1970	km ²	359	25	40	424	20%	-36%	-7%
	% of total	85	6	9	100			
	<i>n</i>	6	6	30	22			
1980	km ²	358	7	18	383	0%	-72%	-55%
	% of total	93	2	5	100			
	<i>n</i>	6	1	12	19			
1990	km ²	597	26	12	635	67%	271%	-33%
	% of total	94	4	2	100			
	<i>n</i>	7	7	13	27			
1995	km ²	673	27	36	736	13%	4%	200%
	% of total	91	4	5	100			
	<i>n</i>	7	8	25	40			
2001	km ²	878	40	30	948	30%	48%	-17%
	% of total	93	4	3	100			
	<i>n</i>	11	9	25	45			

This has been ascribed to the high number of dispersed populations in that period (van Moll 1999). Noticeable was the 'gap' in the distribution between the core populations of Midden-Limburg and Zuid-Limburg. Also, 'gaps' were noted between the German border (the eastern part of Overijssel named Twente and Gelderland-Achterhoek) and Gelderland-Veluwe. The development in the distribution between the population of Gelderland-Veluwe and that of Gelderland-Achterhoek (Montferland) lagged behind, compared with the closing of the gap between Gelderland-Veluwe and Noord-Holland/Utrecht. The latter becoming less isolated. The lack of development in the northern part of Drenthe and the eastern part of Groningen was also conspicuous. Another matter that draws attention was the increase of the density of occupation in the regions of Gelderland-Veluwe, Noord-Brabant-Maasvallei, Midden-Limburg and Zuid-Limburg.

Continuity of occupation

Table 6 shows the numbers of the occupied and

unoccupied 1-km squares in 2001 for each occupational category. All 1-km squares occupied at a given time from 1960 onwards were included. The continuous occupied 1-km squares made up the largest category. The percentages of respectively 'new', 'alternate' and 'vacant after first occupation' were all around 20%. The percentage of reoccupied 1-km squares in 2001 was low (3%) and approximately equal to the percentage of abandoned 1-km squares (4%).

In 2001, more than half (54%) of the 1-km squares occupied also at an earlier time originate from 1980 or before. Of these, 513 1-km squares had remained occupied since their first date of occupation: the continuous 1-km squares in the so-called 'narrow' sense. A number of 178 1-km squares had no history of continuous occupation. These 1-km squares were to be considered as either alternate or reoccupied (table 6).

Table 7 gives a regional overview of the first year of occupation and the totals for each of the occupational categories. The alternate 1-km squares (*n*=150) not occupied in 2001 are not included. For each region also the number of



Disturbed badger sett by clear felling. *Photograph: Kees Campfens / The Census Foundation.*

ever-occupied 1-km squares is given. Table 8 provides the numbers of continuities and discontinuities per year of survey and the percentages of the continuity of occupation. The short-term occupation (1995-2001) percentage amounted to 82%. Compared with the period 1990-1995 this was an increase of 12%. Despite this nationwide increase in some regions, a decrease however was recorded in Overijssel and Peel. In the short term, only the occupation percentage in Gelderland-Achterhoek was far below the national average.

The average percentage of the continuity of occupation in the long term (1960-2001) was 73% (table 8). Most regions did not strongly deviate from this national long-term percentage. Continuity increased considerably in Drenthe, Noord-Holland/Utrecht, Noord-Brabant-Meierij and Noord-Limburg, whereas some decrease was found in the Peel region. Although there was an increase in the short term for

Gelderland-Achterhoek and Noord-Brabant-Meierij, these regions remained far below the national average.

Reoccupied 1-km squares

In 2001, 5% ($n=44$) of the total of occupied 1-km squares was reoccupied (figure 5). For 1995, this percentage was 3%. Reoccupation occurred mainly in all the three regions of Gelderland and in Zuid-Limburg. Almost half of the reoccupied

Table 5. Average distance in kilometres between the core populations present since 1980 (= indexvalue 100). NME = north, middle and east; S = south.

Year	Nether- lands	Index	NME	Index	S	Index
1960	17	61	—	—	17	89
1970	23	82	35	106	17	89
1980	28	100	33	100	19	100
1990	24	86	35	106	14	74
2001	21	75	26	79	11	58

1-km squares in Zuid-Limburg were found in the area between the highways A79 and N278.

Continuous 1-km squares

In 2001, 54% ($n=513$) of the total of occupied 1-km squares was made up from continuous 1-km squares. On the total of 1-km squares occupied at least once since 1960, minus the new 1-km squares of 2001 ($n=1,145$) the continuous 1-km squares amounted to 45% (table 6). Since 1995, this percentage increased by 2% (van Moll 1999). Hence, it may be concluded that the relationship between continuous and discontinuous 1-km squares became a bit more favourable. However, if we compare in a similar manner 2001 with 1995 and limit ourselves to the 1-km squares occupied in that particular year of survey the picture is somewhat different. The percentage of continuous 1-km squares in 2001 was 74%, for 1995 this was 78%. This means some decline, which involved in particular 1-km squares with 1970 or 1990 as the first year of occupation (table 9).

The number of continuous 1-km squares compared with the total of occupied 1-km squares varied for the different regions between 38 and 100%. Friesland and Noord-Limburg had a percentage that about equals the national average of 74%. The percentage of continuous 1-km squares in Gelderland-Achterhoek (50%), Gelderland-Rijk van Nijmegen/Land van Maas en Waal (60%), Noord-Brabant-Meierij (38%) and Zuid-Limburg (64%) was below the national percentage. Most of the continuous 1-km squares



Use of a badger tunnel by two badgers. Photograph: Kees Campfens / The Census Foundation.

go back to the years 1960, 1990 and 1995. The amount of continuous 1-km squares originating from 1960 was 22%. This equalled the percentage of 1990 (table 7). Despite the considerable increase of percentage of continuities (see table 8) a decrease in stability of continuous squares must be noted for the large populations in the Maasvallei and Zuid-Limburg.

Table 6. Distribution of surveyed 1-km squares in 2001 per occupation category per year of initial occupation since 1960 in the Netherlands.

Occupation category	1960	1970	1980	1990	1995	2001	Total	% of ever occupied
Reoccupied in 2001	8	7	2	27			44	3
Continuously occupied since 19..	115	50	59	111	178		513	37
New in 2001						257	257	18
Alternating: occupied in 2001	97	21	16				134	10
Alternating: not occupied in 2001	91	36	23				150	11
Occupied once only	64	32	15	71	71		253	18
Abandoned		8	12	8	23		51	4
Total	383	158	123	232	249	257	1402	100

New 1-km squares

Figure 6 shows the distribution of the new 1-km squares. The number of new 1-km squares amounted to 27% of the distribution in 2001. This was a 6% decrease compared with 1995. The provinces of Drenthe, Overijssel, Utrecht and Noord-Brabant showed an above average percentage (50%, 53%, 42%, 44%) new 1-km squares. Gelderland-Veluwe, Gelderland-Rijk van Nijmegen/ Land van Maas en Waal, Midden-Limburg and Zuid-Limburg remained below the average (table 7).

Alternate 1-km squares

This category falls apart in 1-km squares occupied in 2001 and 1-km squares not occupied in 2001. 14% of the total distribution in 2001 was made up from alternate 1-km squares. In 1995, ($n=892$) this percentage was 16% (van Moll 1999). Alternate occupation and subsequent occupation in 2001 occurred especially in Noord-Brabant-Meierij and Zuid-Limburg. In particular, 1-km squares occupied for the first time in 1960 were involved (table 7).

The alternate 1-km squares that were not occupied in 2001 (table 6) were in particular also 1-km squares occupied in 1960 for the first time (about 60%). Comparing the number of alternate 1-km squares not occupied in 2001 with the number of 1-km squares occupied at least once, the national percentage came to 10%. Groningen had the most 'unfavourable' ratio (50%). The regions of Gelderland-Achterhoek, Gelderland-Rijk van Nijmegen/Land van Maas en Waal, Noord-Holland/Utrecht, West Noord-Brabant and Noord-Limburg also had a quite considerable proportion of around 15%. The regions of Friesland, Drenthe and Midden-Limburg showed a small proportion, around 5%. The proportion between the alternate 1-km squares and the total number ever-occupied 1-km squares was 11% for 2001 (1995: 13%).

1-km squares vacant after first occupation

The number of 1-km squares vacant after first occupation in the period 1960-1995 was 253. In 1995, this number was 222 1-km squares (van

Moll 1999). Compared with the whole group of ever-occupied 1-km squares the percentage hardly changed, respectively 18% in 1995 and 19% in 2001. The absolute number of 1-km squares vacant after first occupation was highest in Gelderland-Veluwe and Midden-Limburg, followed by Noord-Brabant-Maasvallei and Zuid-Limburg. For all three regions in the province of Gelderland, this category of 1-km squares originated from the period 1990-2001. In 1990 and 1995, almost half of the 1-km squares vacant after first occupation were found in Gelderland-Veluwe. In the western part of this region, north of the A12-highway, 61 1-km squares (24%) were qualified as vacant after first occupation. Midden-Limburg had 28 1-km squares remaining vacant after first occupation, of which 19 were occupied in 1960. This was indicative of the disturbance of habitats in that period (table 7). Compared with the 1-km squares occupied at least once in the period 1960-1995 Groningen, Gelderland-Achterhoek and West Noord-Brabant had a high score.

Abandoned 1-km squares

In 2001, 51 formerly continuous 1-km squares were vacant for the first time. This was 7% of the total distribution in 1995. For 1995, a percentage of 10% was established ($n=61$). The provinces of Gelderland (mainly in the region of Gelderland-Veluwe) and Limburg scored far higher than the other provinces (table 10). In Limburg, the region of Zuid-Limburg accounted for eight 1-km squares, six of them located in the far south. Absolutely speaking this may seem high, but proportionally compared with the national average this was 3% below average. On the other hand it must be noted that more than half of the abandoned 1-km squares having a continuous history going back until 1960 were found in the far south of Limburg (table 10).

Continuity in the wider sense

Table 8 gives an overview of the continuities and discontinuities for each year of survey. The national average for continuity of occupation over

the period 1960-2001 was 73%. This means that in that period of the hundred 1-km squares 73 remained occupied in the following year of survey. In the period 1980-1990, the continuity of occupation was 85%. The continuity of occupation in the period 1990-1995 decreased to 70%. The picture for the period 1995-2001 was more favourable: the percentage came above the long period average (82%). In this period, the distribution was considerably more stable (table 8). The continuity of occupation on the short term over the period 1995-2001 reached values below average. In particular, this occurred in the regions of Gelderland-Achterhoek, Gelderland-Veluwe and the Peel-region. In 2001, in almost 36% of the cases ($n=143$) the vacated 1-km squares touched each other. This means that the area that was vacated covers two or more 1-km squares ($n=51$) (figure 7).

In Friesland, Noord-Brabant-Maasvallei, Peel, Noord-Limburg and Zuid-Limburg the continuity of occupation in the long run (1960-2001) equalled or exceeded the national average of 73% (table 8). Especially Noord-Brabant-Maasvallei and Zuid-Limburg had a high score. A very low score was found for Gelderland-Achterhoek. Below average also were Overijssel, Gelderland-Veluwe, Gelderland-Rijk van Nijmegen/Land van Maas en Waal, Noord-Holland/Utrecht and Midden-Limburg.

Translocations

Table 11 shows the number, sites and net result of the badger translocations that took place in the period 1987-2001. There were 26 translocation sites, located in seven provinces (figure 8). 210 badgers were translocated with the aid of an enclosure. The percentage of translocated badgers reported dead after translocation was 32% (67 badgers). The translocations resulted into the occupation of 37 additional 1-km squares. The average number of badgers in each additional occupied 1-km square was about eight. Translocations accounted for at least 4% of the distribution of 2001. Translocations in Friesland resulted into the development of the Tjongervallei core

population. Translocations in Friesland also led in Drenthe to a dispersed population in the forestry of Smilde. Under the influence of translocations in Drenthe, a splinter population in the central parts of Drenthe (Wijster) developed. In Gelderland-Achterhoek, translocations resulted in the formation of the splinter population Winterswijk. Partly under the influence of translocations, the population of Noord-Brabant-Meierij developed from a splinter population into a core population. Also, in Noord-Brabant translocations led to the dispersed population of Loonse en Drunense Duinen (Noord-Brabant-West). The remainder of the translocations contributed more or less to the strengthening of existing populations.

Disappeared setts

In the period 1995-2001, 202 setts (either occupied or vacant) disappeared. This was 8% of the total of researched sett locations. Of these 202 setts, 19% was inhabited in 1995 (39 setts). The disappeared setts still occupied in 1995 were located mainly in Overijssel, Gelderland-Veluwe, Noord-Brabant-Maasvallei and Zuid-Limburg (table 12).

In total, 145 sett locations were recorded as expired and 57 sett locations as destroyed. In the period 1995-2001, destruction of sett locations was particularly observed in Gelderland-Rijk van Nijmegen/Land van Maas en Waal, Noord-Limburg and Zuid-Limburg. The number of destroyed sett locations decreased 39% compared with the period 1990-1995 ($n=94$).

Disturbances

In total, 315 cases of disturbance of badger setts were observed. In 40% of the cases a directly responsible party, such as a nature manager, land owner or works foreman was involved. A considerable part of the observed disturbance was related to agricultural management (18%) and dogs (11%). In 20% of the cases, the sett was dug out or uprooted without anybody that could be held responsible. For the most part disturbances

Table 7. First year of occupation of 1-km squares since 1960 per region per occupation category in 2001.

Region	Reoccupied in	Continuously occupied since					New in	Alternating - occupied in 2001, first occupied in...				Vacant after first occupation					Ab- andon- ed	Ever occu- pied		
		2001	1960	1970	1980	1990		1995	Total	2001	1960	1970	1980	Total	1960	1970			1980	1990
Friesland	3	0	7	7	5	3	22	14	1	4	1	6	2	3	0	2	4	11	2	60
Groningen	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	4
Drenthe	2	0	1	1	8	8	18	20	0	0	0	0	1	1	0	5	3	10	1	54
Overijssel	0	0	1	3	5	4	13	17	2	0	0	2	7	3	1	0	2	13	1	52
Gelderland - Achterhoek	1	1	0	0	0	2	3	8	2	0	0	2	3	1	0	2	4	10	0	29
Gelderland - Rijk v.Nijm/ Land v.MW	6	10	0	4	0	4	18	6	6	0	0	6	6	1	2	8	2	19	2	65
Gelderland - Veluwe	13	4	27	18	47	66	162	48	3	8	1	12	3	11	4	34	32	84	28	390
Noord-Holland/Utrecht	0	0	0	1	4	2	7	5	0	0	0	0	1	2	0	2	1	6	0	22
Peel	0	0	1	0	0	2	3	5	0	0	0	0	0	0	1	0	1	2	1	13
Noord-Brabant																				
Maasvallei	3	25	7	4	11	15	62	56	11	2	2	15	6	2	2	8	2	20	3	181
Noord-Brabant Meierij	0	0	0	0	0	3	3	8	5	0	0	5	1	0	0	0	1	2	0	20
Noord-Brabant Oost	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0	2	0	6
Noord-Brabant West	0	0	0	0	0	0	0	2	0	0	0	0	0	4	0	0	0	9	0	13
Noord-Limburg	4	9	2	4	8	12	35	30	8	1	2	11	5	0	1	2	5	13	3	109
Midden-Limburg	1	5	0	3	9	18	35	10	10	1	0	11	19	0	2	5	2	28	2	94
Zuid-Limburg	11	61	4	14	14	39	132	26	49	5	10	64	2	4	2	2	12	22	8	290
Total	44	115	50	59	111	178	513	257	97	21	16	134	64	33	15	70	71	253	51	1402

Table 8. Number of continuities (A), discontinuities (B) and percentages of continuity in occupation in the long (1960-2001) and short term (1990-1995 and 1995-2001). A continuity (A) is the number of times a square kilometre was occupied in two successive years of survey. A discontinuity (B) is the number of times a square kilometre was no longer occupied after being occupied in the previous year of survey. $C = \sum A + \sum B$; $C1 = \sum A/C * 100$; $D = \sum A4 + \sum B4$; $D1 = \sum \text{short term continuities } 1990-1995: A4/D * 100$; $E = \sum A5 + \sum B5$; $E1 = \sum \text{short term continuities } 1995-2001: A5/E * 100$.

Region	1960-1970		1970-1980		1980-1990		1990-1995		1995-2001		1960-2001		% con- tinu- ities 1960- 2001		% con- tinu- ities 1990- 1995		% con- tinu- ities 1995- 2001	
Column reference	A1	B1	A2	B2	A3	B3	A4	B4	A5	B5	$\sum A$	$\sum B$	C	C1	D	D1	E	E1
Friesland	2	2	9	10	17	1	23	5	27	6	78	24	102	76	28	82	33	82
Groningen	2	2	0	2	0	0	0	0	0	0	2	4	6	33	0		0	
Drenthe	2	1	2	3	3	1	11	7	18	4	36	16	52	69	18	61	22	82
Overijssel	4	9	3	7	7	2	12	1	15	3	41	22	63	65	13	92	18	83
Gelderland - Achterhoek	6	4	1	8	1	0	3	5	4	5	15	22	37	41	8	38	9	44
Gelderland - RijkvNijm	20	12	15	7	17	4	17	17	21	6	90	46	136	66	31	55	28	75
Gelderland - Veluwe	17	4	58	40	85	10	134	76	168	68	462	198	660	70	211	64	234	72
Noord-Holland/Utrecht	4	1	0	6	1	0	5	2	7	1	17	10	27	63	7	71	8	88
Peel	2	0	2	0	3	1	3	1	4	2	14	4	18	78	4	75	6	67
Noord-Brabant -																		
Maasvallei	41	12	40	15	50	8	59	24	71	9	261	68	329	79	80	74	77	92
Noord-Brabant Meierij	4	4	0	4	0	0	2	2	8	0	14	10	24	58	4	50	8	100
Noord-Brabant - Oost	2	1	0	4	0	0	0	0	0	0	2	5	7	29	0		1	
Noord-Brabant - West	2	5	0	6	0	0	0	0	0	0	2	11	13	15	0		0	
Noord-Limburg	25	9	14	15	21	3	28	12	42	8	130	47	177	73	41	68	48	88
Midden-Limburg	17	25	8	10	14	4	22	9	43	4	104	52	156	67	31	71	47	91
Zuid-Limburg	111	24	93	42	108	22	126	36	174	27	612	151	763	80	159	79	197	88
Total	261	115	245	179	327	56	445	197	602	143	1880	690	2570	73	635	70	736	82

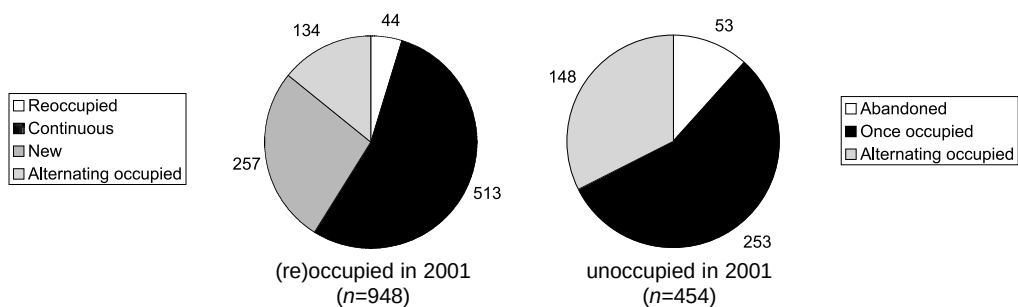


Figure 5. 1-km squares at least once occupied in the Netherlands in the period 1960-2001.

took place in Noord-Brabant and Limburg, in particular Zuid-Limburg. The number of disturbances in Gelderland-Rijk van Nijmegen/Land van Maas and Waal was relatively low. Disturbance by hunting was observed in the provinces of Friesland and Noord-Brabant. In the period 1995-2001, at eight locations poaching was recorded. Six locations were located in Zuid-Limburg and two in the province of Gelderland, both in the region of Gelderland-Veluwe.

Discussion

Character of the research

The survey in 2000-2001 (and of 1995) did not have the character of a "badger census" in the strict sense of the word. In a badger census each known sett location is visited and examined for occupation by badgers. However, by aiming at the habitation per 1-km square already a reliable picture of the spatial distribution of badgers and distribution gaps can be acquired. This suits with the objective for the badger distribution formulated in the badger protection plan. For this a detailed description of the occupation of each individual sett is not needed or necessary. As for the other goals set in the protection plan, i.e. to increase the number of badgers and reaching optimal badger densities (further) ecological research is required. For instance, this would require research on population dynamics and measurement of the character and the carrying

capacity of the habitats.

Number of badgers

Although the actual number of badgers in the Netherlands lies besides the scope of this research, some remarks on this matter can be made. The number of badgers in the Netherlands was estimated between 2,200 and 2,500 individuals in 1995 (Das & Boom 2000, Das & Boom 2002b). With an increase in the distribution of almost 30% between 1995 and 2001, this would mean that the number of badgers comes to an estimated 2,800-3,200 individuals. Earlier, for 1980 a number of 1,200 was estimated and for 2000 a number of 3,500 (Das & Boom 2002c). Rough estimates based on sett surveys came to a number of 1,500 in 1980 and 2,200 individuals in 1990 (Wiertz 1992). Presupposing a constant average of badgers per social group this leads - apart from the number of 3,500 already mentioned - to estimates for the year 2000 of 3,000,

Table 9. Number and first year of occupation of square kilometres continuously occupied in 1995 and in 2001.

Year	1995	2001	Δ 1995-2001	Decrease
1960	120	115	-5	-4%
1970	61	50	-11	-18%
1980	69	59	-10	-14%
1990	136	111	-25	-18%
1995	—	178		
Total	386	513		



Translocation in Land van Maas en Waal (Hernen). Photograph: Kees Campfens / The Census Foundation.

3,700 and 3,200 individuals based on the estimates of 1980 by Das & Boom, 1980 by Wiertz, and 1990 by Wiertz respectively. These estimates are based on extrapolations of the number of badgers from the changes in the number of occupied 1-km squares. However, a realistic number presupposes thorough research on population dynamics (e.g. on average group size, regional differences, mortality), which has not been undertaken in the Netherlands until now.

Development in the distribution

The regions of Overijssel and Gelderland-Achterhoek are still under-developed. In the period 1995-2001, the growth in the distribution is above the national average in Overijssel and Gelderland-Achterhoek. However, if we place this growth in the context of the large amount of unoccupied but suitable habitats in these regions, the increase is relatively small. Moreover, we must mention that in the case of Gelderland-

Achterhoek the contribution of translocation (Winterswijk-area) to the distribution growth has been relatively large.

The development in the distribution varies per region. The area occupied by badgers in the Peel-region on the border of Noord-Brabant and Limburg has grown considerably. This is mainly due to the developments on the Noord-Brabant side of this region. The regions that lag behind most are Gelderland-Veluwe (1%) and the Reestdal (0%) (table 2). Noord-Limburg shows a considerable increase in distribution in the period 1995-2001. In this respect, it differs from the remainder of the province of Limburg where the growth is below the national average. This is in contrast to the period 1990-1995, when the largest increase was established in Midden-Limburg and Zuid-Limburg (respectively 52% and 24%). Also, in Overijssel and in the Reestdal the growth between 1990 and 1995 was considerably higher (both 38%). In regions, relatively large deviations from the national trend appar-

ently occur within a short time span of five years. It may be expected that this holds true in the case of a decline in the distribution. Also, the results show that regional developments are asynchronous.

The overall growth in distribution is considerable: the development of the three largest populations shows that a growth of the distribution area with 35% within a period of five years occurs. This illustrates that the growth is to be considered mainly as restorative growth, meaning the occupation of suitable, but still unoccupied habitat.

Occupation of suitable habitats

The reconstruction of suitable badger habitats shows us that in the year 1900 20% of the total research area consists of suitable badger habitats. In 1995, the quantity of suitable habitats has decreased to 15%. Chances for new occupation of suitable habitats are located particularly in the northern and eastern parts of the Netherlands (Friesland, Groningen, Drenthe, Overijssel and Gelderland-Achterhoek). As the results on the occupation of suitable habitat show, in these parts of the Netherlands a small distribution coincides with a large area of suitable habitat. This applies particularly to Overijssel and Gelderland-Achterhoek which both have a large area with unoccupied suitable habitat.

Because of the geomorphology, i.e. the lack of suitable higher grounds, the populations in Gaasterland most presumably will remain isolated. In the centre of the Netherlands, however, there are only few possibilities for further growth. Gelderland-Veluwe with an occupation rate of 40% is proportionally well occupied. This region is highly forested compared with other regions and there is a favourable proportion between total area and suitable habitat. Increase in the distribution is expected to take place in the western part of this region, i.e. in the Gelderse Vallei. In the centre of Gelderland-Veluwe, the distribution most likely will decrease further. This is due to change of land use (more extensive management) and wildlife management (reduction of

supplementary feeding of ungulates). Possibilities for a continuous distribution in eastern directions are found in the border area of Gelderland-Veluwe, i.e. with the northern part of Gelderland-Achterhoek. A distribution growth in the direction of Noord-Holland and Utrecht is not expected because of the small quantity of area with suitable habitat here. However, further development in the southern part of the wooded bank of the 'Utrechtse Heuvelrug' is probable.

Because of the geomorphology of the rivers area in the central parts of the country, i.e. clay and high groundwater levels, the distribution at the north and south of the main rivers will remain separated (figure 3). Although accessible for badgers, this area probably will never become a component of an unbroken distribution area.

Sufficient suitable habitats for further positive development in the distribution in the south of the Netherlands are to be found in western and eastern Noord-Brabant and Midden-Limburg. A strengthening of the population in the Noord-Brabant-Meierij in the near future is likely. This also applies to the merger of this population with the population in the Noord-Brabant-Maasvallei.

For the areas Noord-Brabant-Maasvallei, Noord-Limburg and Zuid-Limburg the possibilities for extension of the distribution area are limited. In these areas, the badger already occupies a considerable percentage of suitable habitats (50-70%). In the Peel-region, the badger occupies at present even more 1-km squares than the number of 1-km squares that are considered suitable for the region. The regions of Midden-Limburg and Zuid-Limburg are not to be expected to grow into one continuous distribution area. However, most certainly the distance between these populations can be reduced somewhat, since it has been smaller under the same conditions in the past. The causes of this fragmentation in this part of the Limburg province are mainly anthropogenic. The industrial area of the Dutch State Mines (DSM) and the urban areas around Geleen and Sittard together constitute a nearly insurmountable barrier of unsuitable habitats. Contact between the populations of Mid-

den-Limburg and Zuid-Limburg must take a route over German territory. Such a “by-passing” movement has occurred as well in the case of the urban areas of Apeldoorn (Gelderland-Veluwe) and Venlo (Noord-Limburg) (van Moll 1999).

Development per settlement type

The classification in settlement types is meant in the first place to distinguish between the settlements that can be expected to have an influence on the development in the distribution of the badger in the future and those which are not, or much less, influential. The criterion for this distinction must be sought in the chances of survival and expansion of a settlement. Of core populations it is supposed that they can maintain themselves potentially on the long-term (i.e. 20-25 years) as a core population and - given sufficient unoccupied suitable habitats - even can grow in spite of the pressures on the badger population originating from mortality, disturbance and habitat destruction. For splinter populations this is not the case, although these populations will not disappear rapidly as a whole, as the example of Montferland in Gelderland-Achterhoek illustrates. This splinter population is situated rather isolated against the German border. This makes the population vulnerable, partly because of the game regime that applies to the badger in Germany (the season for badger hunting being open during certain months of the year). The local road network also plays a role here (traffic mortality). For these reasons at present little inflow of badgers coming from Germany is to be expected. This is underlined by the disappearance of the dispersed populations in the south of Gelderland-Achterhoek. Most certainly an international approach is needed to increase badger distribution in this region.

In the area of Land van Maas en Waal, by means of translocations, attempts have been made to reconnect the population here with the core population in the area of Rijk van Nijmegen. The population of Land van Maas en Waal exists for a long time in a state of relative isolation.

This is due to the lack of suitable habitats in the north, west and east of this population. In 1960, it was still a core population, but due to the extraction of badgers here, i.e. for reintroduction elsewhere in the Netherlands, this population has become a splinter population. Suitable habitats also disappeared in the south of the area. The connection to the southwest with the population of Rijk van Nijmegen is the more important, but vulnerable. This is because of the road-network and planning developments in the corridor area (mainly housing).

The splinter population of St. Nicolaasga (Friesland) is isolated also due to the lack of suitable habitat. The population will act possibly as a “stepping stone” between the population of Gaasterland and locations situated on higher grounds in the east of Friesland (Tjongervallei) and Drenthe.

The continuous growth in the core population of the Noord-Brabant-Maasvallei makes it most likely that a merger will take place with neighbouring core populations: Noord-Brabant-Meierij, Peel and Midden-Limburg.

Development towards a continuous distribution

The developments in Friesland, Drenthe and Overijssel indicate a possible connection with the large population Gelderland-Veluwe in the future. This is expected in particular because of the presence of suitable habitats in all directions of the splinter populations in the area is in-between (with exception of St. Nicolaasga and Gaasterland).

The objective of the badger protection plan concerning the merger of subpopulations into one continuous distribution is most achieved in Noord-Brabant-Maasvallei and in the province of Limburg. Here two of the three largest populations are growing at a considerable rate. Western Noord-Brabant and the south border of eastern Noord-Brabant however, remained vacant. An explanation for the breach between Midden-Limburg and Zuid-Limburg lies in the small quantity of suitable habitats between these re-



Figure 6. Distribution of newly occupied square kilometres ($n=257$) in the Netherlands in 2001.

gions. The distance to be bridged has increased in the period 1980-2001. This gap at least could be diminished in the future to its former size.

Continuity of occupation

Reoccupied 1-km squares

The largest share of the reoccupied 1-km squares is identified for 1-km squares that are occupied for the first time in 1990. For this age-category the expired time is still relatively short. Because of this, one can consider the chances of reoccupation to be relatively high. Even if the duration of these reoccupations is an open question, the number of reoccupations of already lon-

ger (1960-1980) vacated 1-km squares is considerable: 39%. Reoccupation coincides often with specific protection measures or changes in land use or area management. When evaluating the badger protection plan in the future this category of 1-km squares deserves special attention, because they can shed light on factors that determine the restoration of a badger population.

Continuous 1-km squares

The term 'continuous' should be handled with care. For this research only the data from the years of survey are considered, i.e. the data are not annual. Therefore, in some years between surveys 1-km squares may have been unoccupied

and still be categorized as continuous. It also has to be noted that continuous occupation does not exclude a change of the actual location of habitation within the 1-km square. The used data therefore always gives us no more than the overall line of the occupation of 1-km squares by the badger. Nevertheless the quantity of continuous 1-km squares indicates the size of the stable core in a distribution. For development and maintenance of viable (sub)populations a certain degree of stability of the occupation is of importance. The longer 1-km squares remain continuously occupied the larger their expected importance for reproduction and increase of the population is to be. At least it can be said that the continuity somehow reflects stability in the habitats.

New 1-km squares

The number of new 1-km squares is indicative for the capacity of the badger in the Netherlands to restore under obviously more favourable circumstances. When 27% of the distribution in 2001 exists of newly occupied squares (table 6) this has to be considered as high. Compared with the whole group of ever-occupied 1-km squares since 1960 the percentage is high: 18%. The continuing favourable climate of protection for badgers in the Netherlands seems to manifest itself in a considerable increase in the distribution. This is a consequence of the systematic securing, the restoration and/or opening up of habitats and the compensation of lost habitats in cases of infringements on their integrity. Also, as we have seen, the translocations made a concrete contribution to the increase in distribution. Furthermore, the legal protection of sett locations and the conclusion of agreements for the management of particular badger setts and foraging grounds must be mentioned. Finally, the securing of foraging routes and ecological corridors on innumerable locations (e.g. the construction of 600 badger tunnels at roads and railroads, accompanied by 450 kilometres of fences and 350 km of hedges) have contributed positively to the present distribution; the latter even despite the fact that almost 50% of the technical provisions were found to be not functioning properly. This

was mainly due to a failing construction (Das & Boom 2002a). It can be understood against this background that new impulses from existing badger populations have brought forth new settlements (Das & Boom 2001b).

Another factor that may have contributed to the high number of newly occupied 1-km squares is a change in sett density and/or the number of badgers per inhabited sett location. An increase of the reproduction success and a fall in the mortality among juveniles may be due to moderate climatic circumstances in the previous years. In the period 1990-2001, a strikingly high number of warm and wet winters and warm springs, characterised by predominantly south-western winds, has occurred (KNMI 2002). These conditions may have raised the food supply, particularly earthworms (*Lumbricus terrestris*), in the period that the cubs are suckled (Macdonald & Newman 2002). It must be noted that an increase in density eventually only results in an increase of distribution if the badger enjoys sufficient acceptance and protection in its newly occupied habitats. A systematic study into changes in densities on setts has not taken place in the Netherlands.

Alternate 1-km squares

Within the distribution for 2001 an increase in alternate 1-km squares has been determined. The number of 1-km squares in this category that are occupied for the first time in 1960 is considerably higher than the numbers from later years of survey. A high number of such 1-km squares is found in Zuid-Limburg. This region knows a continuity of occupation above the average. It is probable that the (re)occupation of these 1-km squares here will have a more permanent character. The same applies to Noord-Brabant-Maasvallei. In Gelderland-Veluwe, however, this does not apply; here the continuity of occupation is low and decreases even more and more.

1-km squares vacant after first occupation

Several causes explain the occupation of a 1-km square in just one year of survey. Planning developments may play a role, e.g. in the form of

house or road construction or large-scale changes in land use. 1-km squares vacant after first occupation do not in all cases concern habitats entirely destroyed. Partly the number within this category gives an impression of the number of 1-km squares that possibly qualifies for reoccupation. In 2001, the number of reoccupied 1-km squares is (still) only a fraction of the number of 1-km squares vacant after first occupation (figure 5). In the long term (1960-1995), almost a quarter of all 1-km squares that have been occupied became vacant after first occupation. Particularly the regions that have at present a low occupation rate show high numbers of 1-km squares that became vacant after first occupation. In this respect, a high number of 1-km squares vacant after first occupation in a certain area may be a reference to the potential of that area.

Abandoned 1-km squares

A partial explanation for the high number of abandoned 1-km squares in Gelderland-Veluwe is provided by the reduction or total stop in the supplemental feeding of ungulates in the area. Because of this reduction badgers must fall back on the natural food available in this relatively poor habitat, mostly conifer forests on sandy soils. This results in the enlargement of home ranges and, consequently, in the lower density of occupied setts. Another possible explanation lies in the increased conversion of agriculture enclaves into nature re-

serves. For example, grazing lands, regularly mowed and grazed or mowed and because of these conditions providing badgers with a regular supply of earthworms, are replaced by under-grazed terrain with coarse grasses and woody plants or scrubs or even woodland. For the badger this means a loss of the better forage areas in the habitat that also leads to an enlargement of the home ranges and a decrease of badger density. This process applies not only to Gelderland-Veluwe, but also to the provinces of Noord-Brabant and Limburg. The effect of the density reducing factors mentioned above is open to further research.

Continuity in wider sense

The frequency of occupation of 1-km squares gives us an impression of the "disorder" or "stress" over a period of time within a certain area. In this respect, in the short term Gelderland-Achterhoek (except the recently established population in Winterswijk) and the Peel score below the national average. In both cases it concerns smaller populations where the amount of suitable habitats is restricted. The isolated positions of these settlements provide some explanation for the history of the distribution in both of these areas. The importance of specific sett protection and, if possible, measures dissolving, mitigating or compensating the isolation altogether, is with this all the bigger. The continuity

Table 10. Number of square kilometres first vacant in 2001 (total and per region) and percentage of total occupation in 1995.

Region	Occupation since				Total	%
	1960	1970	1980	1990		
Friesland		1		1	2	4
Drenthe			1		1	2
Overijssel		1			1	2
Gelderland – RvNijm/LvM&W				2	2	4
Gelderland – Veluwe	3	8	3	14	28	55
Peel				1	1	2
Noord-Brabant – Maasvallei		1	1	1	3	6
Noord-Limburg		1		2	3	6
Midden-Limburg		2		2	4	
Zuid-Limburg	5		1	2	8	16
Total	8	12	8	23	51	100

of occupation still increases in the last decade in Gelderland-Achterhoek. In the Peel-region on the other hand a decrease is noted.

The national average for the continuity of occupation over the period 1960-2001 shows that there are considerable fluctuations in the picture of distribution of the badger in the Netherlands (table 8). Because the research makes use of 1-km squares as a unit of research, these fluctuations may only partly be attributed to the natural behaviour of the badger to change location (temporarily or not) of actual habitation within the home range. Once badgers occupy a suitable habitat, they generally will not leave 'spontaneously'. The fluctuations are mainly to be ascribed on the one hand to an unfavourable proportion between growth and mortality. On the other hand it will be the (high) anthropogenic

pressures on badgers and their habitats.

Translocations

The impact of translocations is most likely more positive as described in the results. The mortality recorded after translocation is minimal. Not in all cases the badgers - although each of them has been released with a tattoo mark - are reported back. The output of translocations has been translated into occupied 1-km squares in 2001. This means that 1-km squares occupied directly due to translocations and remaining so up to 2001 are considered as contributions to the distribution. In a following survey inevitably this obvious output will decrease. This is because 1-km squares occupied with "success" may no longer be occupied partly because of displace-



Figure 7. Occupied 1-km squares in 1995, not occupied in 2000-2001 ($n=143$).

ments. When stipulating the correlation between the translocation of badgers and the occupation of setts (occupation of 1-km squares) only direct (temporal) links are considered. Any spin off in the form of extension of the distribution area by the offspring of released badgers or the attraction of ‘wild’ badgers, leading to extra settlements is disregarded. When including this spin off from translocations, a more positive picture of the translocation output could be drawn.

Disappeared setts and disturbances

Although compared with the period 1990-1995 some improvement can be reported, still a large number of setts disappeared. In this period, 284 setts disappeared (11% of the total of researched setts; 1995-2001: 202). This still means that one on every 12 setts disappears within a period of five years. The number of disappeared setts that were inhabited in the previous year of survey halved in 2001. The number of cases where sett destruction has been recorded also halved when compared with the previous survey. It is expected that the absolute number of disappeared setts is higher, since only 57% of the sett locations are

visited.

The decrease in the number of disturbances is possibly explained by an increase of (social) control in the field by humans and the attention the badger is given in planning procedures. Also, the attention generated by protective and mitigating measures, e.g. the legal protection of sett locations and management agreements, needs mentioning.

Conclusions

The development (nationally and regionally) of the badger distribution in 2000-2001 is positive. The badger distribution increases in the period 1995-2001 with 29%. In the period 1990-1995, the increase was 16%. The number of occupied 1-km squares in 2001 amounts to 948; in 1995 a total of 736 1-km squares were counted. In the period 1995-2001, in the regions of Friesland (36%) and Gelderland-Rijk van Nijmegen/Land van Maas en Waal (29%) the increase is average or more. Below average are the regions of Midden-Limburg (21%) and Zuid-Limburg (18%). A standstill has been determined for the Reestdal

Table 11. Translocation sites: location, number, ownership, period, number of translocated badgers, deceased badgers reported back and number of square kilometers occupied due to re-introduction (since 1987). SBB = State Forestry Service; NM = Natuurmonumenten; PL = Provincial Landscapes.

Region	Number		Ownership				Period	Number of Badgers		Contribution in km ²
	SBB	NM	PL	Municipal	Private	Translocated		Deceased		
Friesland	5	3	0	2	0	0	1993-2001	29	13	5
Drenthe	2	0	0	2	0	0	1998	18	2	5
Overijssel	3	1	2	0	0	0	1992-1995	13	12	2
Gelderland – Achterhoek	3	0	0	0	0	3	1997	29	1	6
Gelderland – RvNijm./LvM&W	3	0	0	2	0	1	1987-2000	49	23	7
Noord-Holland/Utrecht	2	0	0	1	0	1	1999	15	4	3
Noord-Brabant – Maasvallei	2	1	0	0	1	0	1992-1999	30	10	2
Noord-Brabant - Meierij	3	0	1	1	0	1	1989-1991	17	1	5
Midden-Limburg	3	3	0	0	0	0	1990-1993	10	1	2
Total	26	8	3	8	1	6	1987-2000	210	67	37

Table 12. Disappeared and disused setts per region in 1995-2001 and setts occupied in 1995.

Region	Disappeared	Disused	Occupied in 1995
Friesland	1	3	0
Drenthe	0	0	0
Overijssel	3	4	4
Gelderland – Achterhoek	3	6	0
Gelderland – RvNijm./LvM&W	12	30	2
Gelderland – Veluwe	5	29	16
Noord-Holland / Utrecht	0	2	0
Peel	0	1	0
Noord-Brabant - Maasvallei	5	19	4
Noord-Brabant Meierij	0	2	0
Noord-Limburg	9	31	1
Midden-Limburg	5	11	3
Zuid-Limburg	14	7	9
Total	57	145	39

population on the border of Drenthe and Overijssel (0%) and Gelderland-Veluwe (1% increase). Also Gelderland-Achterhoek hardly shows any increase, except for the increase to be ascribed to the translocations in this region. The three largest populations of the Netherlands are Gelderland-Veluwe, the Maasvallei and Zuid-Limburg. They account for 84% of the total distribution in 2001. In the period 1995-2001, they end up jointly with an increase above the national average of 29%, i.e. 36%. This, however, can be explained entirely by the increase in the distribution area in the Noord-Brabant-Maasvallei. In the previous period (1990-1995) the increase (12%) in distribution area has been below the national average for that period. In that period, only Zuid-Limburg has shown a growth in distribution that is above average.

The relation between the badger distribution in 2001 and the suitable habitats available has become more favourable, but is certainly not optimal. Of the research area (approximately 25,000 km²) 15% was found to be suitable for the badger. In 2001, the badger occupies 25% of the available suitable habitats. The occupation rate of suitable habitats in the north and east of the Netherlands (8%) is considerably lower than the occupation rate in the middle and south (37%) of the country.

The development of the different settlement

types for the larger populations is positive. The increase in the period 1995-2001 of the area covered by core populations ($n=11$) amounts to 30%. The largest populations are Gelderland-Veluwe, Maasvallei and Zuid-Limburg. The area covered by splinter populations ($n=9$) increases in this period with 48%. The area covered by dispersed populations ($n=25$) decreases in this period with 17%.

In the last 20 years the core populations are merging. In the period 1980-2001, the average distance between core populations decreases with 25% (from 28 to 21 km). In particular, south of the main rivers the distance between core populations has decreased (42%).

The continuity of occupation increases. Since 1960 occupation is determined in 1,402 1-km squares. 73% of these are also occupied in the next year of survey, whereas 253 1-km squares are vacant after first occupation. In 2001 (based on the figures of 1960-1990), 513 1-km squares are continuously occupied, this is 54% of the total distribution. Continuous occupation taking 1960 as the first year of occupation occurs in 115 1-km squares (12%). New in 2001 are 257 1-km squares (27%). The remaining 178 1-km squares (19%) are more than once occupied, but not continuously. The continuity of occupation (in the wider sense) increases from 70% (1990-1995) to 82% (1995-2001).

Figure 8. Translocation sites since 1987.



Translocations contribute to the national distribution. In the period 1987-2001, 210 badgers are translocated from enclosed release sites. Translocations took place in 26 translocation sites in seven provinces. Sooner or later after release around a third of the badgers is reported dead. The contribution of translocation activities amounted to at least 37 1-km squares: this was 4% of the national distribution in 2001.

On Dutch territory 4,400 badger setts were recorded since 1960. During the survey more than 2,500 locations (57%) were visited. In total, 202 research locations in the period 1995-2001

disappeared: this is 8% of the total of sett locations examined. 20% of these disappeared setts were inhabited in 1995. The number of destroyed sett locations decreased by 39% compared with the period 1990-1995.

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Samenvatting

Verspreiding van de das (*Meles meles* L.) in Nederland, periode 1995-2001

In 2000-2001 is een landelijk verspreidingsonderzoek aan de das (*Meles meles*) verricht. Dit onderzoek zou bijdragen aan de tussentijdse evaluatie van het dassenbeheersbeleid van het ministerie van Landbouw, Natuurbeheer en Voedselkwaliteit (LNV). Daarbij richtte het zich op de verspreiding van geschikt leefgebied, bezettingsgraad en continuïteit in bezetting en uitzetacties.

Bovendien werden - buiten de directe verspreidingsdoelen van het beschermingsplan - het verdwijnen van burchtlocaties en de verstoring van dassenburchten tot onderwerp van het onderzoek gemaakt. Behalve met het verspreidingsonderzoek uit 1995 werden de ontwikkelingen in de verspreiding ook vergeleken met burchtonderzoeken uit 1960, 1970, 1980 en 1990. Het onderzoek is vooral gebaseerd op veldwerk. Per kilometerhok (= 1 km²) werd vastgesteld of er sprake was van bezetting door de das, dat wil zeggen, aan de hand van bewoningssporen op en bij dassenburchten.

In eerder onderzoek naar het leefgebied van de das (1995) werd 15% van het onderzoeksgebied (circa 25.000 km²) als geschikt voor de das aangemerkt. In 2001 was 25% van dit potentiële leefgebied door de das bezet. De bezettingsgraad in het noorden en oosten van Nederland (8%) bleek beduidend lager dan die van het midden en zuiden (37%). De toename in de verspreiding sinds 1990 was echter voor het noorden en oosten ruim twee keer zo groot als die in het midden en zuiden van het land, respectievelijk 96% en 44%.

Op Nederlands grondgebied zijn vanaf 1960 circa 4.400 burchtlocaties vastgesteld. Hiervan zijn in 2000-2001 ruim 2.500 locaties (57%) bezocht, waarbij 44% van de locaties bewoond bleek te zijn. Het aantal bezette kilometerhokken in 2000-2001 bedroeg 948; een toename van 29% ten opzichte van 1995 (736 bezette kilometerhokken). De groei in de periode 1995-2001 van de kernpopulaties ($n=11$ in 2001) bedroeg 30%. De splinterpopulaties ($n=9$ in 2001) namen in oppervlak met 48% toe. De verspreide vestigingen ($n=25$ in 2001) namen in deze periode 17% in oppervlak af. De gemiddelde afstand tussen kernpopulaties die vanaf 1980 bestaan, nam in de periode 1980-2001 af met 25% (van 28 naar 21 km).

De regionale groei in de periode 1995-2001 bedroeg in Friesland 36%, het Rijk van Nijmegen/Land van Maas en Waal 29%, en Midden-Limburg 27%. Onder het gemiddelde bleef Zuid-Limburg (18%). Nauwelijks tot geen groei werd

vastgesteld in het Reestdal en op de Veluwe (1% groei). Ook in de Achterhoek was nauwelijks sprake van groei, behalve dan door uitzetacties.

De continuïteit in de dassenverspreiding op kilometerhokschaal nam toe. Vanaf 1960 waren 1.880 (73%) bezette kilometerhokken ook in het daaropvolgende peiljaar bezet. Vanaf 1960 werd bewoning door de das in 1.402 kilometerhokken vastgesteld. Hiervan waren 257 kilometerhokken voor het eerst bezet in 2001. Vanaf 1960 waren 253 kilometerhokken slechts één keer bezet. In 115 kilometerhokken was sprake van continue bewoning sinds 1960. De resterende 892 kilometerhokken waren meer dan eens bezet, maar niet continu.

Van de totale verspreiding in 2001 is 84% geconcentreerd in drie grote populaties (Veluwe, Zuid-Limburg en de Maasvallei). Deze populaties kwamen met een gezamenlijke groei in de verspreiding van 36% in de periode 1995-2001, boven het landelijk gemiddelde uit. Dit was geheel te verklaren uit de toename van het verspreidingsgebied in de Maasvallei. In de periode daarvoor, 1990-1995, lag de groei in deze gebieden nog onder het landelijk gemiddelde (respectievelijk 12% en 16%). Toen concentreerde de groei zich met name in Zuid-Limburg.

In de periode 1987-2001 zijn 210 dassen uitgezet. Dit gebeurde op 26 uitzetlocaties in zeven provincies. Bijna een derde van de dassen is na uitzetting dood teruggemeld. Het aandeel van herintroductie- en uitzetactiviteiten vanaf 1987 in het landelijke verspreidingsbeeld bedroeg minstens 37 kilometerhokken: 4% van de landelijke verspreiding anno 2001.

In de periode 1995-2001 verdwenen 202 burchtlocaties: 8% van het totaal aan onderzochte burchtlocaties. Hiervan was in 1995 20% door dassen nog bewoond (39 burchten). Het aantal vernietigde burchtlocaties (94) daalde in vergelijking met de periode 1990-1995 met 39%.

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Home range of the badger (*Meles meles*) in a heterogeneous landscape in Denmark

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Abstract: Spatial organisation of badgers (*Meles meles* L. 1758) in a heterogeneous landscape in Denmark was studied during 1997-1999. The landscape was dominated by intensively managed agricultural and forest areas, traversed by streams surrounded with bogs and meadows. Seven habitat types were characterised according to land use and vegetation. Home range size estimated by radio-telemetry varied between 2.96 km² and 3.94 km² (100% minimum convex polygons). Individuals from a social group had similar home ranges (95% overlap), whereas home ranges of individuals from neighbouring social groups had little overlap (1-2%). Travelling distances up to 6.9 km per night were observed. Males had larger activity centres than females. Individual habitat selection differed considerably. Most badgers avoided agricultural areas and villages, but no habitat types were preferred or avoided by all individuals. Large home range sizes and long nocturnal travelling distances compared to other temperate regions in Europe indicate that heterogeneous Danish landscapes provide few stable food patches for badgers. We suggest that the natural seasonal and spatial variability of food resources is amplified in areas dominated by managed forests and large-scale arable lands resulting in low population densities of badgers in Denmark.

Keywords: badger, *Meles meles*, home range, space use, habitat use.

Introduction

Badgers (*Meles meles*) live in social groups occupying a common sett and territory (Kruuk 1989). Several studies have illustrated the badgers' ability to accommodate their spatial organisation to environmental conditions, habitat variability and human landuse throughout the geographic range (e.g. Cheeseman et al. 1981, Kruuk & Parish 1987, Nolet & Killingley 1987, Brøseth et al. 1997, Feore & Montgomery 1999, Revilla & Palomares 2002). The flexible spatial organization and ecology results in considerable variations in badger densities (0.12-38 individuals per km²), social group sizes (2 to >20), and territoriality (0.2-25.5 km²) (Johnson et al. 2002, Kowalczyk et al. 2003).

The resource dispersion hypothesis (RDH) is currently the most widely acknowledged expla-

nation for the social group living of badgers (Kruuk & Macdonald 1985, Kruuk 1989). The RDH proposes a set of conditions that permit group formation. The RDH hypothesizes that a patchy, unpredictable but abundant dispersion of food resources determines territory sizes of social groups and that richness of the food patches determines social group size. The social organisation reverts to the general spacing pattern of solitary individuals when the population is under food stress or the population is based on non-patchily distributed food resources (Kruuk & Parish 1987, Revilla & Palomares 2002).

Badgers are usually associated with mosaic landscapes comprising deciduous forests and permanent pastures in northwestern Europe (Neal & Cheeseman 1996). Particularly in the British Isles badgers may occupy small territories and attain high densities, whereas territories are larger and densities are considerably lower in

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forest dwelling populations in Eastern Europe and scrublands in Spain (Johnson et al. 2002, Revilla & Palomares 2002, Kowalczyk et al. 2003). In highly managed landscapes habitat deterioration may restrict badgers to small patches fragmented by large matrixes of sub-optimal agricultural areas reducing abundance and survival of badger populations (Virgós 2001).

The objectives for the present study were to examine home range size and habitat use of badgers in a characteristic, managed heterogeneous landscape in Denmark. No detailed studies on spatial organisation of badgers in Denmark have been published. The study was part of a larger investigation on the ecology of badgers in Denmark (Pertoldi et al. 2000, Pertoldi et al. 2001, Madsen et al. 2002, Pertoldi et al. 2003, Pertoldi et al., in press, Prang et al., in prep.).

Materials and methods

Study Area

The study was performed in eastern Jutland in Denmark (56°27'N, 09°47'E) (figure 1). Mean annual temperature was 8.2°C and mean annual precipitation was 783 mm in the study period (Danmarks Meteorologisk Institut 2004). The mean daily temperature varied between -1.3°C in January and 16.6°C in August. The study area is a mosaic landscape comprising intensively managed agricultural lands and forest areas traversed by streams surrounded by large bogs and meadows. Land cover data were based on a national mapping (Areal Information System, Nielsen et al. 2000). To analyse habitat selection the landscape was categorised in seven biotopes

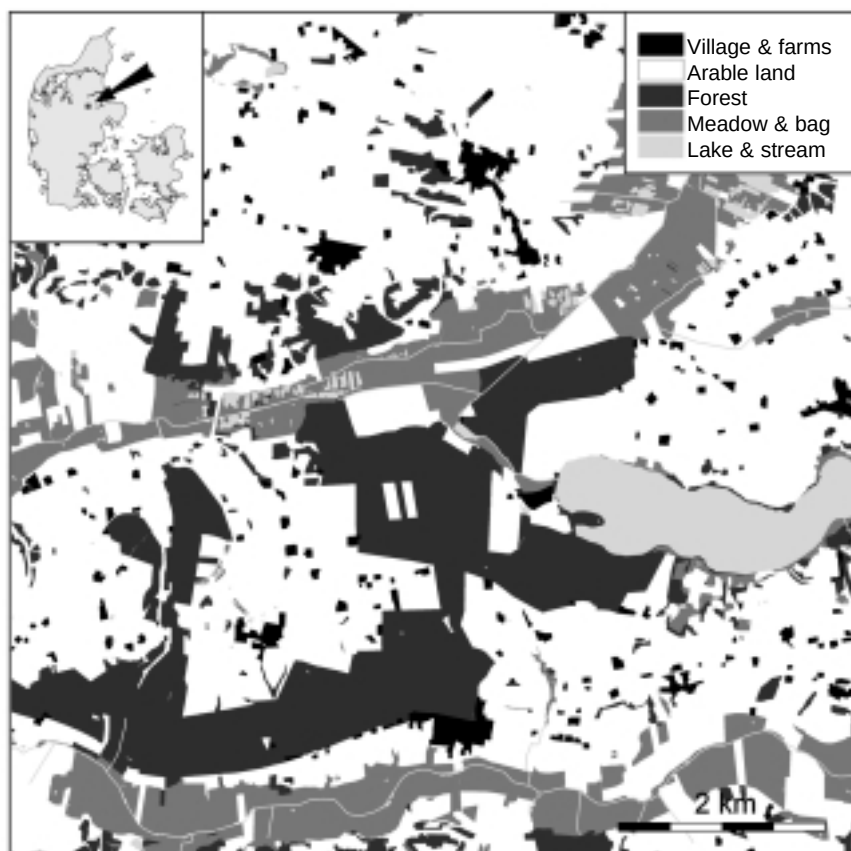


Figure 1. The study area in eastern Jutland in Denmark. The habitat types deciduous forest, coniferous forest and scrubs have been combined for clarity.

according to land use and vegetation: agricultural, coniferous forests, deciduous forests, scrubs, meadows, bogs, and villages and farm buildings. Coniferous forests were dominated by dense stands of Norway spruce (*Picea abies*) with no herb vegetation on the forest floor. Deciduous forests comprised mainly mono-aged beech (*Fagus sylvatica*) stands and minor stands of oak (*Quercus* sp.) and ash (*Fraxinus excelsior*). Old deciduous forests had herb vegetation and undergrowth. Vegetation in scrubs consisted of grassland with trees and bushes. Willow (*Salix* sp.), alder (*Alnus glutinosa*), and birch (*Betula* sp.) dominated the vegetation in the bogs. Meadows were characterised by rich mixed herb vegetation.

Study animals and radio telemetry

Badgers were caught in box traps placed near eight main setts. Trapping was performed in September 1997 and in spring and summer 1998 and 1999. The captured badgers were immobilised with an intramuscular injection of medetomidine (0.12 mg/kg) and ketamine (6 mg/kg) and marked subcutaneous with a microchip. Age was estimated from body weight and tooth wear. Reproductive status of females was recorded. A total of 22 badgers was caught (including twelve cubs). Eight adult and two subadult badgers were fitted with radio-collars (Televilt, Ramsberg, Sweden) (table 1). The bad-

gers were located by triangulation using a handheld antenna. Discontinuous radio-tracking (Harris et al. 1990) was conducted from September 1997 to December 1999. The majority of radio-tracking was conducted during 8-hour sessions over four consecutive nights during spring (March-May) and summer (June-August) in 1998 and 1999. It was attempted to locate each individual badger once an hour throughout the tracking sessions. Total distances travelled by individual badgers were estimated when more than three radio-locations were obtained during an activity period and diurnal resting sites were known.

Home range estimates and habitat use

Spatial analyses were performed in an ArcView GIS environment (Environmental System Research Institute Inc., Redlands, California, USA). Home ranges were calculated using the ArcView extension programme Animal Movement (Hooze & Eichenlaub 1997). Home ranges were estimated as 100% minimum convex polygons (MCP) (Mohr 1947). The MCP home range estimate facilitates comparison with bait-marking studies and it has no assumption about the statistical distribution of observations (Harris et al. 1990). The MCP index is strongly affected by sample size and requires large sample sizes to reach an asymptote (Ford & Myers 1981). In the present study more than 50 radio-locations were

Table 1. Sample periods of radio-collared badgers. M = males, F = females. M2 lost its collar in 1998, but was trapped again in the following spring.

ID	Age	Date of capture	Radio-tracking period	Cause of termination
M1	Adult	September 1997	3 months	Transmitter lost
M2	Adult	March 1998	3 months	Transmitter lost
		February 1999	3 months	Transmitter lost
M3	Adult	March 1998	3 months	Transmitter lost
M4	Adult	March 1998	18 months	
M5	Adult	March 1998	2 months	Transmitter lost
M6	Adult	March 1998	17 months	Traffic killed
F1	Subadult	April 1998	19 months	Traffic killed
M7	Adult	February 1999	3 months	Transmitter lost
F2	Subadult	April 1999	7 days	Transmitter failure
F3	Adult	June 1999	6 months	

required to obtain asymptotic MCP home range sizes. Overlap between home ranges was calculated as percentage overlap between individuals' MCP. Activity centres were derived as fixed kernel home range estimates (Seaman & Powell 1996). The study area was defined as the minimum convex polygon encompassing all radio-locations and a surrounding 3 km buffer zone. Availabilities of the different habitat types described above were determined as the proportions of the habitats in the study area and in the MCP home ranges of individual badgers. Likewise, for each badger the proportion of radio-locations within each habitat type was calculated. Two methods were used to analyse the habitat utilisation on the same data: the compositional analysis (Aebischer et al. 1993) and the method described by Neu et al. (1974). The two methods have different scope of analysis and different shortcomings affecting the validity of the analysis, often at the statistical level. The problems are discussed below.

Results

A total of 1044 radio-locations were collected. Home range sizes and habitat use were estimated from 577 radio-locations of active badgers. Radio-locations of M4 from the second year were excluded from home range size and habitat use analyses as frequent trappings of M4 (occasion-

ally twice a night) confounded their validity. Based on trapping record and observations the maximum size of social groups was four and two cubs.

Individual home ranges varied between 2.96 km² and 3.94 km² (table 2). Individuals from the same social group (M6 and F1) had a 95% overlap of the home ranges (figure 2). M1 also belonged to this social group. All locations of M1 were within the home ranges of M6 and F1. Insufficient numbers of radio-locations were obtained to estimate M5's and M7's individual range. They were trapped at the same main sett and had 85% overlap of ranges. The home range of their social group was estimated to 4.23 km² by combining the radio-locations of M5 and M7.

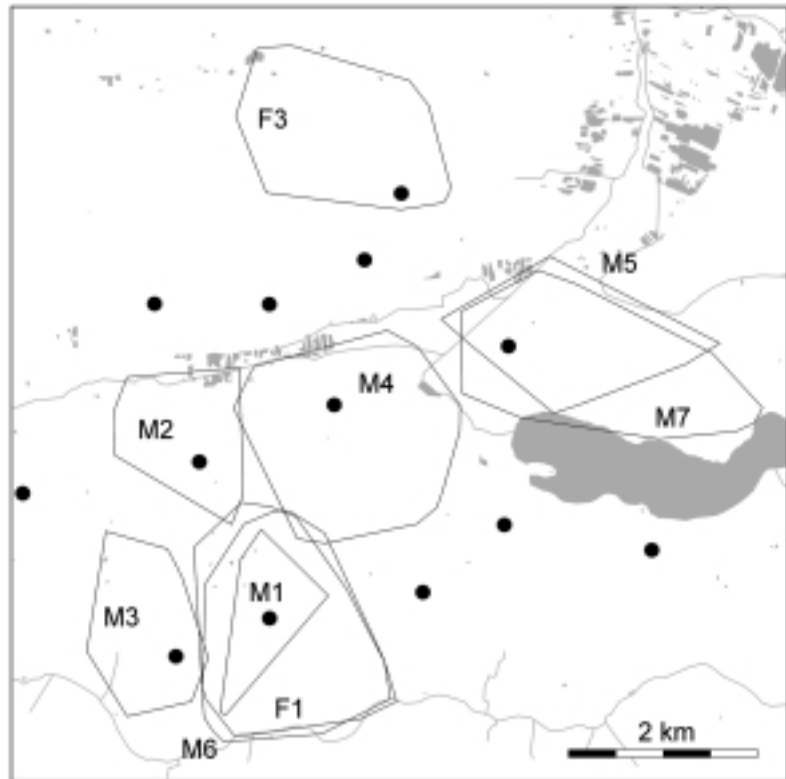
Home range overlap between neighbouring social groups was 1-2%. Home ranges of social groups were stable between years. A bait-marking study performed in the year prior to the radio-tracking (Madsen 1999) identified territory boundaries similar to home ranges of M6 and F1 as determined by radio-tracking. An adult female trapped at their main sett was radio-tracked in 1992 (Taastrøm 1993). Its home range overlapped with 97% of the present range of the social group. Combining results from radio-tracking and bait-marking studies the home ranges of M2's and M3's social groups were respectively 2.39 km² and 2.29 km².

Mean total distance travelled by individual badgers was 3.42 ± 1.44 km (range 1.67-6.90

Table 2. Home range sizes (km²) estimated as 100% minimum convex polygons (MCP) and fixed kernel isolines. Kernel estimates are 95% (K95), 90% (K90), 75% (K75), and 50% (K50) isolines. The analyses of M4 were based exclusively on the radio-locations from 1998. *Home range estimates only indicative figures as numbers of radio-locations were insufficient.

ID	Active radio-locations	MCP	K95	K90	K75	K50
M1	23	1.04*				
M2	48	1.62*				
M3	29	1.77*				
M4	74	3.94	5.03	4.02	2.32	0.59
M5	31	2.55*				
M6	109	3.84	5.00	4.33	2.34	0.54
F1	139	3.54	4.02	3.11	1.47	0.43
M7	29	3.69*				
F2	3	—				
F3	95	2.96	1.61	0.95	0.23	0.11

Figure 2. Home ranges (100% minimum convex polygons) of badgers and dispersion of active main setts. Figure frame as in figure 1. Grey areas indicate lakes and streams.



km) ($n=30$). No difference was detected between nocturnal travelling distances of males and females ($t=1.08$, $df=28$, N.S.). Activity periods up to 8 hours per night were observed. The area covered by males on single nights (MCP) tended to be larger than areas covered by females (males: $n=12$, mean 0.95 ± 0.73 km², range 0.14–2.08 km²; females: $n=18$, mean 0.56 ± 0.46 km², range 0.09–1.93 km²; $t=1.78$, $df=28$, $P=0.09$). Males covered larger areas per night than females during the summer season (June–August) (males: $n=7$, mean 1.15 ± 0.66 km², range 0.14–1.89 km²; females: $n=15$, mean 0.60 ± 0.48 km², range 0.09–1.93 km²; $t=2.23$, $df=20$, $P<0.05$). Up to 65% of the total individual home range (MCP) was covered during a single night. Estimated from fixed kernel isolines males had larger activity centres than females (table 2).

The compositional analysis revealed that the radio-tagged badger population used the available area randomly (table 3), i.e. no habitat type

was preferred or avoided by all individuals (study area: $\lambda=0.0751$, N.S.; MCP area: $\lambda=0.0675$, N.S.).

Analysis as described by Neu et al. (1974) showed that the habitat use of badgers was significantly different from habitat availability ($\chi^2=453.97$, $df=54$, $P<0.001$). Large variability of individual habitat selection caused the high χ^2 -value and no habitat type could be characterised as key habitat for all individuals. However, most individuals avoided agricultural areas and villages, and preferred deciduous forests. Habitat use within individual home ranges varied. Habitat availability within M6's and F1's individual home ranges was similar ($\chi^2=0.61$, $df=6$, N.S.) but while F1 used habitats as available in its home range ($\chi^2=4.76$, $df=6$, N.S.), M6 tended to avoid agricultural areas ($\chi^2=23.18$, $df=6$, $P<0.001$). M4 used habitats as available within its home range ($\chi^2=10.90$, $df=6$, N.S.). F3 had very high percentage of agricultural lands in its home

Table 3. Percentage of habitat availability and habitat use by badgers in a heterogeneous landscape in Denmark.

Habitat type	Habitat availability	Overall habitat use	
		Mean $\pm$ S.D.	Min.-max.
Agricultural	66.65	46.51 $\pm$ 15.94	27.59-72.41
Coniferous	8.02	13.80 $\pm$ 10.15	0.00-31.03
Meadows	6.70	4.73 $\pm$ 4.17	0.00-12.90
Bogs	6.24	7.49 $\pm$ 5.31	0.00-13.79
Deciduous	6.10	20.84 $\pm$ 11.40	0.00-37.93
Urban	4.75	2.06 $\pm$ 3.29	0.00-8.70
Scrubs	1.54	4.57 $\pm$ 3.55	0.00-8.70

range (86%) and showed a strong preference for deciduous forest ($\chi^2=153.47$, $df=5$, $P<0.001$).

Discussion

Spatial organisation of badger populations across Europe correlates with environmental variables as determined by annual differences between maximum and minimum temperatures (Johnson et al. 2002). Furthermore, territory size is determined by the spatial dispersion and availability of earthworms, the principal food for badgers in most European populations (Kruuk 1989, Neal & Cheeseman 1996, Kowalczyk et al. 2003). Home ranges of badgers in Denmark were larger than observed in other populations in the temperate region of Europe (Cheeseman et al. 1981, Kruuk & Parish 1987, Nolet & Killingley 1987, Herrmann et al. 1997). Home range sizes in Denmark were comparable to more harsh environments dominated by poor conifer forests in Norway, unimproved grasslands in Ire-

land, and scrublands in Spain (table 4) (Brøseth et al. 1997, Feore & Montgomery 1999, Revilla & Palomares 2002).

Travelling distances of badgers in Denmark were longer than reported in high-density populations in England (Neal & Cheeseman1996) but comparable to travelling distances measured in low-density populations in Spain (Revilla & Palomares 2002). Length of travelling distances and foraging trips increases with reduced availability of food resources (Kruuk 1989). Adult males travel longer distances, spend more time along territory boundaries and visit boundary latrines more than subadult males and females (Roper et al. 1993, Neal & Cheeseman 1996, Revilla & Palomares 2002). In the present study we did not detect such differences between males and females probably because of small sample size. However, males had larger activity centres and covered larger areas during a single activity period compared to females. Parental care may have influenced the size of activity centres and habitat utilisation of the females. F1 was a non-

Table 4. Data on density and territory size in badger populations in Europe (means or min.-max.).

Country	Territory size (km ²)	Density (ind./km ²)	Reference
England, Gloucestershire (mean)	0.22	28.53	Cheeseman et al. 1981
England, Wytham Woods (mean)	0.60	17.35	Johnson et al. 2002
Germany	0.60-1.10	1.9-2.9	Herrmann et al. 1997
Ireland, Castleward	0.50	11.90	Feore & Montgomery 1999
Ireland, Katesbridge	1.27	1.60	Feore & Montgomery 1999
Ireland, Glenwhirry	3.45	0.86	Feore & Montgomery 1999
Norway	5.4	–	Brøseth et al. 1997
Poland, Białowieza	12.8	0.15-0.21	Kowalczyk et al. 2003
Scotland, Aviemore	1.21	2.2	Kruuk & Parish 1987
Spain, Doñana NP	4.12	0.2-1.0	Revilla & Palomares 2002
The Netherlands	0.78	3.8-6.0	Nolet & Killingley 1987

breeding female when it was trapped. It was observed at a sett with a cub and may have functioned as a helper in the first year of the study. Its diurnal resting pattern during the second year and observations of cubs suggests that F1 had cubs (van Teeffelen et al. 2001). F3 was emaciated and had recently lactated when it was trapped in June. Four cubs were later trapped at the same sett.

The study area was centred in a forest area and trappings were conducted at setts in the forest area. Although densities of setts in areas dominated by agricultural lands are probably lower than in forest, the home ranges located in areas dominated by agricultural lands were not larger than home ranges with substantial forest areas. The absence of common habitat preferences for all individuals suggests that the badgers exploited food resources occurring in all the different habitats.

Earthworms (*Lumbricus* sp.) are the principle food item for badgers, but cereals and small mammals have a higher importance in Denmark (Madsen et al. 2002) than recorded in other food studies of badger populations in the temperate region of Europe (Kruuk 1989, Neal & Cheeseman 1996). Permanent pastures and deciduous forests are important for badgers as these habitats may house large populations of earthworms (Hofer 1988, Brøseth et al. 1997). A small study indicated that earthworm biomasses were low in our study area (401 kg/ha in pastures, 21 kg/ha in deciduous woodlands) (Madsen 1999). Earthworm biomasses in pastures and deciduous woodlands in high-density badger areas in England (Wytham Woods) were estimated to 971 kg/ha and 837 kg/ha, respectively (Hofer 1988). Only a few small patches were managed as permanent pastures in the study area. Most grass fields were intensively managed monocultures for ensilage production included in crop rotation schemes. As earthworms are long-living species, these grass fields may hold relatively small biomasses of earthworm. Furthermore, these grass fields may have minor importance to badgers as feeding patches as periods with low grass, which makes earthworms accessible for badgers, are

short (Kruuk 1989). A small proportion of the meadows in the study area were grazed by cows (*Bos taurus*) or sheep (*Ovis aries*) but since meadows were often flooded during winter, they were an unfavourable habitat for earthworms.

The analysis of habitat utilisation by animals is a complex subject at the limit of the current methodology. The methods, which are commonly used or recommended, have their advantages and disadvantages, but no method is suitable for all studies (Neu et al. 1974, Alldredge & Ratti 1986, White & Garrot 1990, Aebischer et al. 1993). The compositional analysis focuses on habitat utilisation of the whole population with the number of animals as the sample size (Aebischer et al. 1993). This approach means that pooling data across animals is justifiable only if they do not differ, but all show the same preference/avoidance. This assumption is not fulfilled in the present study, as the animals showed individual variation in behaviour. In contrast to this the Neu-method uses Bonferroni confidence intervals, which make it possible to analyse the habitat utilisation of the individuals, where the tested variable are formed by the the radio-locations. However, the Neu-method uses the assumption that each individual observation has to be statistical independent. This assumption can be violated in several occasions in the present study. The positions of sequentially collected radio-locations from a tagged animal may be serially correlated and areas may be unavailable to an animal, as it may be constrained by the presence of other animals. The second assumption is probably not fulfilled in the present study as some of the individuals originate from the same sett. Furthermore, the activity of an animal is probably also affected by animals from neighbouring setts. We attempted to reduce this interaction by defining the minimum convex polygon as the area available to the animals.

The dispersion of habitat patches containing the important food resources determines territory sizes of badgers (Kruuk 1989). In accordance with the resource dispersion hypothesis, badgers may be characterised as a contractor species in high population density areas with relatively sta-

ble food resources (Kruuk & Macdonald 1985). We need a more comprehensive assessment of the spatial distribution of the food resources and social group size to make accurate classifications of habitat qualities and evaluate the RDH for badgers in Denmark. However, despite a small sample size and methodological limitations in the present study, the large home range sizes and long travelling distances per night suggest that the heterogeneous landscape in Denmark with intensively managed arable lands and managed forests provide relatively few food patches for badgers. We suggest that the larger seasonal and spatial variability of food resources in intensively managed landscapes results in larger home ranges and lower population densities of badgers in Denmark compared to other populations in temperate regions of Europe.

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Samenvatting

Homerange van de das (*Meles meles*) in een heterogeen landschap in Denemarken

Het ruimtelijk gedrag van de das (*Meles meles* L. 1758) werd onderzocht in een heterogeen landschap in Denemarken in de periode 1997-1999. Het studiegebied werd gedomineerd door intensieve landbouw en productiebos, en doorsneden door watergangen, veengebied en graslanden. Ten behoeve van dit onderzoek werden in het landschap, naar beheer en begroeiing, zeven habitat-typen onderscheiden.

Posities van de dieren werden bepaald met behulp van radio-telemetrie. De groottes van de hiermee geschatte homeranges varieerden tussen 2,96 km² en 3,94 km² (100% minimum convex polygons).

Dieren van een sociale groep deelden hun homerange (gemiddeld 95% overlap tussen homeranges), terwijl homeranges van dieren uit naburige groepen weinig overlap hadden (gemiddeld 1-2%). Verplaatsingen tot 6,9 km per nacht werden waargenomen, waarbij mannelijke dieren

grotere activiteitscentra hadden dan vrouwen. Habitatvoorkeuren verschilden aanzienlijk tussen individuele dieren. De meeste dassen vermeden landbouwgebied en dorpen, maar geen enkel habitat-type werd gemeden of geprefereerd door alle individuen.

Vergeleken met studies in andere gebieden in Europa waren in dit studiegebied homeranges groter en nachtelijke trektochten langer. Dit lijkt erop te wijzen dat het heterogene Deen-

se landschap de das weinig stabiele foerageerlocaties biedt. We stellen voor dat de natuurlijke variatie in ruimte en tijd van voedselbronnen groter is in gebieden met veel productiebossen en grootschalige landbouw, met als gevolg grote homeranges en een lage populatiedichtheid.

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Habitat selection by female otters with small cubs in freshwater habitats in northeast Spain

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Abstract: Otters (*Lutra lutra*) are found in aquatic environments. This study, however, found differences in the use and importance of patches at different moments of the otter life cycle. We studied five natal dens and 38 rearing sectors of small otter cubs in Mediterranean freshwater habitats of southwestern Europe. The results show a strong relationship between the presence of such rearing sectors and the availability of food and the presence of complex dens. Females with small cubs selected the deepest and widest stretches, with more ponds and calm waters, a greater abundance of food and a greater availability of potential and used dens. Some of the rearing sectors were used for generations. Our results highlight the importance of certain stretches for the breeding of the otter. Conservation of these areas should be a basic tool in the management of species such as the otter.

Keywords: otter, *Lutra lutra*, cubs, breeding, habitat, conservation.

Introduction

The otter (*Lutra lutra*) disappeared from much of its European range during the 20th century (Mason & Macdonald 1986, Macdonald & Mason 1994). Habitat destruction was mentioned as a cause of this and, it became recognised that the otter was sensitive to habitat changes and provided an indicator of habitat quality (Jenkins 1980, Mason & Macdonald 1986, Lunnon & Reynolds 1991, Prauser & Röchert 1991). A general point of view emerged that the species needs natural riverbanks, well-developed and structured vegetation, and unpolluted water. However, otters living in marine environments in northern Europe, or in semiarid or Mediterranean environments of Spain or northern Africa, permanently stay in places where vegetation or water is very scarce or non-existent, in reservoirs or man-made irrigation channels, in urban areas, and even close to industrial complexes (Mason & Macdonald 1986, Kruuk 1995, Strachan & Jefferies 1996, Kruuk et al. 1998, Ruiz-Olmo & Delibes 1998, Kranz & Toman

2000). So, otters can be found living in any type of aquatic environment, whether marine or freshwater, natural, man-made or altered, especially when population saturation occurs.

However, several studies have shown that some places are only used by otters to move between stretches of river and other patches are used more intensively (Kruuk 1995, Ruiz-Olmo et al., in press). To a certain degree, otters show habitat preferences, for example with respect to food abundance, potential resting sites or safe conditions (Kruuk et al. 1990, Kruuk 1995, Ruiz-Olmo 1995a, López-Martín et al. 1997, Kruuk et al. 1998, Ruiz-Olmo 2001b, Madsen & Prang 2001, Ruiz-Olmo et al., in press), but some of these preferences do not totally coincide with certain habitat features traditionally thought to influence otter movements and preferences, such as vegetation cover or disturbance (see also Durbin 1998). Furthermore, not all places where indirect otter signs are found are equally important. Fretwell (1972) discusses habitat quality, defined in terms of the fitness that a habitat confers on its occupants, and this can vary according to species, sex, age, and time.

Today, an approach based merely on the *habitat* of the otter (considered as a *distribution* concept), can contribute very little to further know-

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ledge of this issue, just as the idea of legally protecting or managing every where that otter tracks or spraints are found hardly appears to be practical. More focused conservation techniques could focus on the specific needs that this carnivore species has at certain times in its biological cycle, especially during breeding, feeding, and resting (Reichman & Smith 1990, Durbin 1996, Oli et al. 1997, Fernández & Palomares 2000). In case of breeding and rearing new-born cubs, such needs can be a limiting factor for a population because this is a time of high energy requirements (Gittleman & Oftedal 1987, Oftedal & Gittleman 1989), especially in a species such as the otter, that has a considerably higher metabolism than would be expected for its body mass (Iversen 1972, McNaab 1989).

As with other solitary mustelids (Powell 1979), the female otter takes sole care for rearing the young (Macdonald & Mason 1986, Kruuk 1995). The selection of a suitable habitat that ensures a minimum mortality of cubs and mothers until dispersal (10-16 months old in the case of the otter; Mason & Macdonald 1986, Watt 1993, Kruuk 1995), is an important factor, as is the case with other carnivores (Laurenson 1994, Laurenson 1995).

This approach should help us in providing a more detailed understanding of the real habitat needs of the species. This study tries to determine whether a selection of habitat occurs in the reproductive period by characterisation of: 1. the places where cubs are born and spend the first few weeks of their life, and 2. the places where they spend the first few months of their life, after emerging from the natal dens.

Methods

Study area

Data were obtained from several river basins situated in northeast Spain: Middle Cinca (between the Grado and Ballobar), Ésera, Isábena, Noguera Ribagorçana, Noguera Pallaresa, Upper Segre (upstream from the town of La Seu d'Urgell),

Bergantes, Matarranya, Algars, Muga, Fluvià and small rivers and channels on the Alt Empordà plain. Their characteristics and the human geography are described in Folch et al. (1986), Terrades et al. (1989), and Ruiz-Olmo et al. (2001a, 2001b, 2002). In accordance with previous studies (Delibes 1990, Ruiz-Olmo & Delibes 1998, Ruiz-Olmo 2001), the stretches of river where the presence of otters is known to be stable, albeit for only part of the year, were selected. Thus, only those watercourses and water bodies within 1,279 1x1 km grid-squares (UTM grid) were considered.

In the Ebro Basin below 800 m, the dominant species in the otter's diet is barbel (mainly *Barbus graellsii*, but also *Barbus haasi*), French nase (*Chondrostoma miegii*) and, in more recent times, the American crayfish (*Procambarus clarkii*) (Ruiz-Olmo & Palazón 1997, Ruiz-Olmo 1998). At altitudes above 800 m, the main food of otters consists of brown trout (*Salmo trutta*) and, in springtime, amphibians (*Bufo bufo*, *Rana perezi* and *Rana temporaria*). At the local level, otters feed on other important prey-items such as the viperine snake (*Natrix maura*) and other Cyprinids. In the Fluvià and Muga river basins, the main species are American crayfish, fish (a minimum of eight species), amphibians, and water snakes (J. Ruiz-Olmo, A. Batet, J. Jiménez & D. Martínez, unpublished data).

Detection of cubs and dens

The field work was mainly focused on litters with small cubs of two to six months old in rearing sectors. This is the period between when the cubs begin to come out of the den (Mason & Macdonald 1986, Kruuk 1995, Durbin 1996) and the age when, on reaching 90% of their total length (TL) it becomes difficult to distinguish them from the mother (Ruiz-Olmo et al. 2002). In this period cubs are easily distinguished, are more vulnerable, have lesser locomotive and swimming abilities, and don't capture prey on their own (Kruuk 1995). Their dependence on their mother is high, and therefore the quality of habitat is very important.

During direct observations TL of the cubs was used (in 10 cm intervals) in relation to that of the mother. For live captured animals or carcasses, TL and weight were obtained to an accuracy of ± 0.5 cm and ± 10 g, and compared with 90% of minimum TL and weight of reproductive Iberian females (Ruiz-Olmo et al. 2002). Finally, clearly defined footprints or tracks of small cubs encountered were measured (total length of the front and rear paws including the claw), according to the obtained functions (Ruiz-Olmo et al. 2002).

A *natal den* was considered as a den used by a female to give birth to her young and in which the cubs remain during the first one or two weeks of life without going outside, although the female may transfer them from one place to another. A *breeding sector* refers to a stretch of river where a natal den has been detected, whereas a *rearing sector* was a sector where 2-6 months-old cubs were detected. For comparisons, a 500 m length stretch with the middle point placed either in the den or at the point where cubs were detected, was used.

In order to study the generational use of such type of sectors, data were compiled between 1984 to 2001. However, for the statistical comparisons, we used only rearing sectors occupied by small cubs from 1998 to 2001.

We used direct observation during visual censuses and vigils (Ruiz-Olmo 1995b and 1998, Ruiz-Olmo et al. 2001a, Ruiz-Olmo et al. 2002, Ruiz-Olmo et al., in press), the collection of carcasses of dead cubs or alive cubs found (with precise information on the capture site), cubs captured for radio-tracking studies, the footprints of cubs (Erlinge 1967, Erlinge 1968, Macdonald & Mason 1988, Sidorovich 1991, Dülfer & Roche 1998, Ruiz-Olmo et al. 2002), and the natal dens detected.

Natal dens are difficult to find in freshwater ecosystems without radio-tracking because there is often no external evidence of their presence (Moorhouse 1988, Durbin 1996), although Kruuk (1995) has shown in marine environments that smooth earth is found around the entrance opening, and often it has dried mud on the grass

outside with telltale footprints. Natal dens found by radio-tracking were recorded, as were dens with mud and grass remains, together with telltale signs of the presence of small cubs (Kruuk 1995). In one case the repair of an electricity power station, caused the water level to drop, leaving the den exposed. Other methods included the intensive monitoring of foot-prints at the entrance of dens where rearing occurs on a regular basis. The detection of dozens of foot-prints of one particular individual entering or exiting a den, followed by dozens of foot-prints of small cubs several weeks later (eight or more), together with dozens or hundreds of spraints, was considered to be a natal den.

Breeding habitat selection

The values of 71 attributes (table 1) were determined in the rearing sectors. Also, a stratified sample of 100 stretches of 500 m long was randomly selected according to the length of the watercourse and riverbanks in each river basin (3 on the Middle Cinca, 10 on the Ésera, 6 on the Isábena, 10 on the Noguera Ribagorçana, 18 on the Noguera Pallaresa, 9 on the Upper Segre, 5 on the Bergantes, 11 on the Matarranya, 6 on the Algars and 20 in the Muga-Fluvià-Empordà plain complex); two were in areas totally and temporally destroyed during human works and were not surveyed. The accessible part of the slope was prospected in both type of stretches.

Fish abundance was determined through published information, where available or obtained by electrofishing during a period of known presence of cubs (Ruiz-Olmo 1995a, López-Martín et al. 1998, Ruiz-Olmo et al. 2001a, Ruiz-Olmo et al. 2002, Saavedra 2002). However, in some cases this option was not available, and we have instead used data from table 2 (as for crayfish and amphibians).

A detailed search of the riverbank was made for places that were potentially suitable for dens, or that showed signs of having been used for breeding or rearing cubs. Safety against predators (various wild species and dogs) and environmental exposure (high temperatures in summer,

Table 1. Attributes studied for each 500 m stretch. (*) Attributes included in a stepwise logistic model. Habitat structure was recorded as six categories: 0 represents 0% cover, 1 represents 1-20%, 2 represents 21-40%, 3 represents 41-60%, 4 represents 61-80% and 5 represents 81-100%. Structure diversity was calculated as follows: for the substrate the sum of values of rocks, stones, gravel, sand and earth, and for vegetation, the sum of values of long grass, short grass, rushes, helophytic vegetation, brambles, and each type of riparian forest. Food was calculated as was described in the section on methods; values were corrected by means of a logarithmic transformation (ln). Bankside slope was recorded as four categories: 1 represents <10%, 2 represents 11-25%, 3 represents 26-50% and 4 represents >50%. Accessibility was recorded as four categories, 1 represents <1 min, 2 represents 1-10 min, 3 represents 11-30 min and 4 represents >30 min.

Category of attribute	Attributes
Cub rearing sectors characteristics	Presence / absence Altitude (m) (*) Bankside slope
Water in stretch	Surface (m ²) Maximum speed (m/s) (*) Tributaries (number) (*) Small streams (number) Length of calm waters (m) (*) Maximum depth (m) (*) Average width (m) (*) Presence of waterfalls (*)
Ponds in the river	Number with depth >1 m and >2 m (*) Surface in ponds with depth >1 m and >2 m Average width in ponds >1 m depth
Food availability(see text)	Fish Crayfish Total food (fish + crayfish + amphibians) (*)
Den availability	Rocky dens systems (number) Number of holts in rocky systems Total rocky and other dens systems (number) (*) Total holts (number) (*)
Habitat structure; <2 m and <10 m from water	Big rocky blocks and rocky cliffs (*) Stones Gravel Sand Earth Long grass (>0.1 m in height) (*) Short grass (<0.1 m in height) Rushes (e.g. <i>Juncus</i>) Helophytic vegetation (*) Brambles (e.g. <i>Rubus</i> , <i>Coriaria</i>) (*) Small/Immature riparian forest Height/Mature riparian forest Small/Sparce riparian forest Height/Sparce riparian forest

Table 1. [Continued]

Category of attribute	Attributes
Structure diversity; <2 m and <10 m from water	Substrate (*) Vegetation
Human structures and landscape <500 m	Irrigation small ditches (*) Urban (villages, towns) Paved roads Paved + unpaved roads Unirrigated crops (*) Fertile plain Irrigated intensive crops Fruit trees Forest (*) Grassland Bush Esclerophyl small forest Accessibility from paved road Accessibility from unpaved road Distance from village (m) Distance from inhabited house (m)

Table 2. Scale used to estimate the abundance of fish, crayfish and amphibians.

Scale of abundance	Electrofishing (g /m ²)	Fish Visual estimation*	Crayfish Visual estimation	Amphibians Visual estimation
0	0	0 seen	0 seen	0 seen
1	0.01 – 1.0	1 seen	1 seen	1 seen
2	1.0 – 13.0	2 to 20 seen	2 to 20 seen	2 to 20 seen
3	13.0 – 20.0	Frequent	Frequent	Frequent
4	20.0 – 48.0	Abundant	Abundant	Abundant
5	> 48.0	High abundance	High abundance	High abundance

* Based on the significant relationship ($P < 0.05$) found in the study area between the visual estimation of fish observed in a 600 m stretch and the average biomass available (Ruiz-Olmo & López-Martín 2000).

low temperatures in winter, fluctuations in the water level) were considered by means of some of the considered attributes (those related to potential dens and vegetation). The entrance had to be large enough to allow an adult to enter (diameter equal to, or larger than 15-20 cm; Reuther 1991, C. Reuther, personal observations) and had to lead to sufficiently deep chambers. According to results of radio-tracking studies in the study area (Ruiz-Olmo 1995a, Jiménez & Palomo 1998, Jiménez & Ruiz-Olmo, in press), potential places for dens (specially for breeding) were limited to rock formations (loose rock, large rocks, rocky ledges), deep tree roots with holes, thick masses of tangled living vegetation

carried downstream by floods, and helophytic vegetation systems. In the case of dense vegetation, a search was carried out, with special emphasis being put on frequently used passages.

Statistical analysis

Two types of analysis have been used to compare the attributes:

1. A PCA multivariate analysis (based on the correlations matrix) to reduce the number of variables to be analysed. A stepwise logistic regression, in order to establish an equation (using only the main variables selected), so that predictions can be made of the stretches

with the highest probability of use by otters when rearing their cubs. This type of analysis uses data of the dependent variable (presence-absence of a cub rearing sector) to generate the regression for one or more habitat variables. A logit transformation must also be used for it to fit a logistic curve of the data (Collett 1991, Lovett et al. 1997) to establish which parameters affect the use of ponds in marine habitats, and where other aspects of its use can be consulted.

2. A univariant comparison for main attributes in the model, using the Student *t*-test and Mann-Whitney *U*-tests.

Results

Natal dens

Five natal dens were found, with the birth of young being verified in four of these. Rocks served as dens for the majority (three cases), with one in reeds and the other in thick, bank-side vegetation. Four dens were in stretches with continuously flowing water throughout the year, although in one case there were several years when it dried up completely (but not the year of breeding). Three were less than 500 m from a village, and four were less than 100 m from an asphalt-surface road. Average distance to the nearest inhabited house was $225 \text{ m} \pm 112 \text{ m}$ (150 to 450 m) and to the nearest village $620 \text{ m} \pm 466 \text{ m}$ (150 to 1,450 m). The biggest difference was the distance to the water's edge, which oscillated between 2 m and 249 m ($53.4 \text{ m} \pm 109.9 \text{ m}$), although the entrances in three of the cases were less than 5 m from the water.

Rearing sectors

A total of 38 rearing sectors were detected (2 on the Middle Cinca, 3 on the Isábena, 10 on the Noguera Ribagorçana, 7 on the Noguera Pallaresa, 3 on the Upper Segre, 3 on the Bergantes, 2 on the Matarranya, 5 on the Algars, 2 on the Fluvià, and 1 in a water channel on the Alt Empordà

plain). The presence of ponds (over 1 m deep) was detected in 97% of the stretches studied; still water, backwaters, irrigation or similar types of dams were also detected in 97% of cases; an average water width of greater than 5 m was found in 92% of all cases and a maximum water depth of more than 1.4 m in 76% of cases. As for den availability, at least one potential den for small cubs was found in 87% of all rearing sectors, with potential dens amongst rocks existing in 66% of the stretches. The one found at the highest altitude was at 1,050 m.

Model

Stepwise logistic regression was applied to 20 of the attributes (marked in table 1), selected after a PCA multivariate analysis for reduction of variables. The analysis showed that the presence of small cub rearing sectors was most strongly related to the availability of food in the environment, followed by den complexity (with more entrances) (table 3). Between these two, it was possible to correctly classify the presence of small cub rearing sectors in 79.2% of the stretches. Other variables that entered the model were water current speed and the presence of small irrigation ditches. Analysis of other attributes did not significantly lead to a decrease in the residual deviation. The resulting equation was as follows:

Logit (probability of the presence of small cubs) = $-17.962 + 4.874 (\text{food}) + 0.350 (\text{den entrances}) - 1.545 (\text{water speed}) + 2.012 (\text{small irrigation ditches})$

The univariant comparative analysis of stretches with rearing sectors (i.e. with small cubs) and random stretches for the variables in the model, again showed the preference of otter females with small cubs for stretches with lower water speed ($P=0.042$), longer stretches of calm waters ($P=0.0005$), fewer waterfalls ($P=0.035$), a greater abundance of food ($P<0.0001$), more small overgrown irrigation ditches ($P=0.019$), greater availability of potential dens for cubs ($P=0.0001$; in the case of rocky stretches $P=0.0027$) and with more den entrances ($P=0.004$).

Table 3. Logistic models using maximum likelihood estimates fitted to the presence-absence of small otter cubs in the different stretches, following the final model (difference in deviance approximates the *Chi*-square distribution with respective degrees of freedom, d.f.).

Variable added	Model deviance	Difference in deviance	df	% correct classification
+ Food	20.128	20.128	1	76.4
+ Den entrances	28.50	8.378	1	79.20
+ Water speed	36.768	8.262	1	83.72
+ Presence of small irrigation ditches	44.043	7.275	1	86.05
Variable	Regression coefficient	se	Probability coefficient = 0	
Food	4.874	1.086	< 0.0001	
Den entrances	0.350	0.121	0.0038	
Water speed	-1.545	0.537	0.0040	
Presence of small irrigation ditches	2.012	0.746	0.0070	

Other attributes that could be related with these precedents include, small cubs rearing sectors were also found more frequently at sectors with tributaries ($P=0.034$), with more ponds, with deeper (>1 m: $P=0.045$; >2 m: $P=0.0005$) and wider ponds ($P=0.05$), at the deepest stretches ($P=0.006$), at stretches with less grass ($P=0.002$), with more helophytic vegetation ($P=0.0007$), and with a higher abundance of brambles ($P=0.003$).

There was no evidence that attributes connected with the substrate of the riverbed, vegetation diversity or human structures correlated with the presence or absence of rearing sectors.

Generational use of the rearing sectors and conservation

Of the 21 rearing sectors monitored for reuse over years (in six cases the rearing sector remained active up to 18 years later), 15 (71%) turned out to be used regularly by females with small cubs which confirms that a large number of dens and rearing sectors are used over different generations. In some dens monitored by our team, it has been verified that otters breed in the same location every year, except after heavy drought, catastrophic flooding or food shortages. The causes for the non-reuse of rearing sectors in one or more years include particularly catastrophic flooding (up to 73% of the sectors were

affected in some years), drought (27%), highway construction work (5%), and the changes in the levels of reservoirs (5%). 39% of the rearing sectors studied ($n=38$) were affected either totally or partially by construction works or similar human activities at some point during the period covered.

Discussion

Natal dens

Data of this type is very scarce in the literature (Harris 1968, Taylor & Kruuk 1990, Moorhouse 1998). The otters studied here gave birth to their young and reared them during the first few weeks in places that were not necessarily away from human activity. In our study area, the otter is respected and is not hunted (Ruiz-Olmo 2001) and this may be a possible contributory factor. It might be adduced that certain otters could be forced to breed near to human beings at times of population saturation, however, some of these natal dens, were first found during years when the otter population was at a lower level and far from saturation.

Otters can use various types of places to give birth and rear their young during the first few weeks of their life (Harris 1968, Moorhouse 1988, Taylor & Kruuk 1990, Durbin 1996). Nev-

ertheless, the most frequently used type of structure in freshwaters in northeast Spain were rock systems, and quite often these were the only type of structure available (Ruiz-Olmo 1995a, Jiménez & Palomo 1998, Ruiz-Olmo 2001). The fact that one of the females followed by radio-tracking gave birth 249 m from the river, leads us to believe that appropriate dens are scarce. However, rock systems that the Iberian otter can use do frequently occur near to the water, as we found on three separate occasions. Taylor & Kruuk (1990) found a natal den in reeds less than 2 m from a small watercourse (less than 1 m wide) in northeast Scotland. In the same area, Durbin (1996) found a natal den 150 m from the main river but next to (3.5 m) a small tributary 0.7 m wide. On the Shetland Islands, Kruuk (1995) found natal dens far from the sea (between 100 m and over 1 km), although they were very close to their own supply of fresh water. The Mediterranean rivers that we have studied and where rearing sectors have been found, often carry much less water and are not so wide as in northern Europe, and the abundance and density of these rivers and small tributaries are also much lower than in northern Europe.

The higher abundance of potential wild predator species of the otter in the Iberian Peninsula (wolf (*Canis lupus*), Iberian lynx (*Lynx pardinus*), golden eagle (*Aquila chrysaetos*), Iberian imperial eagle (*Aquila adalberti*), eagle owl (*Bubo bubo*), etc.), could also partially explain why natal dens area far away from watercourses could be less advantageous.

Rearing sectors and dens

Female otters selected stretches to rear small cubs with high food availability, suitable dens with abundant exits, deeper and calm water, and good accessibility for the cubs (small irrigation ditches, backwaters). If the otter is a food-limited species (Kruuk 1995, Kruuk & Carss 1996), then its breeding success and cubs' survival depend on the abundance of food (Kruuk et al. 1987, Kruuk et al. 1991, Elmeros & Madsen 1999, Ruiz-Olmo et al. 2001a, Ruiz-Olmo et al.

2001b) and choice of sectors with plenty of suitable prey should be expected. The presence of sufficient food near where the cubs are kept, represents an important energy saving strategy as this reduces female movements (as was found by Saavedra 2003, Jiménez 2005), reduces the vulnerability of the cubs and the mother and thereby contributes to maintaining or increasing the breeding success rate.

The presence of safe dens for the cubs was also an important habitat selection factor. Such places can be very abundant in certain areas, although our results show that this is not the case in others, with 55% of the randomly selected stretches lacking any kind of structure that would be appropriate for the presence of such dens. In reference to resting sites (where the otter is less selective and uses many different ones in its home range; Ruiz-Olmo et al. 1995, Jiménez & Palomo 1998), Beja (1996) found a low frequency of use of different dens in southwestern Portugal, and pointed out that this could be a limited resource in some areas. Dens used by otters in marine environments in Northern Europe are limited by the geology of the terrain, with limitations being imposed by certain types of soil (Kruuk et al. 1989, Kruuk 1995, Yoxon 2000).

Finally, the availability of water and the form in which it occurs played an important role in our study area. Ponds and small irrigation ditches were favoured as these offered protected spaces where small cubs can safely learn to swim during the first weeks after leaving the den (Kruuk 1995) with less danger of being carried away by the current or drowned. Kruuk (1995) found similar results in Scotland and the Shetland Islands, where females used areas with calmer water whereas males frequently used more exposed places with a faster current. Selection of deep and wide ponds is (most likely also) related to the greater availability of the fish that otters prey on and where most of the available fish biomass is concentrated (Ruiz-Olmo 2001, Ruiz-Olmo et al. 2001a, Ruiz-Olmo et al. 2001b). This indicates that the selection of ponds is due to the availability of food rather than to the otter's need for water.



Fresh water habitat in the study area typically favoured by otter females to rear cubs. *Photograph: Jordi Ruiz-Olmo.*

Small irrigation ditches (less than 1 m wide) could also be a reserve of water and food during times of drought, small dams can block the streams, but the water often remains for more weeks or months in such ditches.

The occurrence of good breeding and rearing sectors may be limited, and the repeated use of some dens, by successive generations of otters, appears to support this observation. Similar patterns of repeated use has also been noted in dens in marine environments in Northern Europe (Kruuk 1995).

Conclusions

According to our results, female otters show definite preferences in selecting sites in which to rear their small cubs. Preferred variables related to the availability of food and water, current speed, water depth, and availability of den complexes. Distance from to human activity did not

play any role in this selection, neither (with the exception of the presence of helophytic vegetation (positive relation) and grass (negative relation)) did vegetation cover or plant diversity in the vicinity of the water.

Our results show that good breeding and rearing sectors also undergo human pressure (works, forest fires, gravel extraction, roads, reservoirs) and drastic changes due to natural agents (catastrophic flooding, heavy snowfall, etc.). This means that special attention needs to be paid if the otter population is to be conserved and correctly managed. Actions needed involve the mapping of rearing sectors, monitoring and protecting such areas and, if necessary, their regeneration.

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Samenvatting

Habitatselectie door vrouwelijke otters met jongen in zoetwater-habitats in noordoost-Spanje

Otters kunnen worden gevonden in aquatische omgevingen. Er konden verschillen worden vastgesteld tussen sectoren op verschillende momenten van de levenscyclus zowel in gebruik als belangrijkheid. Wij hebben vijf nestholten bestu-

deerd en 38 sectoren in Mediterrane zoetwater-habitats in zuidwest-Europa waarin jonge otters opgroeiden. Stapsgewijze logistische regressie toonde een sterke relatie aan tussen de aanwezigheid van bepaalde sectoren en de aanwezigheid van voedsel en de aanwezigheid van complexe nestholten. De vrouwtjes met jongen selecteerden de diepste en breedste stukken, met meer vijvers en rustig water, een grotere rijkdom aan voedsel en een grotere beschikbaarheid van potentiële en gebruikte holten. Sommige van de sectoren waar de jonge otters opgroeiden, werden generaties lang gebruikt. Onze resultaten onderstrepen het belang van bepaalde sectoren voor de voortplanting van de otter. Het behoud van deze gebieden zou het basale instrument moeten zijn in het beheer van de soort.

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Het voorkomen van de gewone baardvleermuis (*Myotis mystacinus*) en Brandts vleermuis (*Myotis brandtii*) in Nederland

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Samenvatting: In dit artikel worden de resultaten gepresenteerd van een onderzoek naar het voorkomen van de nauw verwante soorten *Myotis brandtii* en *Myotis mystacinus* in Nederland. In de periode 1987 tot en met 2005 werden in totaal 180 baardvleermuizen gedetermineerd op basis van morfologische kenmerken van dieren in overwinteringsverblijven, van dood gevonden dieren en van dieren die werden gevangen met mistnetten in de zomer. *Myotis mystacinus* werd in alle delen van Nederland vastgesteld. Een exemplaar van *Myotis brandtii* werd gevangen in een mistnet in september 2001 in Zuid-Limburg bij de Koelenboschgroeve en twee andere dieren werden overwinterend aangetroffen in Fort Asperen in het midden van ons land. Deze gegevens wijzen erop dat *Myotis brandtii* veel zeldzamer is (1,7% *Myotis brandtii*) dan verondersteld in eerder onderzoek aan de hand van museummateriaal (12,2% *Myotis brandtii* van 135 gedetermineerde *Myotis mystacinus/brandtii*). Meer onderzoek is nodig om de status en de populatiegrootte van *Myotis brandtii* in Nederland te bepalen, met name onderzoek met mistnetten in de zomerperiode in geschikte gebieden in Midden- en Zuid-Nederland.

Trefwoorden: baardvleermuizen, Brandts vleermuis, *Myotis mystacinus*, *Myotis brandtii*, gebitskenmerken, Nederland.

Inleiding

De baardvleermuizen *Myotis mystacinus* en *Myotis brandtii* zijn nauw verwante soorten die zeer sterk op elkaar lijken. In veel Europese landen is de verspreiding van beide soorten pas de laatste decennia in kaart gebracht. Omdat zij in het veld niet van elkaar zijn te onderscheiden zonder het hanteren van de dieren was de kennis over de verspreiding van beide soorten in Nederland voornamelijk gebaseerd op bestudering van museumcollecties (Hoogenboezem 1982). Aangezien er niet meer dan enige tientallen baardvleermuizen in deze collecties beschikbaar zijn en het merendeel van deze dieren is verzameld in de jaren twintig en dertig van de vorige eeuw, kan gesteld worden dat de verspreiding van beide baardvleermuizen in Nederland slecht bekend

was. Bovendien is driekwart van dit materiaal afkomstig uit Zuid-Limburg. In de periode 1970-1988 zijn slechts van 15 locaties in Nederland nader gedetermineerde baardvleermuizen bekend door toevallige vondsten (Glas & Voûte 1992). Ook het onderzoek met bat-detectors heeft weinig nieuwe vindplaatsen van beide soorten baardvleermuizen aan het licht gebracht; in de periode 1986-1993 werd zelfs geen enkele Brandts vleermuis (*Myotis brandtii*) gemeld en werden slechts enkele nieuwe vindplaatsen van de gewone baardvleermuis (*Myotis mystacinus*) gevonden (van der Coelen & Verheggen 1997a, van der Coelen & Verheggen 1997b). Vanwege veranderingen in de Nederlandse wetgeving (Flora- en Faunawet) is er een toenemende behoefte aan informatie over de status en het voorkomen van zowel de Brandts vleermuis als de gewone baardvleermuis.

De Stichting Vleermuisonderzoek heeft na uitvoerige afweging van de voor- en nadelen van een dergelijk onderzoek het initiatief genomen

om in de winters 1998/1999, 1999/2000 en 2000/2001 steekproefsgewijs een aantal baardvleermuizen in winterobjecten nader op soort te onderzoeken. In dit artikel worden de resultaten van dit onderzoek gepresenteerd, aangevuld met de resultaten van determinatie van toevallige vondsten en vangsten met mistnetten uit de periode 2001-2005.

Methode

Baardvleermuizen zijn in de winterobjecten onderzocht op gebitskenmerken (zowel mannetjes als vrouwtjes) en de vorm van de penis (mannetjes). Bij het hanteren van levende baardvleermuizen zijn slechts enkele kenmerken van het gebit bruikbaar, namelijk de grootte van de protoconus op het cingulum van P^3 en de relatieve hoogte van de beide voorste praemolaren in boven- en onderkaak. Vooral laatstgenoemd kenmerk is in de meeste gevallen goed te zien bij gebruik van een loep van tenminste 10x vergroting. Bij *Myotis mystacinus* is P^2 veel lager dan P^1 (zie figuur 1) en P_2 veel lager dan P_1 , terwijl de beide

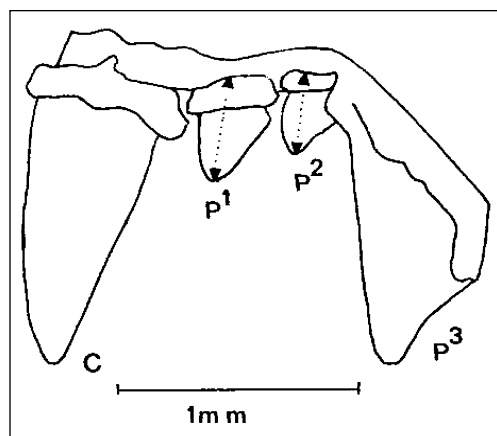
praemolaren in boven- en onderkaak bij *Myotis brandtii* ongeveer even hoog zijn. De meeste auteurs beschouwen het verschil in hoogte in boven- en onderkaak als een belangrijk kenmerk. Er zijn meer kenmerken aan het gebit bekend als onderscheid tussen beide baardvleermuizen, maar deze andere kenmerken zijn in het veld bij het hanteren van levende dieren niet bruikbaar omdat ze niet (voldoende) zijn te zien. De praemolaren aan zowel de onder- als bovenzijde van het gebit zijn over het algemeen wel goed zichtbaar.

Daarnaast zijn in de periode 1987-2005 23 vondsten van baardvleermuizen gedaan. De meeste exemplaren zijn binnengebracht in het kader van rabiësonderzoek bij het ID in Lelystad. Sinds het voorjaar 2002 heeft de Veldwerkgroep van de Vereniging voor Zoogdierkunde en Zoogdierbescherming (VZZ) de mogelijkheid om onderzoek aan vleermuizen met behulp van mistnetten uit te voeren. Hierdoor zijn ook op enkele andere plaatsen aanvullende waarnemingen van baardvleermuizen verzameld.

Resultaten

In de winters 1998/1999, 1999/2000 en 2000/2001 zijn in totaal 134 baardvleermuizen nader op naam gebracht in overwinteringobjecten in Drenthe (5 dieren), Gelderland (49 dieren), Noord-Holland (9 dieren), Zuid-Holland (29 dieren), Zeeland (12 dieren), Noord-Brabant (9 dieren) en Limburg (21 dieren). Het betreft niet alleen dieren die in hun winterslaap zijn gestoord, maar ook dieren die toevallig in wakkere toestand werden aangetroffen in de onderkomens, dieren die dood werden gevonden en mannelijke dieren in winterslaap waarbij het geslachtsdeel voldoende zichtbaar was. Van de 134 gehanteerde dieren hadden er 84 betrekking op mannetjes en 48 op vrouwtjes. In twee gevallen is het geslacht niet vastgesteld. Er zijn 132 dieren gede-termineerd als gewone baardvleermuis en twee exemplaren als Brandts vleermuis.

De 23 vondsten van baardvleermuizen in de periode 1987 tot en met 2005 zijn vooral afkomstig uit het zomerhalfjaar en zijn verspreid over



Figuur 1. Hoektaand en praemolaren in de linker bovenkaak van de gewone baardvleermuis (*Myotis mystacinus*); de pijlen geven aan hoe de hoogte van P^1 en P^2 is bepaald (naar Hoogenboezem 1982).

Figure 1. Upper left canine and premolars of whiskered bat (*Myotis mystacinus*); the arrows show how the height of P^1 and P^2 has been measured (after Hoogenboezem 1982).

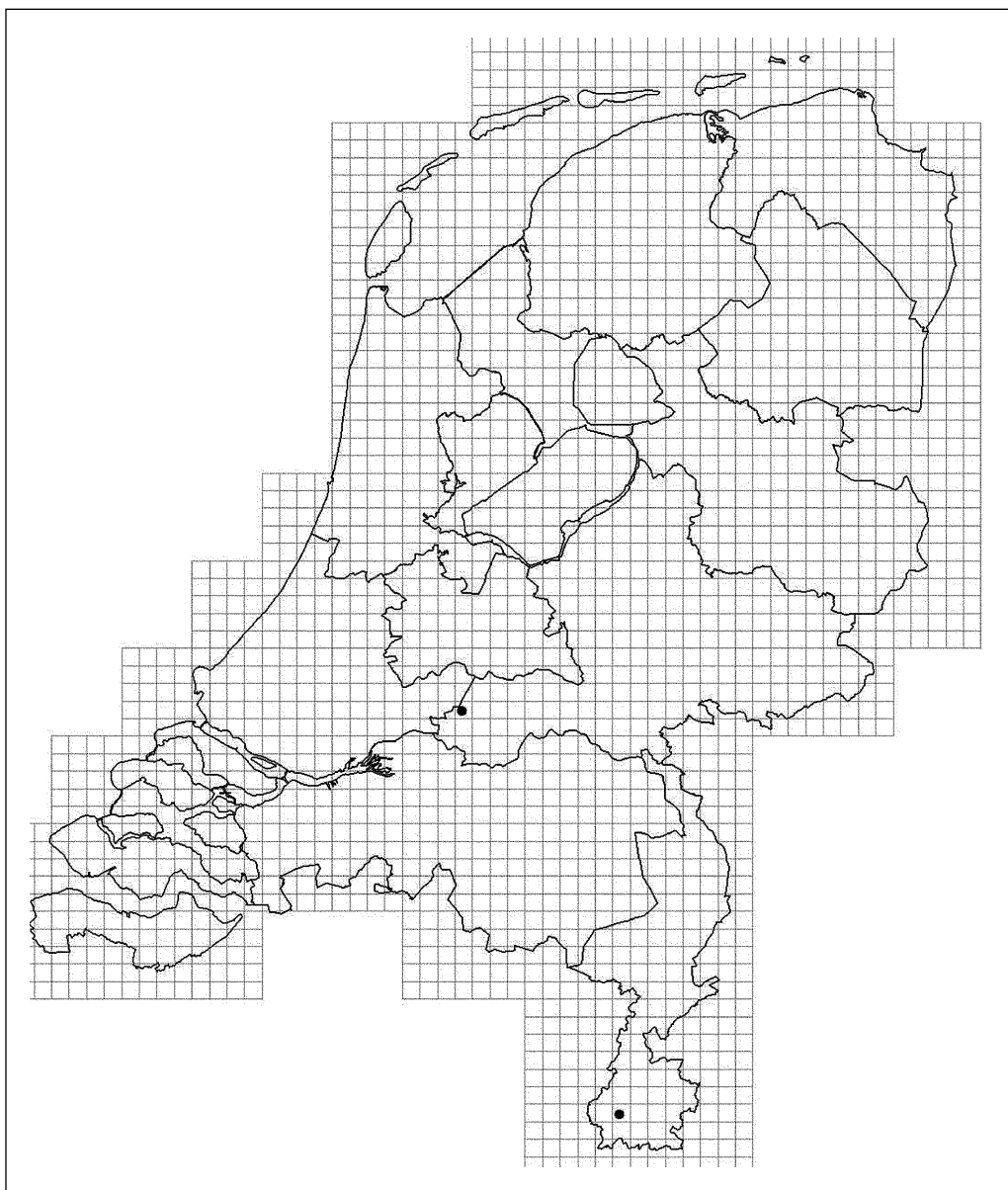


Figuur 2. De verspreiding van de gewone baardvleermuis (*Myotis mystacinus*) in Nederland 1988-2005.
 Figure 2. Distribution of the whiskered bat (*Myotis mystacinus*) in the Netherlands 1988-2005.

heel Nederland. In alle gevallen bleek het om de gewone baardvleermuis te gaan.

Tenslotte zijn in september 2001 in Zuid-Limburg op drie plaatsen in totaal twaalf baardvleermuizen met mistnetten gevangen. Het ging om 11 *Myotis mystacinus* (alle mannetjes) en 1 *Myo-*

tis brandtii (mannetje) en wel voor de ingang van de Koeleboschgroeve. In de omgeving van Wageningen zijn in september 2002 tien baardvleermuizen gevangen die alle betrekking hadden op *Myotis mystacinus* (8 mannetjes en 2 vrouwtjes).



Figuur 3. De verspreiding van de Brandts vleermuis (*Myotis brandtii*) in Nederland 1988-2005.
 Figure 3. Distribution of the Brandt's bat (*Myotis brandtii*) in the Netherlands 1988-2005.

Uiteindelijk zijn op de bovenstaande drie manieren 180 baardvleermuizen op uiterlijke kenmerken onderzocht. Eén exemplaar hiervan was op grond van de tandkenmerken niet nader op naam te brengen. In totaal waren 176 exemplaren hiervan gewone baardvleermuizen en 3

exemplaren Brandts vleermuizen. De verspreiding per uurhok is weergegeven in de figuren 2 en 3. Zoals deze laten zien zijn er overal in het land waarnemingen van gewone baardvleermuizen. De Brandts vleermuis werd op twee locaties aangetroffen: voor de Koeleboschgroeve in



Foto 1. Een Brandts vleermuis (*Myotis brandtii*) in Fort Asperen op 23 januari 2001. Foto: Kamiel Spoelstra.
 Photo 1. A Brandt's bat (*Myotis brandtii*) in Fort Asperen on 23 January 2001. Photograph: Kamiel Spoelstra.

Zuid-Limburg en in Fort Asperen, op de grens van Gelderland en Zuid-Holland.

Discussie en conclusies

De aanwezigheid van de Brandts vleermuis is in 1980 al vastgesteld in de Koeleboschgroeve (Hoogenboezem 1982). In de omgeving van Fort Asperen was de soort nog niet eerder aangetroffen, hoewel de melding niet ver is verwijderd (30 km in noordoostelijke richting) van de enige andere vindplaats van de soort buiten Zuid-Limburg, namelijk te Bilthoven op 7 september 1968 (Hoogenboezem 1982). Het exemplaar dat op 14 april 1960 is verzameld op de Westwal van Goes (RMNH 16836) (Hoogenboezem 1982) is destijds, zoals bleek bij controle van de museumcollectie op basis van de penisvorm en de beide voorste praemolaren, ten onrechte als *Myotis brandtii* gedetermineerd.

Het percentage van *Myotis brandtii* dat des-

tijds in de Nederlandse musea van *Myotis mystacinus/Myotis brandtii* aanwezig was, bedroeg 12,2% (Hoogenboezem 1982). Ruim driekwart van het materiaal, gebaseerd op 135 exemplaren, was echter afkomstig uit Zuid-Limburg en slechts 22,5% uit de overige delen van Nederland. Een aanvullend onderzoek aan 26 levende mannetjes van *Myotis mystacinus/Myotis brandtii* in de Koeleboschgroeve leverde destijds 11,5% *Myotis brandtii* op. Op grond van het onderhavige onderzoek lijkt het erop dat de Brandts vleermuis in Nederland heel wat zeldzamer is dan op grond van eerder onderzoek werd verondersteld. Tijdens dit onderzoek, gebaseerd op 179 op naam gebrachte baardvleermuizen, is slechts een percentage van 1,7% van *Myotis brandtii* (drie exemplaren) aangetroffen. De onderzochte dieren kwamen verspreid uit het hele land; 18% kwam uit Zuid-Limburg. Tijdens het onderzoek van Hoogenboezem (1982) zijn 133 baardvleermuizen onderzocht in Zuid-Limburg tegenover 33 dieren tijdens dit onderzoek. Deze



Foto 2. Bijna alle onderzochte baardvleermuizen bleken betrekking te hebben op de gewone baardvleermuis (*Myotis mystacinus*). Foto: Kamiel Spoelstra.

Photo 2. Almost all investigated bats appeared to be whiskered bats (*Myotis mystacinus*). Photograph: Kamiel Spoelstra.

aantallen zijn te klein om uitspraken over een eventuele trend te kunnen doen. Bovendien is het onderzoek van Hoogenboezem voornamelijk gebaseerd op materiaal in museumcollecties, verzameld in een periode van meer dan vijftig jaar.

Van de 154 gedetermineerde baardvleermuizen in of bij de winterobjecten waarbij het geslacht kon worden bepaald, had 68% ($n=104$) betrekking op mannetjes en 32% ($n=50$) op vrouwtjes. Deze scheve sexe-verhouding kan deels veroorzaakt zijn door het feit dat alleen dieren zijn onderzocht die vrij aan het plafond hingen of tegen de wand. Een meerderheid van de baardvleermuizen kruipt weg in spleten en gaten, waarbij mannelijke dieren vaker vrij hangen en/of solitair de winterslaap door brengen (Daan & Wichers 1968). Uit onderzoek in andere landen zoals Noorwegen (J. van der Kooij, monde-

linge mededeling) blijkt dat er geen verschillen in hangplaatsen zijn gevonden tussen *Myotis mystacinus* en *Myotis brandtii*. Het is dus niet aanemelijk dat het selectief onderzoeken van meer vrij hangende dieren tot een andere verhouding tussen beide soorten baardvleermuizen zou leiden.

Volwassen Brandts vleermuizen hebben over het algemeen een meer lichtbruin tot roze gekleurde oorbasis en snuit dan volwassen gewone baardvleermuizen, die overwegend zwart van kleur zijn (Schober & Grimmberger 1999). Ohlendorf (1999) vond bij onderzoek op basis van 1250 *Myotis brandtii* dat vrouwtjes tot en met drie jaar oud nog zwartige oren hebben; pas bij vier jaar is er een bruinige tint. Oudere volwassen vrouwtjes vertonen pas een lichtbruine tot roze oorkleur.

Bij de onderzochte dieren tijdens dit onderzoek is tevens naar de kleurdeling van snuit en oorbasis gekeken. Dit heeft tot weinig bruikbare informatie geleid. Een interpretatie van kleurtinten door verschillende personen is bij voorbaat al moeilijk vergelijkbaar. De algemene indruk is dat de beschreven kleurverschillen van oorbasis en snuit van beide soorten baardvleermuizen wel opgaan maar niet als betrouwbaar determinatiekenmerk gebruikt kunnen worden. Zo zijn enkele dieren met een relatief lichte oorbasis en snuit gevonden die op basis van de tandkenmerken en penisvorm toch als *Myotis mystacinus* zijn gedermineerd. Mogelijk wordt de Brandts vleermuis door de lichtbruine tot roze oorbasis en snuit tijdens tellingen in objecten waar vleermuizen overwinteren vaker verward met de talrijk aanwezige watervleermuis (*Myotis daubentonii*) dan wordt verondersteld. Extra aandacht aan de grootte van de achterpoten en de vorm van de oorpunten kan in dergelijke gevallen uitsluitsel geven.

In recente literatuur worden nog andere verschillen tussen *Myotis mystacinus* en *Myotis brandtii* gegeven. Zo vermeldt Krapp (2001) dat het uiteinde van het oor bij *Myotis brandtii* hooguit tot de snuitpunt reikt, terwijl het oor bij *Myotis mystacinus* 1-3 mm voorbij de snuitpunt steekt. Tupinier (2001) vermeldt daarentegen dat het oor bij *Myotis brandtii* 1-3 mm over de snuitpunt komt terwijl Tupinier & Aellen (2001) bij *Myotis mystacinus* beschrijven dat het oor net over de snuit steekt.

Kowalski & Ruprecht (1981) en Hackethal & Grimmberger (1984) wijzen op het verschil tussen de beide *Myotis*-soorten door het al of niet ontbreken van een huidplooi aan het hielspoor. Schober & Grimmberger (1987, 2001) geven dit kenmerk voor beide soorten, terwijl Tupinier (2001) expliciet vermeldt dat dit kenmerk niet onderscheidend is.

Vervolgonderzoek

Vervolgonderzoek is nodig om essentiële vragen te kunnen beantwoorden over de status van zo-

wel de Brandts vleermuis als de gewone baardvleermuis in Nederland. Het is op dit moment onbekend of er van de Brandts vleermuis in Nederland een levensvatbare populatie aanwezig is en in wat voor soort onderkomens de soort voorkomt (zowel in de zomer als in de winter).

Onderzoek met mistnetten in potentiële zomerbiotopen en tijdens de nazomer voor de ingangen van winterobjecten lijkt hiervoor de beste methode. Omdat meldingen van Brandts vleermuizen zijn geconcentreerd in midden-Nederland en Zuid-Limburg zijn dit de meest voor de hand liggende gebieden om nader te onderzoeken. Aangezien het werken met mistnetten aanzienlijk minder verstorend is voor baardvleermuizen dan het hanteren van dieren tijdens de winterslaap verdient dit sterk de voorkeur.

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Summary

The occurrence of whiskered bat (*Myotis mystacinus*) and Brandt's bat (*Myotis brandtii*) in the Netherlands

In this study a total of 180 bats were examined for the univocal identification of the closely related species *Myotis brandtii* and *Myotis mystacinus* between 1987 and 2005. Bats were identified by the use of morphological characteristics during hibernation and captures by mist nets. All bats found dead during this time span were examined as well. Three bats were identified as *Myotis brandtii*, 176 as *Myotis mystacinus*, and one bat could not be identified. *Myotis mystacinus* was found in all parts of the Netherlands. One specimen of *Myotis brandtii* was found in September 2001 in southern Limburg near a hibernating site and two were found hibernating in a Fortress near Asperen in the central part of the Netherlands. The present study confirms the occurrence of both *Myotis mystacinus* and *Myotis brandtii* in the Netherlands during the period 1987-2005. The outcome of this study shows that *Myotis brandtii* is much less common (1.7% *Myotis brandtii*) than indicated in an earlier study (12.2% based on 135 specimens). Additional research is necessary to confirm the status and population size of *Myotis brandtii* in the Netherlands by the use of mist nets in and near potential habitats.

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