POPULATION ECOLOGY AND CONSERVATION OF THE BARN OWL *Tyto alba* IN FARMLAND HABITATS IN LIEMERS AND ACHTERHOEK (THE NETHERLANDS)

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Barn Owl (Photo Jos Korenromp)

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ABSTRACT Over the last decades, the Barn Owl population has markedly decreased in range and breeding numbers in The Netherlands as in most western European countries. For effective conservation and population management, it is essential to know which factors are responsible for this decline. The present study deals with the Barn Owl population in the eastern part of The Netherlands. Population trends and demography (productivity, dispersal, mortality) were studied in two different districts (Liemers and Achterhoek) over two consecutive nine-year periods (1967-75 and 1976-84). Trends in population levels and demographic parameters are analysed in relation to external (environmental) factors, especially food supply, winter weather conditions, nest site availability and changes in rural landscapes and in farming practices.

In Liemers the Barn Owl population has decreased markedly since 1960, especially in areas which have been subject to urbanisation and to large-scale land consolidation aimed at agricultural intensification. In contrast, in Achterhoek the Barn Owl population increased in the period 1965-85; landscape diversity is much better preserved in this district. More Barn Owls breed in small-scale mixed farmland than in large-scale uniform farmland. A significant, positive, correlation was found between the Barn Owl breeding density and the length of hedgerows, lines of trees and woodland edges.

Both in Liemers and Achterhoek, no clear trends over time were noticed as regards breeding performance, dispersal patterns and mortality in adult Barn Owls. However, first-year mortality in Liemers in the second period (1976-84) proved to be higher than in the first period (1967-84) and in both periods in Achterhoek. In Liemers, productivity was too low to compensate for the high mortality in which road deaths took a heavy toll. This district proved to be a 'sink area', where the Barn Owl population persists only due to continuous net imports of owls. In contrast, Achterhoek is a 'source area' where productivity exceeds mortality. The relative importance of the various demographic parameters for the population balance is presented in a diagram (Fig. 25), which also gives a quantitative assessment of the sink (Liemers) and the source (Achterhoek).

The key factors which limit Barn Owl numbers proved to be time- and region-dependent. In the 1980s, a continuing decline took place in the most devastated landscapes of Liemers, accounted for by progressive agricultural intensification and also by urbanisation and the expansion of the main road network. In contrast, the Barn Owl population increased in the better preserved mixed farmland of Achterhoek. The loss in nest site availability in the study region (which was great in the early years of the study period) has been offset by a major nestbox campaign, which proved to be very successful. Today over 90% of the Barn Owl pairs in Liemers and Achterhoek use these nestboxes for breeding. The mean number of young raised in nestboxes was significantly higher than that of 'free' nest sites. In Liemers the improved nest site availability could not stop the

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population decline. The proximate factors causing this decline are the loss of foraging habitat (disappearance of vole-rich areas, large-scale reduction of hedgerows) and the sharply increased traffic density (causing high road mortality rates). In the small-scale mixed farmland of Achterhoek, however, the Barn Owl population grew in parallel with the increased supply of nestboxes. This supports evidence that nest site availability is the environmental limiting factor in well-preserved landscapes with a rich and buffered food supply. The relationships between the most important external (environmental) factors and the main internal (demographic) parameters, as found in this study for the 1980s, are presented in a diagram (Fig. 35).

A number of recommendations can be made for the protection of the Barn Owl and its habitat. These are summarized at the end of this article. Conservation measures should be linked to a land use strategy which favours not only the Barn Owl, but also broader conservation interests including historic-cultural values and the scenery in the wider countryside. Such a strategy will be profitable for other endangered birds and other scarce species associated with farmland. Monitoring of population trends of breeding birds in the study region showed that birds from semi-natural habitats (open water, marshland, woodland) are relatively safe if they are non-migratory or winter in Europe. In contrast, many species breeding in farmland are threatened, in which Africa-migrants run double risks. There are better prospects for farmland birds with limited dispersals, such as the Barn Owl. Conservation measures regarding the local habitat (increasing the diversity in farmland environments including the supply of appropriate nest sites) certainly offer an opportunity for maintaining and increasing their breeding populations within a relatively short period of time (10-15 years).

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1. INTRODUCTION

1.1 Background

In Europe the Barn Owl *Tyto alba* is widely distributed in lowland and hilly country where there is a sufficient supply of small mammals, particularly voles *Microtidae*, mice *Muridae* and shrews *Soricidae*. Within its European range the Barn Owl usually avoids natural or semi-natural habitats such as dunes, marshes, heaths and woodland. Nowadays it inhabits predominantly man-made landscapes, generally areas which have been cultivated for various agricultural practices (Glutz von Blotzheim & Bauer 1980, Cramp 1985).

Over the last decades, the Barn Owl population has markedly declined in range and breeding numbers in most countries of western Europe, e.g. in Ireland and Britain (Sharrock 1976), Denmark (Dybbro 1976), Germany (Bauer & Thielcke 1982, Nicolai 1993), The Netherlands (Braaksma & de Bruijn 1976, Teixeira 1979, SOVON 1987), Belgium (van der Straeten & Asselberg 1973) and France (Yeatman 1976). Probably this concerns long-term downward trends, which are unconnected with periodic population fluctuations as caused by cycles in the abundance of voles, the main prey of the Barn Owl (e.g. Schönfeld & Girbig 1975, de Bruijn 1979, Taylor *et al.* 1992). In a number of countries, the Barn Owl has been enlisted as a threatened species ('Red Data Bird'), e.g. in Germany (Bauer & Thielcke 1982), France (Jarry & Terrasse 1983), The Netherlands (Osieck 1986, Osieck & Hustings 1994) and Britain (Batten *et al.* 1990). It is only recently that signs of partial and local recovery have been presumed or noticed (Percival 1991, van der Hut *et al.* 1992).

The long-term decrease of the Barn Owl is variously attributed to natural factors such as adverse climate conditions (Honer 1963, Shawyer 1987), deaths by human intervention (trapping, shooting, being locked in), the use of toxic pesticides (Joiris & Martens 1971, Prestt & Ratcliffe 1972, Newton *et al.* 1991), increase in road deaths (Kaus 1977, Shawyer 1987, Illner 1992) and the loss of breeding sites (Peitzmeier 1969, Bühler 1977, Bunn *et al.* 1982). Besides these, a number of authors attribute the widespread numerical decline of The Barn Owl mainly to the loss of habitat as caused by urbanisation of the countryside, and by changes in agriculture, leading to a decrease in foraging areas and food supply (Sparks & Soper 1970, Braaksma & de Bruijn 1976, Bauer & Thielcke 1982, Epple & Hölziger 1987, Batten *et al.* 1990). Long-term integrated studies are urgently needed to gain insight into these complicated processes. In such studies, surveys of internal (demographic) population parameters are required in combination with external (environmental) data in order to determine the factors, which are limiting the Barn Owl numbers. For, the study of environmental limiting factors is essential for effective conservation and population management (Newton in Perrins *et al.* 1991).

1.2 Aims

For a deeper understanding of the relations between the Barn Owl and its environment, a number of aspects of the species' ecology and population dynamics have to be clarified. The present study deals with the Barn Owl population of a 900 km^2 study area in the eastern part of The Netherlands. This area can be divided in two districts (Liemers and Achterhoek) which differ markedly in landscape structure. Here population studies have been carried out continuously since 1965. All major Barn Owl habitat types found in The Netherlands are represented in the study area due to the landscape diversity here. The aims of this long-term study are:

1. Monitoring population levels over a long period so that it is possible to distinguish long-term population trends from short-term fluctuations, which are characteristic of Barn Owl populations.
2. Studying main aspects of the population ecology on a regional scale, particularly habitat selection and feeding ecology.
3. Analysing trends in demographic parameters, viz. reproduction, dispersal and mortality.
4. Investigating relationships between trends in population performance and relevant environmental factors, e.g. winter weather conditions, food supply, nest site availability, urbanisation, expansion of the road network, and changes in farmland habitats and land use.

The scope of this study is to integrate information on population levels with that on reproduction, dispersal patterns and mortality, to achieve an integrated picture of the Barn Owl population dynamics on a regional scale. In order to detect trends both in space and time, differences have been analysed between two study districts (Liemers and Achterhoek) over two consecutive nine-year periods (1967-75 and 1976-84). The outcomes are analysed in relation to environmental factors in order to find explanatory factors behind the owl's population trends. In some parts of the study, data from the period 1985-93 have been processed.

1.3 Outline of the paper

The outline of this paper is as follows. In Chapter 2 and 3, the study area and the methods and materials used are described. Chapter 4 deals with the distribution, breeding densities and population trends of the Barn Owl in both study districts. Then the habitat selection and the feeding ecology are reviewed (Chapter 5 and 6). The demography of the Barn Owl population is analysed in the Chapters 7-9, which deal respectively with the breeding performance, dispersal patterns and mortality (including causes of death) in Liemers and Achterhoek. In Chapter 10 these population parameters are brought together and discussed in relation to external factors, especially vole densities, duration of snow cover, deaths caused by human intervention (including road deaths and pesticides) and the effect of nestboxes on the population. Furthermore, the influences of habitat changes and land use on the Barn Owl population are taken into account. In the final chapter, special attention is paid to bird species which are, like the Barn Owl, linked with farmland habitats. For it is clear that radical changes in landscape features and farming practices not merely affect a single species, but whole communities of ecologically associated species (Bezzel 1982, Fuller 1982, de Bruijn 1982, de Molenaar 1983, O'Connor & Shrubb 1986).

The over-all aim of this study is to contribute essential knowledge for conservation and management of important natural values in farmland, which forms the greater part of the countryside in western Europe. With its mixture of open fields, grasslands, hedgerows and coppices, farmland habitats can support a diverse avifauna with many scarce species of conservation interest. The maintenance of this diversity throughout the countryside is just as essential as the conservation of isolated areas of semi-natural habitats, such as woodlands and moors (Fuller 1982, Batten *et al.* 1990).

2. STUDY AREA

The study area (Fig. 1) is situated in the eastern part of The Netherlands near the German border (5°58'-6°50' E, 51°50'-52°02' N) and comprises roughly an area of 60 by 15 km. With a total area of 900 km^2 this covers about 3% of the Dutch territory. The study region is divided into two parts by a small river, the Oude IJssel. The western part, named Liemers (350 km^2), is mainly a holocene (alluvial) district; the eastern part, named Achterhoek (550 km^2), is a pleistocene (diluvial) district. Landscape structure and habitats in Liemers and Achterhoek differ markedly: these regions are classed under two different physio-geographic provinces of The Netherlands (Zonneveld 1985). A division of the study area by landscape types is shown in Figure 2 and explained in section 2.1 (Liemers) and section 2.2 (Achterhoek). Supplementary landscape-ecological information can be found in Visscher (1975) and in the Scientific Atlas of the Netherlands (1963-1977).

2.1 Liemers

Liemers consists predominantly of riverine and polder areas. Amidst these flat landscapes (elevation 10-15 m. above sea-level) a chain of hills rises up to 100 m.: this is the wooded moraine ridge of Montferland. The human population of Liemers is concentrated in dispersed villages which are interconnected by a rather dense network of main and secondary roads.

The broad valleys of the Rhine (Rijn), the IJssel and the Oude IJssel form the natural boundaries of Liemers. During the Holocene, meandering rivers built up a complex of banks (natural levees) and valleys. A number of villages are located on the relatively high levees of Rhine and IJssel. Here many farmsteads are located, too, which are lying either in small groups or more dispersed. Many farms in the river landscape are centuries old. The sandy clay deposits of the Rhine levees are very suitable for agricultural and horticultural practices; they are also used for growing fruits. On the inland sand dunes along the Oude IJssel, a chain of villages is found, as well as a number of country estates with associated woodlands.

Along the rivers one can still find old river branches with fens (swamps), alternating with wet grassland complexes (holms). An example of such a semi-natural fen landscape is most beautifully preserved in the Oude Rijn Nature Reserve near the small city of Zevenaar.

In the NW and SE of Liemers extensive grassland polders are found in the basin-clay areas ('back-swamps'). Originally no farms and only a few roads were built here, but these polder landscapes have been subject to more intensive

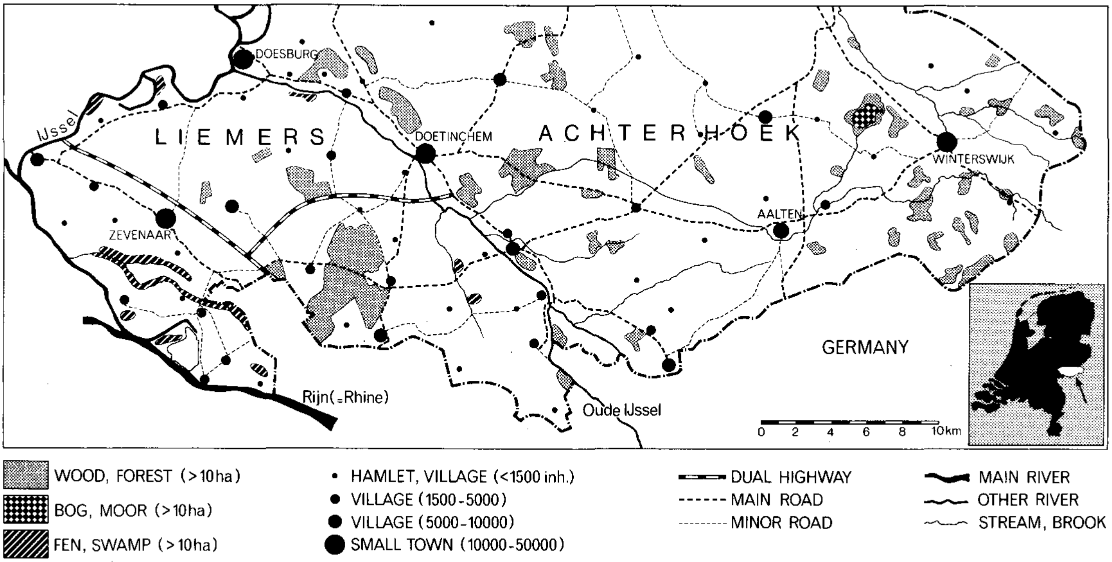


Fig. 1. The study region: Liemers and Achterhoek.

cultivation in recent decades. Land consolidation and drainage operations have made the back-swamps more accessible; many hedgerows were cleared during these operations.

The high moraine ridge of Montferland is covered with woods. Nowadays this area is a Nature Reserve. Northwards the high ridge passes into a rolling sandy area. This small-scale pleistocene landscape, which lends itself to mixed farming, is similar to many parts of Achterhoek (see next section).

To review, the following landscape types are characteristic of Liemers (Fig. 2): polder landscape, river landscape, fen landscape and wooded moraine ridge.

2.2 Achterhoek

Achterhoek is a sandy district extending from the valley of the Oude IJssel eastwards to the German border. During the Pleistocene large parts of this region were covered by fine aeolian sands (so-called 'cover-sands'). The western part of Achterhoek consists of a gentle rolling landscape (15-25 m. above sea-level), the eastern part is a more elevated plateau (35-40 m.). Achterhoek is rather sparsely populated and less industrialized than Liemers.

The cover-sand landscape of western Achterhoek consists of low ridges alternating with small valleys and depressions. Dispersed farms are situated on the ridges, each farm being confined to a small area of higher ground with arable fields in its immediate neighbourhood. The intervening lower ground between the ridges is used as meadow. The small-scale pattern of this landscape type is accentuated by numerous rows of trees, hedgerows and many woodlots (mainly coniferous and mixed forests).

The landscape of eastern Achterhoek around the village of Winterswijk consists of plateau remnants intersected by small stream valleys. For centuries the relatively higher grounds were used for arable fields. Generally their extent was such that they could support only a limited number of farms concentrated in small groups (forming a hamlet in the neighbourhood of the fields) or a still more loose configuration of dispersed farmsteads. The fertile stream valleys and other relatively low parts are used as grasslands. The proportion of woodland is larger than in the

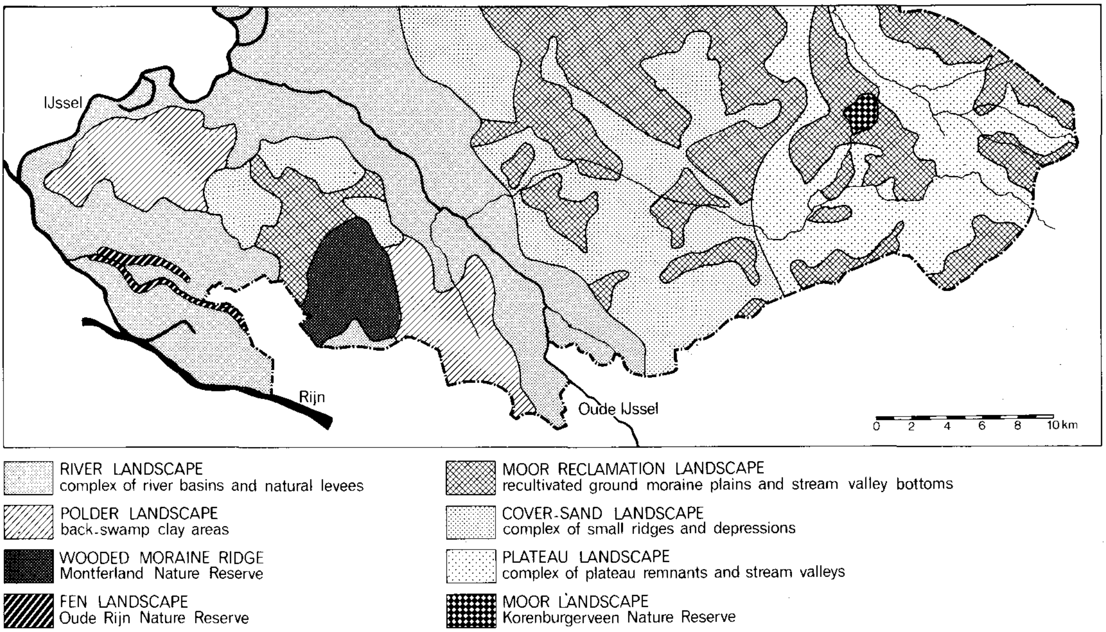


Fig. 2. Landscape types in the study region.

cover-sand area, with more deciduous forests, which is due to rich soils found locally on the Winterswijk plateau.

Both in the cover-sand region and on the plateau, lower areas are found with soils influenced by ground water, as a result of boulder clay (ground moraine) not far below the surface. Until the beginning of the 20th century, large moorlands with wet heaths and raised bogs were found here. These remain in only two or three complexes, of which the Korenburgerveen Nature Reserve is the most important. Elsewhere the ground moraine plains and the stream valley bottoms have been reclaimed. These moor-reclamations are being cultivated as damp grassland complexes.

To review, the following landscape types are characteristic of Achterhoek (Fig. 2): cover-sand landscape, plateau landscape, moor landscape and moor-reclamation landscape.

2.3 Review of the main landscape types

It is possible to make a classification of the landscape types found in the study region based on their geomorphological foundation, human occupancy and the characteristic habitat-complexes present. The main groups are formed by (a) semi-natural landscapes (marshland, moorland and woodland), (b) mixed farmland (agricultural landscapes with a great diversity of habitats and many small landscape elements and with a mosaic of arable fields and grasslands), and (c) uniform farmland (large-scale agricultural landscapes, usually grassland-complexes, with local forestry plantations). The landscape types found in the study region can be classed under the main types as follows:

a. Semi-natural landscapes:

- fen landscape (Oude Rijn Nature Reserve);
- wooded moraine ridge (Montferland Nature Reserve);
- moor landscape (Korenburgerveen Nature Reserve).

b. Mixed farmland:

- river landscape (complex of river valleys and natural levees);
- cover-sand landscape (complex of small ridges and depressions);

- plateau landscape (complex of plateau remnants and stream valleys).

c. Uniform farmland:
- polder landscape (back-swamp clay areas);
- moor-reclamation landscape (cultivated ground moraine plains).

In a forthcoming chapter (dealing with the habitat selection of the Barn Owl) each landscape type is subdivided into habitat-complexes based on characteristic habitat features and human land use (see review in Table 6).

3. GENERAL METHODS AND MATERIALS

This study integrates information on population levels of the Barn Owl with that on demographic parameters (reproduction, dispersal, mortality). Trends in population performance are analysed in relation to environmental factors. The results are placed in a wider context by comparing the population trends with those of other scarce bird species in the study area. In this chapter the general methods used are discussed, dealing with the following problems:
1. Monitoring of Barn Owl populations.
2. Analysis of demographic parameters, viz. reproduction, dispersal and mortality.
3. Surveys of population trends in a number of scarce and characteristic breeding birds in the study region

Methods specific for other problems studied will be described under the appropiate chapters of this paper. These include aspects of the population ecology of the Barn Owl (particularly habitat selection and feeding ecology: Chapters 5 and 6) and the survey of a number of environmental factors (with special respect to weather conditions, food supply, nest site availability and changes in habitat features and land use: Chapter 10).

Statistical analyses in this study have been performed using the computer software packages SPSS and Statistix 4.0 (programmes run by W. Nijdam and J.M. Tinbergen, respectively). A probability value (p) of 0.05 was used as the threshold level of significance in statistical analyses.

3.1 Monitoring Barn Owl populations

The Barn Owl is an exceptionally difficult species to count accurately because of its widely dispersed distribution pattern and its elusive nocturnal nature. They are very easy to miss. This was poignantly demonstrated by the fact that a pair of Barn Owls nested in a barn on the author's own farmstead, but were not noticed by us until they had young to feed. The only way to obtain accurate population data is to survey thoroughly a defined sample area (census plot) in which all possible nest sites and daytime roosting sites are searched for and checked for the presence of Barn Owls or fresh marks typical of this species (pellets, shed feathers, white droppings on roofs or below entrance holes). The results of these surveys must be combined with sightings and vocal records of Barn Owls (territorial screeches and screams of adults, hissing and snoring calls of young).

Barn Owl population surveys should be carried out in areas large enough (at least 75-100 km^2) in order to cover several breeding pairs and should be chosen at random so as to represent the main habitats in the study region (see also Percival 1990). Barn Owl numbers can be influenced markedly by cyclic fluctuations in the main prey species, that is the Common Vole *Microtus arvalis* on the continent (Baudvin 1975, Schönfeld & Girbig 1975, Braaksma & de Bruijn 1976, de Bruijn 1979) and the Field Vole *Microtus agrestis* in Britain (Taylor *et al.* 1988, 1992). Therefore censuses should be carried out for several years, preferably for at least 6-7 successive years in order to cover two vole cycles.

Long-term population surveys under these basic conditions have been continuously carried out in a 900 km^2 study region in the eastern part of The Netherlands. In the period 1964-66, the author started his intensive search after the breeding occurrence of the Barn Owl in Liemers and Achterhoek. Hundreds of potential breeding places all over the region were visited in order to trace the species' former and recent occurrence. This census included visits to farms, churches, castles and other types of suitable building. To a lesser extent tree sites were also investigated, but this proved to be unprofitable because nowadays the species hardly nests in hollow trees in The Netherlands (presumed to be less than 3% of all nest sites, see also Braaksma & de Bruijn 1976). Beside these extensive field surveys, requests for Barn Owl data were made to local ornithologists, priests, landowners, farmers, game-keepers and other countrymen. Appeals for co-operation were also made in appropiate local magazines. As far as possible, all reports were followed by site visits by the author or experienced fellow-workers. Processing of data regarding former breeding occurrence were restricted to the period since the severe winter of 1955/56. Statements of such former occurrence were only validated when unmistakable old marks of Barn Owls (see above) could be found in the territory concerned, or when the former breeding occurrence could be confirmed by two trustworthy informants. In fact, nearly all reliable records of breeding Barn Owls proved to be of two

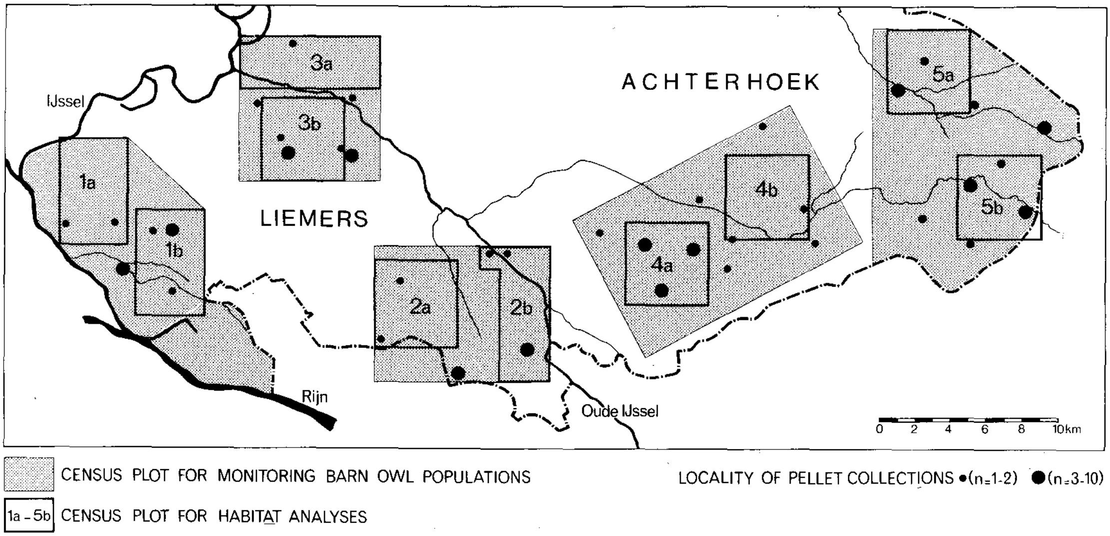


Fig. 3. Map of the study region, showing (a) the five defined census plots for monitoring Barn Owl populations (shaded areas); (b) the ten census plots for habitat analyses (marked 1a-5b); (c) the locations of pellet collections (in two size categories).

kinds: either the owls were reported to breed 'always' (meaning annually) in the territory concerned, or the owls were said to have bred 'incidentally' (usually only in one or two years breeding). The first category was classed as 'regularly occupied territories' and the latter as 'irregularly occupied territories'. Altogether about 90 Barn Owl breeding territories occupied after 1955 were registered in this way in the study region during the mid 1960s. About 55 of these territories had a regular occupancy history.

From 1967 onwards, the attention has focused upon five defined census plots (each between 75 and 125 km^2) distributed over the study region. These census plots are shown (grey shaded) in Figure 3. Three of them are located in Liemers (total area size 250 km^2) and two in Achterhoek (together 250 km^2). These survey sample areas were selected in such a way that all farmland habitats present in the study region are well represented in the census plots. Plot I and plot II (W. Liemers and E. Liemers) consist mainly of polder and river landscapes, plot III (N. Liemers) comprises river landscape and adjoining cover-sand landscape, plot IV (W. Achterhoek) consists mainly of cover-sand landscape and moor reclamations whereas plot V (E. Achterhoek) consists of plateau landscape and moor reclamations. These census plots were thoroughly searched annually for Barn Owls, in the manner described above. The author's work was gradually facilitated by a growing number of active voluntary fellow-workers. There were about 10 in the mid 1970s and 25 in the mid 1980s, this increase being stimulated by the establishment of the Achterhoek-Liemers Working Group for Barn Owl Protection. Over the years, local networks comprising in total over 500 countrymen (mainly farmers) have been build up, and supply data on the occurrence of Barn Owls. Every year all suitable nest sites in the census plots are checked for the occurrence of Barn Owls. In spring (April-May) information is gathered about the presence of Barn Owls without visiting the actual nest sites so as to avoid disturbance during the incubation period. In the period June-July all nest sites are visited (mostly twice) in order to establish the breeding performance and to ring the owlets. Late in summer (August-September) the nest sites are usually visited again in order to check for the occurrence of late or second broods.

In a number of cases adult owls were located in the main breeding season (April-August) in areas where no nests were found even after thorough searching of all potential nest sites. These birds were ultimately filed as 'non-breeders'. All other survey results in this study about breeding Barn Owls concern pairs which have actually bred (clutch laid). Thanks to these very intensive, consistent monitoring activities we feel confident to have registered annually over 90% of the actual total of Barn Owl breeding pairs in the intensive census plots from 1967 onwards. In total, the census data comprise 346 breeding pairs (Liemers: 108, Achterhoek: 238) over the period 1967-84. In addition, 122 non-breeding adult owls (Liemers: 51, Achterhoek: 71) were recorded in the five census plots over this period.

3.2 Studying demographic Barn Owl population parameters

Reproduction. Data on brood success have been systematically collected over the whole study period. This has be done in order to investigate temporal and spatial variation in reproduction, to see whether changes in breeding performance may have affected the over-all population dynamics. No data on clutch size have been collected (other than circumstantially) for the purpose of minimizing disturbance of the adult owls during the courtship and the incubation period. However, whenever possible we tried at least to obtain information about the brood size (number of young in the nest) and the over-all brood success (number of young fledged). Disturbance at the nest was kept at a minimum by visiting the sites in the evening and trying to plan the visits to the nest when the young were at an age of 3-6 weeks (taking information of the local inhabitants and observations of the owl's behaviour and vocal records of the young into account). At this stage the owlets were systematically marked with Arnhem-rings of the Netherlands Bird Ringing Centre. During late summer visits (August-September) information was gathered about second broods and loses of nestlings following ringing (based on communications of local habitants and findings of dead owlets in or below the nest). Brood success has been defined as the number of fledglings leaving the nest well (at an age of 8-10 weeks).

For the purpose of this study, the over-all breeding performance (mean brood success) was calculated inclusive of the completely failed broods (0 young fledged). In all, fledging success of 273 broods (Liemers: 73, Achterhoek: 200) could be established over the period 1967-84.

Dispersal. At the start of this study, an intensive ringing scheme of nestlings was set up in order to investigate variation in space and time in dispersal patterns (Fig. 4). In the period 1967-84, a total of 663 nestlings were marked with Arnhem-rings (Liemers: 157, Achterhoek: 506). To limit disturbance, no systematic work has been done as regards capturing and marking of adult owls. In the period 1967-84 only 24 adult owls were incidentally ringed of which 6 have been recovered subsequently. Out of a total of 663 nestlings ringed in the period 1967-84, a total of 164 (=24.7%) birds were reported up to 1-1-1990 at The

Fig. 4. Every year the census plots were searched for Barn Owl broods and the young were ringed in order to obtain data on reproduction, dispersal and mortality. Photo R. Jonker.

Netherlands Bird Ringing Centre after fledging. 21 of these reports concerned birds which were found dead within 30 days after ringing in or near the nesting place (0-2 km), whereas 10 owls were captured alive and released again subsequently. These 31 recoveries have been left out of account. The further analysis has concentrated on the remaining 133 ringing recoveries. Regarding the general dispersal pattern it can be said that 50 owls were found dead within the study region (both Liemers and Achterhoek), 45 were found in other parts of The Netherlands and 38 abroad. The latter category comprises 34 emigrants to Germany and 4 emigrants to France. On the other hand, 25 Barn Owls ringed in 1967-84 as nestlings outside the study region were found dead in Liemers and Achterhoek (up to 1-1-1990), six of them being immigrants from Germany.

Mortality. Data on mortality of both first-year and adult owls are needed to study quantitative aspects of the population balance. The ringing data mentioned under the previous heading were also used for analysing mortality rates. From the 133 returns of owls ringed as nestlings in the study area, 91 (68%) were found dead in the first year after ringing, whereas 42 recoveries concerned birds found dead subsequently. Mortality rates in Barn Owls are both age- and time-dependant. This is a consequence of annual fluctuations in survival rates as shown by the work of Schönfeld *et al.* (1977), Bairlein (1985) and Percival (1990). Our own analysis of these aspects had to be restricted to some extent as there were a limited number of recoveries in single years. For the total population and the whole study period, age-specific mortality could be determined by using life table analysis in which for each year class the number of birds alive at the beginning of the year is known, as well as the number of birds dying over the year. In this way first-year mortality and annual adult mortality rates can be determined, as well as age-specific life expectation (cf. Hickey 1952, Haldane 1955, Schifferli 1957, Henny 1969). The same method was used for studying spatial and temporal variation in mortality rates: for both Liemers and Achterhoek first-year mortality and mean adult mortality were calculated for two consecutive periods (1967-75 and 1976-84). These mortality rates are subject to potential biases as caused by the limited amount of data although they fit well with values found in other European studies (cf. Glutz von Blotzheim & Bauer 1980). For the near future it would still be advisable to compare the results of this regional analysis with that of the total comprehensive Dutch ringing database using advanced statistical techniques in analysing age- and time-specific variation in mortality rates (White 1983, Anderson *et al.* 1985, Lakhani 1987).

Causes of death. Another aspect of mortality is the analysis of factors causing the death of Barn Owls. During the research we collected information on about 140 Barn Owls found dead in the study region in the period 1967-84. This regards full-grown birds (no nestlings). These data were obtained from two main sources: (1) ringing recoveries stored in the databases of The Netherlands Bird Ringing Centre, totalling 77 reports; (2) personal findings and information gathered and checked by the author and fellow-workers of the Achterhoek-Liemers Working Group for Barn Owl Protection, totalling 63 reports. In analysing the ringing reports, the original references were used; these were mainly letters from the finders in the ringing archives. Data from the second source comprise both personal findings and reliable information obtained from conversations with local farmers and other countrymen, mostly during the annual monitoring of Barn Owl territories. The finders were questioned about the species identity, the precise condition of the bird, the recovery data and location and the recovery circumstances. A number of specimens found dead was sent to the Central Veterinary Institute (CDI) at Lelystad for analysis of the cause of death (including parasitological and toxicological research). All finds which the author could not verify beyond question as regards the species' identification or the finding location were rejected. In doubtful or obscure recovery circumstances, the cause of death was classed in the category 'unknown'. Ultimately for 90 out of the 140 Barn Owls found dead, the death cause or detailed recovery circumstances are known (ringing reports: 48, other checked information: 42). The causes of death were grouped into the following main categories: road traffic deaths, collided with other obstacles, killed by human intervention (unintentionally as well as deliberately), starvation (especially in harsh winters with vole scarcity) and poisoning by toxic pesticides.

Different information sources (ringing reports against other checked information) gave differing ratios regarding the cause of death. As a result of extensive conversations with finders of ringed Barn Owls, it became clear that a number of mortality causes was under-represented in ringing reports. The reason for this is dual: (1) The cause of death is not so conspicuous and therefore often not mentioned by the finder in the recovery report (starvation, pesticides); (2) The cause of death is intentionally concealed in the finder's report, which happens in cases of killings of this legally protected bird. A number of these birds were reported as road victims by the finder, although in reality they had been deliberately killed, on closer investigation on our part! Moreover, in road victims the cause of death is easily recognizable and these are therefore recorded relatively frequently as such in the ringing reports. So we must conclude that road deaths are over-represented in the ringing statistics, at the expense of a number of other causes of death. This probably holds too for earlier studies of the Dutch Barn Owl population (Braaksma & de Bruijn 1976, de Jong 1983), because the mortality figures in these studies are based mainly on ringing recoveries. In the present study, analysis of the various causes of death is based both on ringing reports and other checked information. Therefore the bias will be less.

3.3 Surveying population trends in scarce and characteristic breeding birds in the study area

In the early 1960s, the study area (Liemers and southern Achterhoek: Fig. 1) appeared to be very rich avifaunistically. About 135 bird species proved to breed here (out of a total of 156 species breeding in the whole of The Netherlands), according to the author's observations and information known by elder bird wachters both in Liemers and in Achterhoek. Preliminary to later current local surveys, the author and some other enthusiastic young field ornithologists began systematically to collect quantitative data on breeding bird species in this region. The basic idea later crystallized into a scheme to monitor a number of scarce and characteristic breeding bird species in order to trace population trends in 'ecological critical species' like the Barn Owl. At first, 75 species were selected for surveying in order to establish a baseline for future population monitoring. This group of birds comprised a representative sample of species from different families and habitats (marshland, farmland, woodland). In parallel with the Barn Owl mapping, Liemers and Achterhoek were traversed in the period

1963-67 and all characteristic habitat types were searched for territories of the selected bird species in April-July. The survey areas were censused at least in one year by the author or his fellow-workers, and were usually visited three times during the breeding season. A number of night visits in search for special species were made in appropiate habitats. Supplementary information was acquired from all locally known bird watchers. Some important bird areas (e.g. Oude Rijn Reserve, Montferland, Winterswijk region) were monitored for scarce birds in several years, and visited many times. Some other areas (viz. uniform farmland and extensive forest plantations) were relatively under-represented in these surveys. Census methods included point counts and transects as well as territory mapping depending on both the species and the habitat type surveyed. The fact is that in the 1960s standardized census methods were hardly known. These have been developed and became widespread during the 1970s and 1980s since increasingly more time, money and manpower was available for ornithological surveys (Berthold 1976, Teixeira 1979, Marchant 1983, Hustings *et al.* 1985).

During the late 1970s and early 1980s this survey work was repeated, but this time within the framework of regional and even national monitoring projects in which many volunteer observers were involved using standardized methods in surveying breeding birds. The results from this comprehensive field work are compiled in a number of excellent regional avifaunas (van den Bergh *et al.* 1979, Vogelwerkgroep Zuidoost-Achterhoek 1985, Lensink & Vogelwerkgroep Arnhem 1993) and stored in national ornithological databases (SOVON archives 1976-84). Basic material from these sources could be used and were supplement with data from our own surveys and the unpublished data from local bird watchers to complete a second population survey (1978-82) of scarce and characteristic breeding birds in Liemers and Achterhoek.

During the field work in the 1960s and later in the evaluation phase it became clear that some of the species originally selected could not be counted adequately by us during the first survey (1963-67) with the methods in use then, for a number of reasons: (1) The species was too numerous or too widely distributed to be counted accurately (e.g. Little Owl *Athene noctua*, Rufous Nightingale *Luscinia megarhynchos*, Golden Oriole *Oriolus oriolus*); (2) Other species were too difficult to be censused adequately by us as a result of insufficient census techniques (e.g. Water Rail *Rallus aquaticus*, Woodcock *Scolopax rusticola*); (3) A third group of species proved to be seriously underestimated by us because we under-valued the efforts required (e.g. Lesser Spotted Woodpecker *Dendrocopus minor*, Firecrest *Regulus ignicapillus*, Hawfinch *Coccothraustes coccothraustes*); (4) Finally, some species showed large fluctuations in numbers in successive years making it difficult to perform comparable population estimates between the two survey periods (Common Quail *Coturnix coturnix*, Green Woodpecker *Picus viridis*, Wood Warbler *Phylloscopus sibilatrix*). No population estimations were made for the species in which the survey results are biased by such main errors. On the other hand, a number of species turned up in 1965-80 as new regional breeding birds which could be monitored adequately (e.g. Gadwall *Anas strepera*, Tufted Duck *Aythya fuligula*, Fieldfare *Turdus pilaris*, Bearded Tit *Panurus biarmicus*).

For the aim of this study, the trends in at last 50 breeding birds in the study region are analysed by comparing the population levels in the periods 1963-67 and 1978-82. These comprise species in which the population estimates for both periods are sufficiently reliable and comparable. For each species an estimate of the total number of breeding pairs is given, in which the range expresses both fluctuations in numbers and the exactness of the survey performed. The abundance is divided into 8 classes, each successive class roughly doubling the size of the last. The population estimates can be biased with respect to the real numbers of birds. However, they are primarily used for establishing marked population trends. These were only stated for species which have increased or decreased by two or more abundance classes, meaning at least a fourfold change in surveyed numbers between the two periods compared. From of the 50 species analysed, a total of 11 (22%) showed marked increases in breeding numbers as against a total of 17 (34%) showing marked decreases; in 22 species (44%) no apparent trends were found in breeding numbers in the period 1965-80. For most species concerned corresponding trends were noticed (though not always equally well documented) in other surveys over the last decades, both on a regional and on a national scale (*loc. cit.*). The birds with marked changes in population numbers are analysed in this study as regards their migratory habits and habitat choice. This will augment ecological information needed for a better understanding of the underlying factors in bird population changes, such as have been observed in the Barn Owl.

4. DISTRIBUTION AND BREEDING DENSITIES

4.1 Breeding occurrence in Liemers and Achterhoek

Over the last decades, many data have been collected on the state of the Barn Owl population

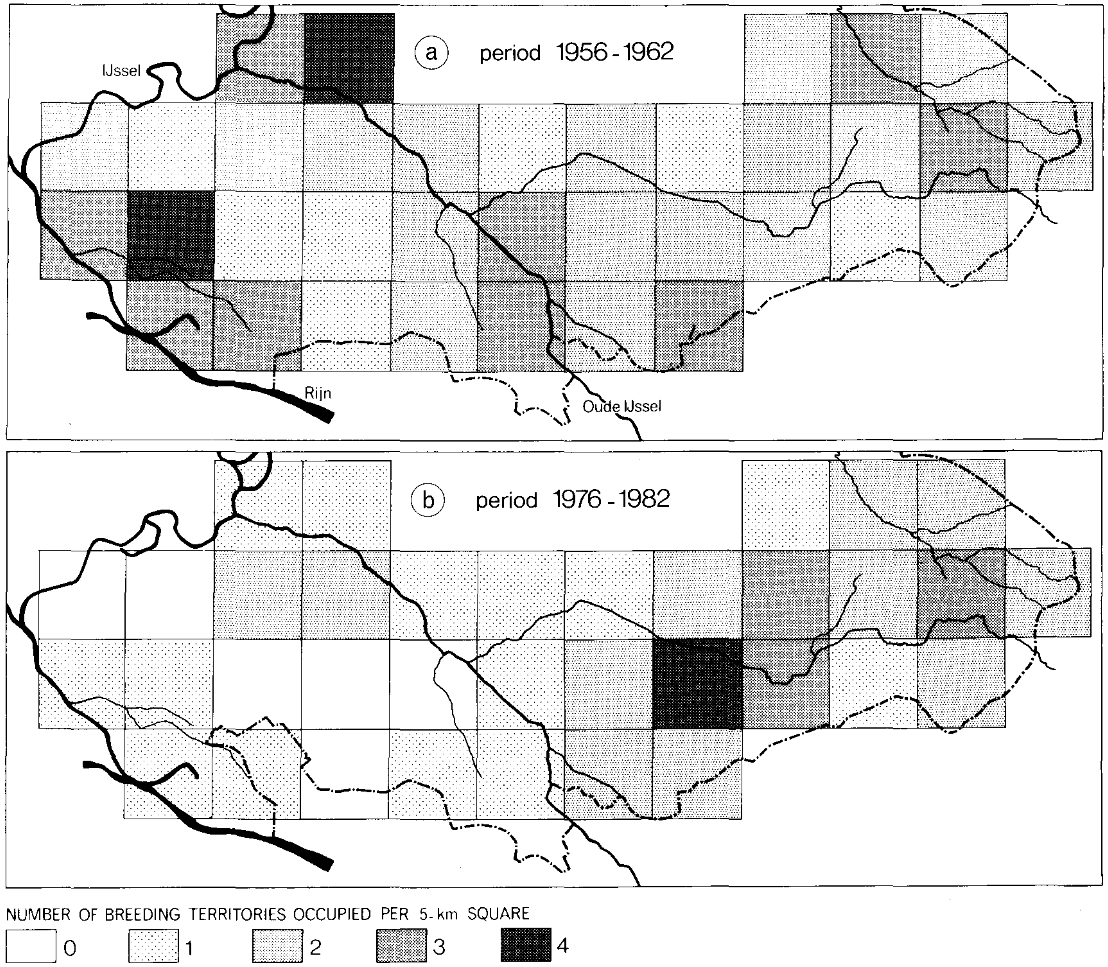


Fig. 5. Distribution pattern and breeding density of the Barn Owl in the study region in the periods 1956-62 and 1976-82. The breeding occurrence is given per 5-km square (=25 km^2). The total number of occupied breeding territories amounted to 76 in the first period and 49 in the latter period.

in The Netherlands. In good vole years around 1960, as many as 3000-3500 pairs of Barn Owl were breeding in The Netherlands. After the adverse winters of 1961/62 and 1962/63, the Dutch breeding population had fallen to only 400-800 pairs in 1966-68. In 1973-75 the population was estimated at 250-600 pairs and in 1982-84 at 300-500 pairs. These data are based on annual nationwide population censuses made by S. Braaksma together with many regional fellow-workers. In the period 1988-90 a partial recovery of the Barn Owl population took place, particularly in the northern and eastern part of The Netherlands, according to the national survey (J. de Jong, pers. comm.). Distribution maps and more detailed census results can be found in Braaksma & de Bruijn (1976), Teixeira (1979), SOVON (1987) and van der Hut *et al.* (1992).

Figure 5 shows the breeding occurrence of the Barn Owl in the study area (Liemers and Achterhoek) in the period 1956-62 and in the period 1976-82. For each period the number of

Table 1. Barn Owl population level in census plots in Liemers and Achterhoek during consecutive periods 1956-62, 1963-68, 1969-75 and 1976-82 (based on data in Appendix 1 and Appendix 2).

Census plot	Area (km^2)	Density (breeding pairs/100 km^2)				Index of population level			
		1956-62	1963-68	1969-75	1976-82	1956-62	1963-68	1969-75	1976-82
W. Liemers (L1)	95	7-11	4-7	2-3	1-2	100	60	30	15
E. Liemers (L2)	80	6-10	5-8	3-4	1-3	100	80	45	25
N. Liemers (L3)	75	7-10	4-7	3-5	3-5	100	60	45	45
W. Achterhoek (A1)	125	4-7	3-5	5-8	7-9	100	75	120	145
E. Achterhoek (A2)	125	4-7	3-5	4-7	4-7	100	75	100	100
Liemers (L1+L2+L3)	250	7-10	4-7	3-4	2-3	100	65	40	30
Achterhoek (A1+A2)	250	4-7	3-5	4-8	5-8	100	75	110	120

NOTES. Figures of density refer to average and maximum number of breeding pairs per 100 km^2 in the period concerned. The index of population level is calculated from the mean of the density figures in this table (basic years for calculations: 1956-62 = 100).

occupied breeding territories is given per 5 by 5 km square (25 km^2). Some traditional breeding territories contained two or more different nest sites used in successive years: for the purpose of the study these are considered to constitute one territory, as shown in Figure 5. This picture gives a good over-all view of the distribution pattern and relative breeding densities of the Barn Owl in the study area in the two periods compared. For the whole study region (900 km^2), the Barn Owl population can be estimated at 50-60 breeding pairs in the first period (1956-62), whereas it was 30-35 pairs in the latest period (1976-82). These numbers refer to the population size in years with a high population level of the Common Vole *Microtus arvalis*, the main prey species of the Barn Owl.

In the picture shown in Figure 5, two trends can be clearly distinguished: (1) a decline in the total number of occupied breeding territories, (2) a shift in the main centre of population density in the study area during the past decades, viz. from west (Liemers) to east (Achterhoek). These trends are further worked out in Table 1 which is based on survey results summarized in Appendix 1. The first part of Table 1 shows the Barn Owl breeding density (pairs/100 km^2) in the intensively surveyed census plots in the study region in four consecutive periods (1956-62, 1963-68, 1969-75 and 1976-82). The second part of this table shows the trend of the Barn Owl population in the five census plots expressed in an index for the population level with the period 1956-62 as base for calculation. The most remarkable decrease of the Barn Owl population was found in the census plot W. Liemers (-85% in the period 1956-82); in contrast, a considerable increase was found in the census plot W. Achterhoek (+45% in the period 1956-82). For the whole of Liemers, a sharp decline in population density was observed over the period 1956-82, starting in the beginning of the 1960s (with the disastrous winters of 1961/62 and 1962/63) and continuing until the beginning of the 1980s. In Achterhoek the Barn Owl population decreased too in the 1960s but here a remarkable recovery took place thereafter.

These trends can be further analysed on the basis of data in Table 2 showing the distribution of Barn Owl territories over the various habitat types of the study area. It can be seen that most Barn Owls breed in mixed farmland, less in uniform farmland and none in semi-natural landscapes. The preference of Barn Owls for

Table 2. Breeding occurrence of the Barn Owl in the various landscape types of the study area: period 1956-62 compared with period 1976-82. Figures in brackets show percentages.

Type of landscape	Area size (km^2)		Number of Barn Owl breeding territories			
			Period 1956-62		Period 1976-82	
SEMI-NATURAL HABITATS						
Fen landscape	6	(0.7)	-	(-)	-	(-)
Wooded moraine ridge	29	(3.2)	-	(-)	-	(-)
Moor landscape	5	(0.6)	-	(-)	-	(-)
UNIFORM FARMLAND						
Polder landscape	79	(8.7)	4	(5.3)	2	(4.1)
Moor-reclamation landscape	213	(23.5)	4	(5.3)	2	(4.1)
MIXED FARMLAND						
River landscape	269	(29.7)	36	(47.4)	10	(20.4)
Cover-sand landscape	179	(19.8)	16	(21.0)	18	(36.7)
Plateau landscape	125	(13.8)	16	(21.0)	17	(34.7)
Total	905	(100%)	76	(100%)	49	(100%)

NOTE. Habitat features of the landscape types are given in Table 6.

farmland with a great habitat diversity (riverine, cover-sand and plateau landscape) above uniform farmland (polders and moor-reclamations) proved to be statistically very significant (conditional Poisson test, $p < 0.001$). The sum total of occupied Barn Owl territories dropped from 76 (period 1956-62) to 49 (period 1976-82). The numerical decline of the Barn Owl in the period 1956-82 can be related to changes in population density in specific landscape types. A marked decrease has taken place in the holocene river landscape (typical of Liemers), whereas the Barn Owl population in the pleistocene cover-sand and plateau landscapes (typical of Achterhoek) remained stable or even increased. In the period 1956-62 about 47% of the Barn Owl territories were situated in the riverine area as against 42% in the whole cover-sand and plateau region. In the period 1976-82 the same ratio was 20% as against 71%, as can be seen in Table 2. The decrease of the Barn Owl in the river landscape in the study region is statistically significant (χ^2 test, $p < 0.01$).

This remarkable shift in landscape types favoured by Barn Owls over the last twenty years is illustrated in more detail in Figure 6 which shows the population trends in three census plots (E. Liemers, N. Liemers and W. Achterhoek) in four consecutive periods (1956-62, 1963-68, 1969-75 and 1976-82). Here a distinction is made between irregularly occupied Barn Owl territories (which held a Barn Owl breeding pair in only one or two years in the period concerned) and regularly occupied territories (which held a breeding pair in three or more years). The upper part of Figure 6 shows the Barn Owl population trend in the census plots E. Liemers and N. Liemers. As can be seen, in the polders only a few Barn Owl pairs are breeding. In the river landscape a considerable number of traditional territories was found up to the 1960s. Afterwards the number of regularly occupied territories decreased gradually here; in the riverine area only a few Barn Owls territories were regularly occupied during the latest census period. The lower part of Figure 6 shows the Barn Owl population trend in

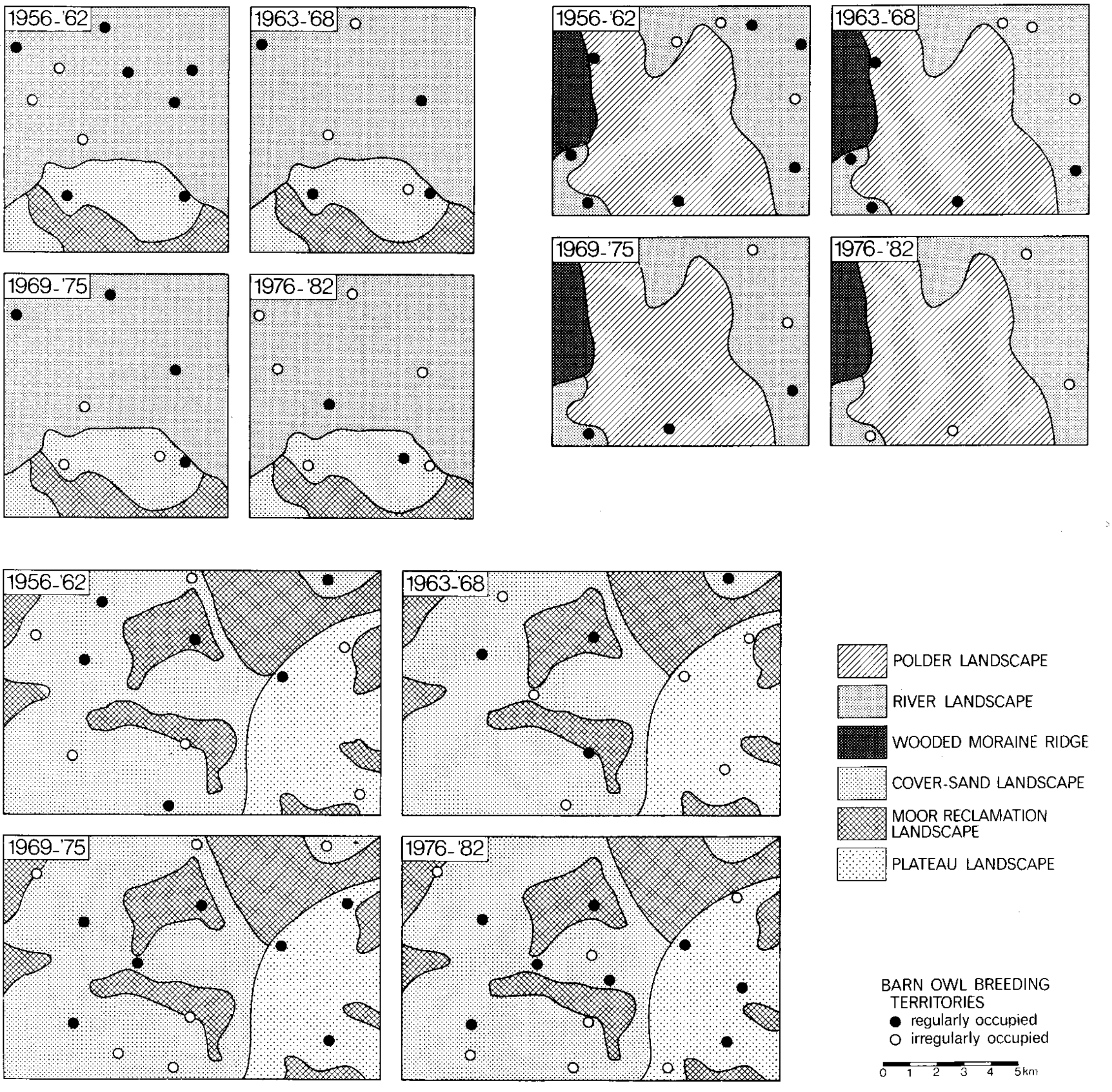


Fig. 6. Breeding occurrence of the Barn Owl in three census plots (E. Liemers, N. Liemers and W. Achterhoek) in four consecutive periods (1956-62, 1963-68, 1969-75 and 1976-82). Open circles indicate irregularly occupied territories (which held a breeding pair in one or two years of the period concerned), solid circles indicate regularly occupied territories (which held a breeding pair in three or more years).

the census plot W. Achterhoek. Here it can be seen that in the uniform moor-reclamations practically no Barn Owls are breeding. Their favourite breeding territories are nearly all located in the cover-sand and plateau landscapes. In the latter landscape types definitely no decrease in occupancy rate of Barn Owl breeding territories was found in the period 1956-82.

4.2 Breeding densities and population trends

From Figures 5 and 6 one can not derive absolute breeding densities in single census

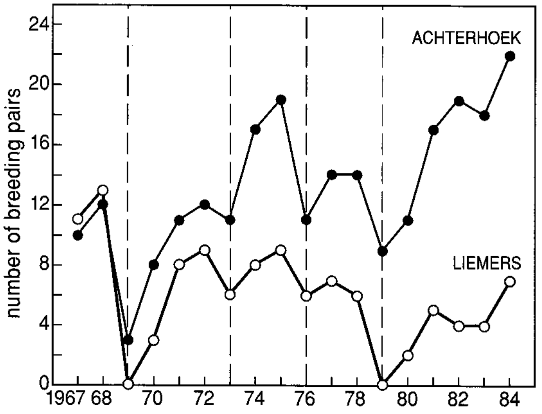


Fig. 7. Annual numbers of Barn Owl breeding pairs in the defined census plots in Liemers (total area size: 250 km^2) and in the census plots in Achterhoek (total area size: 250 km^2) in the period 1967-84. Dotted lines indicate minima in the Barn Owl population corresponding to troughs in the cycle of the Common Vole *Microtus arvalis.*

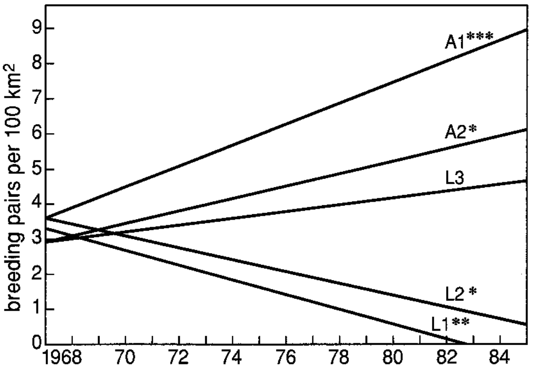


Fig. 8. Trends in breeding densities of the Barn Owl in the five census plots in the period 1967-84. For two areas (A1 = W. Achterhoek, A2 = E. Achterhoek) breeding densities increased, for two areas (L1 = W. Liemers, L2 = E. Liemers) breeding densities decreased, for one area (L3 = N. Liemers) no significant trend could be shown. The fitted lines as computed using linear regression analysis are given (based on data in Appendix 2). Significance levels are indicated as follows: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

years nor in specific sub-areas owing to the fluctuating occupancy rate of breeding territories in successive years (see de Bruijn 1979). However, exact values can be given for the period 1967-84 due to counts made in five census plots ranging in size from 75-125 km^2 (see Fig. 3). These plots were carefully searched for breeding pairs of Barn Owls every year as described in section 3.1. The annual numbers of breeding pairs in the three sample plots in Liemers (250 km^2 altogether) and in the two plots in Achterhoek (250 km^2, too) are graphically shown in Figure 7. In this figure periodic dips in the numbers of breeding pairs both in Liemers and Achterhoek can be seen, corresponding to cyclic troughs in the vole population (1969, 1973, 1976, 1979). Regarding long-term trends, the Achterhoek population apparently shows an increase in numbers whereas the Liemers population seems to decline over the period 1967-84. Firstly, the population trend over time was tested as regards the total numbers (both breeding and non-breeding birds) in the census plots in Liemers and in Achterhoek. Therefore a linear regression analysis was made of the annual numbers of Barn Owls over the period 1967-84, based on the data in Appendix 2. This analysis showed a significant decrease in Liemers ($p < 0.05$) and a significant increase in Achterhoek ($p < 0.005$).

Significance in trends in breeding numbers over time (1967-84) was tested for each census plot separately using linear regression (Fig. 8). The results of the annual counts as given in Appendix 2 were converted to breeding pairs per 100 km^2 so that the densities could be compared. For both sample plots in Achterhoek (A1 = W. Achterhoek and A2 = E. Achterhoek) the breeding densities increased (A1: $p < 0.001$; A2: $p < 0.05$). For two of the three sample plots in Liemers (L1 = W. Liemers and L2 = E. Liemers) the breeding densities decreased (L1: $p < 0.01$; L2: $p < 0.05$) while in one plot (L3 = N. Liemers) no significant trend in breeding density could be shown.

The Barn Owl population level can be expressed by giving the range of the breeding densities (minimum and maximum value) and the mean breeding density for the whole study period (1967-84). Taking the three census plots in Liemers together (=250 km^2), the annual number of breeding pairs ranged from 0 to 13, corresponding to 0-5.2 (mean 2.4) breeding pairs per 100 km^2. It should be realized that the population densities in the holocene landscape types of Liemers were much higher in the late 1950s (see Table 1). Anyhow, in 1984 during a peak of the Common Vole as many as six Barn Owl pairs (raising 21 fledged young) were found in N. Liemers in a 65 km^2 area of a river landscape adjoining a cover-sand region.

Taking the two census plots in Achterhoek together (=250 km^2), in the period 1967-84 the annual number of breeding pairs ranged from 3 to 22, corresponding to 1.2-8.8 (mean 5.3) breeding pairs/100 km^2. These densities in the pleistocene landscapes of Achterhoek are even higher than the population densities in this region during the late 1950s (Table 1). During the vole peak year 1981, in the census plot W. Achterhoek (cover-sand landscape with moor-reclamations), a concentration of six breeding pairs (raising 26 young) was found in an area of only 35 km^2. In the whole census plot W. Achterhoek (125 km^2) a total number of 13 pairs bred in 1984, corresponding to a breeding density of 10.4 pairs/100 km^2.

4.3 Population levels compared with other populations

Generally speaking, the highest population densities were found in the following landscape types of the study area: in the river landscape (over 10 breeding pairs/100 km^2 in peak vole years until the 1960s), in the cover-sand landscape (5-10 breeding pairs/100 km^2) and in the plateau landscape (5-7 breeding pairs/ 100 km^2 in good vole years). It has to be said that these values are relatively high. In fact, they were hardly representative of the Dutch situation: maximum densities exceeding 5 breeding pairs per 100 km^2 have been claimed for only a very few localities in the eastern and southern parts of The Netherlands in the period 1963-84.

After a number of good vole years, the Dutch Barn Owl population peaked in 1990 thanks to a very high population level of the Common Vole *Microtus arvalis*. In that year in 25 square plots of 10 by 10 km (100 km^2) more than 10 breeding pairs of the Barn Owl were established in The Netherlands (van der Hut *et al.* 1992). Six of those plots (=24%!) were located in the present study region: two in N. Liemers (with 11-12 breeding pairs/100 km^2) and four in Achterhoek (with 11-13 breeding pairs/100 km^2). As for the period 1967-84, these density figures refer to pairs which actually bred (confirmed broods).

Comparison with population data from other

Table 3. Population density of the Barn Owl in Western and Central Europe in the period 1960-1985 based on long-term monitoring studies.

Study region (nation)	Census period	Area size (km^2)	Population density (breeding pairs/100 km^2)			Source
			min. (year)	max. (year)	mean	
W. Germany (FRG)	1960-72	840	0.2 (1969)	4.5 (1968)	1.7	Wülfing in Schneider (1977)
E. Germany (GDR)	1968-74	1000	1.5 (1969)	5.4 (1971)	3.3	Schönfeld *et al.* (1977)
SW Scotland (GB)	1981-85	2200	2.2 (1985)	5.1 (1981)	3.2	Taylor *et al.* (1988)
Liemers (NL)	1967-84	250	0 (1969)	5.2 (1968)	2.4	this study (see note)
Achterhoek (NL)	1967-84	250	1.2 (1969)	8.8 (1984)	5.3	this study (see note)

NOTE. Density figures for Liemers and Achterhoek (period 1967-84) are calculated from basic data in Appendix 2.

Fig. 9. Traditional breeding site of the Barn Owl in the river landscape. Photo Onno de Bruijn.

areas should be carefully made. In most regions of western Europe, as in the study area, Barn Owl populations fluctuate considerably in numbers from year to year. As stated before, censuses should be made for several years (at least 6-7 successive years, in order to cover two vole cycles) and within areas large enough, also chosen at random (at least 75-100 km^2, representing the main habitats in the study region). Examination of published data on Barn Owl population densities shows that only a few records fulfil these conditions. These are reviewed in Table 3. Globally speaking, the densities found in these long-term studies are about of the same order as the densities established during the present Dutch study. Strikingly, both the lowest density (0 pairs/100 km^2) and the highest density (8.8 pairs/100 km^2) were established in the Dutch study region, in Liemers (1969, 1979) and in Achterhoek (1984) respectively.

5. NEST SITES AND FORAGING HABITATS

In western and central Europe, Barn Owls occur in lowland and hilly country in Atlantic or moderately continental climates with winter snow averaging less than 40 days duration and less than 7 cm depth. Within this range they inhabit open but not treeless landscapes offering adequate prey (voles, mice, shrews). For the greatest part, these habitats are formed by land used for various types of agricultural practices. Mixed farmland habitats with a great diversity of small landscape elements are preferred in which a rich food supply over the seasons and the years is best guaranteed (Glutz von Blotzheim & Bauer 1980). A more specific habitat is formed by young forest plantations in Britain in the first years when farmland (mainly sheepwalk) is taken over by forestry. Here, Barn Owls are attracted by huge numbers of voles and the same applies on the continent on complexes of arable fields which are taken out of production (set-aside).

Adjacent to good foraging habitats, Barn Owls need suitable daytime roosts and nest sites. These are characteristically found in old buildings in villages and hamlets as well as in scattered farmsteads including outhouses which offer dark and undisturbed places with free access (Cramp 1985). Nowadays this species rarely breeds in hollow trees in most parts of its distribution range, with Britain as a striking exception (see Bunn *et al.* 1982).

5.1 Breeding sites and nest sites

The global scheme outlined above can be further worked out on the basis of conditions found in the Dutch study region. In Table 4 the different types of breeding sites of Barn Owls have been classified, as observed in Liemers and Achterhoek in the period 1956-84. Most breeding sites were situated in farm buildings with over 85% of all broods established. In the study region, Barn Owls prefer old farmsteads with a number of outhouses (barns, granaries etc.) as breeding sites, and among these, somewhat untidy farmyards surrounded by old trees are favoured (Fig. 9). Many of them have been inhabited by breeding Barn Owls for several decades, some even longer. The owls nested inside the farm buildings on lofts, rafters, amongst bales of hay or -very typically in the study region- in dovecotes (Fig. 10). From 1967 onwards most of these were replaced by special Barn Owl breeding boxes (see below). Besides the farmsteads, a number of churches have also been occupied for long periods by breeding Barn Owls, particularly in Liemers. The owls live in the church towers and in dark lofts seldom entered by people; here the eggs are laid in some dark corner, preferably in a more or less enclosed site. Furthermore castles, windmills and old houses have been used occasionally as places for breeding. 'Natural' nest sites such as hollow trees are very rarely observed (only 2 out of 95 sites in the study area with only 1% of all broods established). This nesting scheme fits the general Dutch pattern (Braaksma & de Bruijn 1976).

During the first years of our research we developed special Barn Owl nesting boxes in order to compensate the loss of favourable nest sites. The most successful type appeared to be a wooden nestbox about 75 cm long, 40 cm wide and 50 cm deep with an entrance hole of about 15 cm x 15 cm. These boxes are placed in dark and quiet corners well above the ground within suitable buildings with free access to the owls

Table 4. Breeding site selection of Barn Owls in Liemers and Achterhoek (period 1956-84). Figures show (a) total numbers of breeding sites recorded, and (b) total numbers of broods established in the particular type of breeding site.

Type of breeding site	Liemers		Achterhoek		Total study area	
	(a) sites	(b) broods	(a) sites	(b) broods	(a) sites	(b) broods
Farm buildings	25 (64%)	85 (73%)	49 (88%)	256 (91%)	74 (78%)	341 (86%)
Churches	6 (15%)	14 (12%)	4 (7%)	14 (5%)	10 (11%)	28 (7%)
Castles	3 (8%)	8 (7%)	- (-)	- (-)	3 (3%)	8 (2%)
Other buildings	3 (8%)	7 (6%)	3 (5%)	10 (4%)	6 (6%)	17 (4%)
Hollow trees	2 (5%)	2 (2%)	- (-)	- (-)	2 (2%)	2 (1%)
Total	39 (100%)	116 (100%)	56 (100%)	280 (100%)	95 (100%)	396 (100%)

Fig. 10. Young Barn Owls in an old dove-cote. Photo Jos Korenromp.

(Fig. 11). In the period 1967-84 more than 200 of these Barn Owl nestboxes were provided all over the study area, in co-operation with local farmers and other countrymen. In Liemers 75 nestboxes were placed in suitable buildings in the period 1967-84, giving an average density of about 20 boxes per 100 km^2 by the mid 1980s. In Achterhoek 135 boxes were set up in the same period, which gives an average of 25 boxes per 100 km^2. The distribution of all the nestboxes in the study area in the period 1967-84 is shown in Figure 12. This also shows which boxes have been occupied.

The nestbox campaign proved to be successful. In places were Barn Owls used to breed (traditional territories), the nestbox was habitually adopted by the owls in the next breeding season. A number of breeding sites which had been left became re-occupied within a few years. Table 5 reviews the use of the nestboxes by breeding Barn Owls within a 10-year period following their placement. The over-all occupancy rate of the nestboxes by breeding Barn Owls was about the same in Liemers as in Achterhoek (32% and 36% of the supplied boxes, respectively). However, in Liemers the nestboxes were occupied less frequently than in Achterhoek.

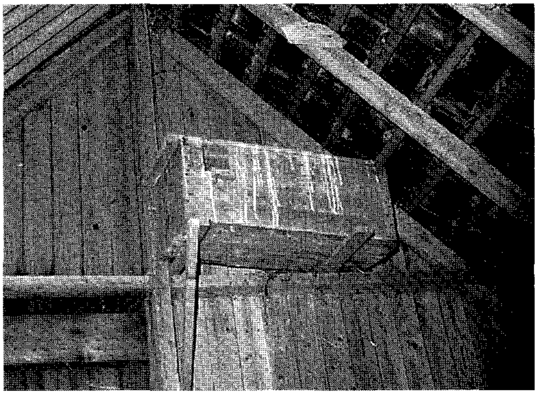


Fig. 11. An occupied Barn Owl nestbox. Photo Onno de Bruijn.

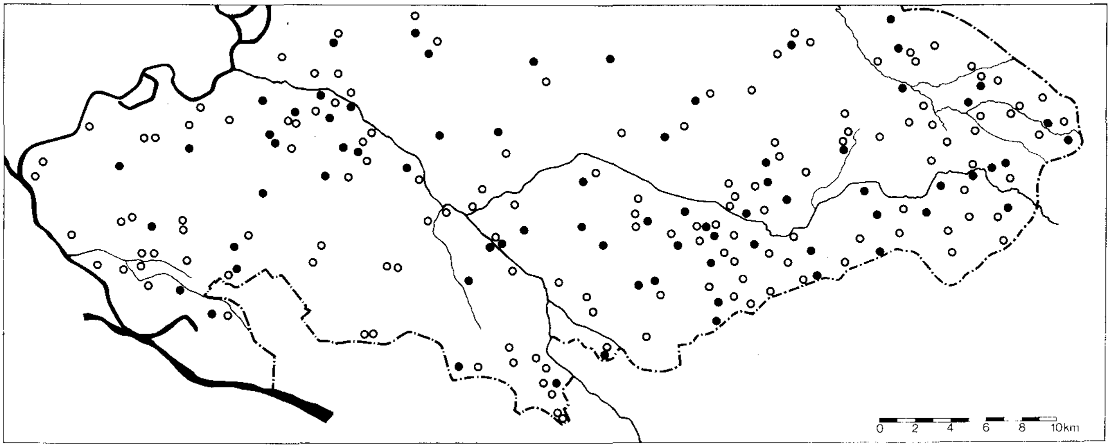


Fig. 12. Locations of Barn Owl nestboxes placed in Liemers and Achterhoek in the period 1967-84. Solid circles indicate nestboxes which have been occupied at least once by breeding Barn Owls in the 10-year period following their placement. Open circles indicate nestboxes which remained vacant in the 10-year period after placement.

Analysing the frequency of occupancy of the nestboxes, in Liemers 79% of the successful boxes were used only in 1-3 years by breeding Barn Owls, as against 17% in 4-7 years. Just one nestbox (=4%) was used more frequently: a breeding site in N. Liemers which has been occupied in 8 out of the 10 years after placing the box (with a total of 30 young fledged). In Achterhoek, 42% of the successful boxes were used in 1-3 years and 39% in 4-7 years. No less than 9 boxes (=19%) were used still more frequently, of which three boxes were even occupied every 10 year by breeding Barn Owls (delivering 24, 31 and 37 raised young per box).

The mean frequency of occupancy of the nestboxes appeared to be significantly higher in Achterhoek than in Liemers, averaging 4.5 as against 2.8 out of 10 years as shown in Table 5 (one-sided t test, $p < 0.005$).

Altogether, the results of our nestbox scheme in the study region have been surprisingly good, as can be demonstrated for the intensively censused areas. During the initial stage (period 1967-75) of this conservation programme less than 25% of the Barn Owl broods (39 out of 172) were established in nestboxes. In parallel with the growing number of boxes available, more than 75% of the Barn Owl broods (133 out of

Table 5. Frequency of occupancy of Barn Owl nestboxes in Liemers and Achterhoek over the 10-year period following on their placement. Figures are based on occupancy of the nestboxes by Barn Owl pairs which were actually breeding (clutch laid).

District	Number of nestboxes	Occupied by breeding Barn Owls	Number of years occupied										Mean frequency of occupancy (years) in 10-year period
			1	2	3	4	5	6	7	8	9	10	
Liemers	75	24 (32%)	7	7	5	1	1	1	1	1	-	-	2.8
Achterhoek	135	48 (36%)	9	6	5	6	6	6	1	2	4	3	4.5

NOTE. Figures concern nestboxes which were set up in study area from 1967 until the beginning of 1984 (see Figure 12). Survey results include data up to and including 1993.

Table 6. Structure of traditional Barn Owl home ranges in various landscape types in the study area. Single Barn Owl home ranges are indicated by letters (A-P). The size of the dots indicates surface-covering of the habitat-complexes in home range concerned.
Key: • = 4-10%, ● = 11-25%, ⬤ = 26-50%, **⬤** = > 50% surface-covering.

Habitat-complex based on land use	Polders		Reclaimed Moors		River landscape				Cover-sand landscape				Plateau landscape			
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
1. BUILT-UP AREAS																
1.1 village, hamlet		•	•		•	•				•	•				•	
2. FARMLAND																
2.1 predominantly grassland, open scenery	⬤	⬤	⬤	●	●	●		●		•		•	●	•		•
2.2 predominantly arable fields, with loosely grouped farmsteads, open scenery	•	●						●	•		●	●	⬤		•	⬤
2.3 complex of arable fields and grasslands, with many farmsteads, open scenery			●	●			●			●						
2.4 predominantly grassland, with many hedgerows or rows of trees	**⬤**	⬤	●	⬤	•	●	●	●	●	●	●	●	•	●	⬤	•
2.5 complex of arable fields, orchards and grasslands, with many dispersed or loosely grouped farmsteads					**⬤**	⬤	⬤	●								
2.6 complex of arable fields and grasslands, with many hedgerows, rows of trees, woodlots and many dispersed farmsteads							●	●	**⬤**	**⬤**	⬤	⬤	●	⬤	⬤	●
3. SEMI-NATURAL HABITATS																
3.1 fen/marsh: complex of shallow water, reed fens and valley bogs					•	●	•									
3.2 moor/bog: complex of poor-fens, heaths and raised bogs														•		
3.3 woodland: predominantly coniferous and mixed forests				●						•		•		•	•	•
3.4 woodland: predominantly deciduous forests							•	•	•				•	•	•	●

NOTES. (1) The home ranges A-B and E-H are situated in Liemers, the home ranges C-D and I-P are situated in Achterhoek. (2) Home ranges extending over two landscape types were classed under the landscape type containing the nest site and the greatest part of the hunting grounds.

175) were situated in nestboxes in the next period (1976-84), and in the period 1985-93 more than 90% of all Barn Owl broods in the study area were raised in breeding boxes! Over the last decades, this nestbox scheme has proven to be an important weapon in the struggle for the conservation of the Barn Owl population.

5.2 Structure of Barn Owl home ranges in various landscape types

Barn Owls show a tendency to hold on to definite breeding sites and foraging areas. For a species like this (in which the adult birds are mainly resident) the term 'home range' as defined in Newton (1979) is appropiate, implying the nesting territory (with one or more nest sites) and the hunting grounds of a pair. An aerial photograph of a characteristic home range in Liemers is shown in Figure 13, a traditional home range in Achterhoek in Figure 14. On these photographs a number of typical habitat-complexes based on land use can be distinguished within the landscape types shown.

In order to detect the habitat-complexes of vital importance to Barn Owls, Table 6 was composed. This table shows the structure of 16 regularly occupied Barn Owl home ranges in the study region, each based on an area coverage of the order of 5-10 km^2. On the vertical axis of Table 6, habitat-complexes typical of the study area are classed in three main groups: built-up areas, farmland and semi-natural habitats. On the horizontal axis, Barn Owl home ranges are arranged according to the landscape types as found in the study area. Only such home ranges were selected as have been regularly occupied by breeding Barn Owls in both the periods 1967-75 and 1976-84 (so-called 'traditional home ranges'). The habitat structures of the territories shown in this table represent the field situation around 1975. Based on this scheme and supplemented by many field observations, habitat selection of the Barn Owl can be analysed by landscape type. In the text below, the numbering of habitat-complexes agrees with the code used in Table 6.

Polder landscape. Only a very few Barn Owls live in the polders due to a limited number of appropiate breeding sites: these basin areas were periodically flooded and are therefore almost without human occupancy. Moreover the polders are poor in prey species: only Common Voles and Common Shrews live here in considerable numbers. The only two known traditional nest sites are located in a church in a small village and in a centuries old barn on a mound. The foraging areas are characterized by large grassland areas, both open complexes (type 2.1) and the type with many hedgerows (2.4). Owls living here can hardly survive in poor vole years.

Moor-reclamation landscape. The reclaimed moors constitute a rather uniform landscape sharing a number of habitat features with the polder landscape. As in the latter type, only a few Barn Owls pairs nest here: as few as two traditional home ranges are known to us despite the large area of reclaimed moors in the study region (Table 2). Here the owls breed in dovecotes in farms which were built after reclamation of the moors in the 1920s and 1930s. They hunt Common Voles and Common Shrews in the surrounding grassland areas, both open complexes (type 2.1) and the type with many hedgerows (2.4). This last, and a few areas with mixed farming (type 2.3) could provide some alternative prey to the owls in periods of vole scarcity.

River landscape. Barn Owl home ranges in the riverine area show much more variation than in the polders. The owls nest in old villages and country seats on the natural levees, and in large farms which are situated either in small groups or more dispersed. The Barn Owls hunt in castle parks and over churchyards and farmyards, and in bad weather also within old barns. Outside in the riverine area they prefer complexes of arable fields with orchards on the natural levees (type 2.5) and areas with mixed farming enriched with hedgerows and small woodlots (type 2.6). Furthermore the owls visit rough dike-slopes and extensive grassland areas in the river valleys (types 2.1 and 2.4).

Cover-sand landscape. Here the owls inhabit the relatively small farms typical of this area. Their habitat requirements are perfectly fulfilled in the small-scale mixed farmland (elevated arable grounds and lower grasslands), the more because of the presence of so many woodlots, hedges and rows of trees where many different prey species are found (type 2.6). The hunting flights lead Barn Owls also to grassland-complexes (preferably with many hedges, type 2.4) in adjoining moor-reclamations, as observed.

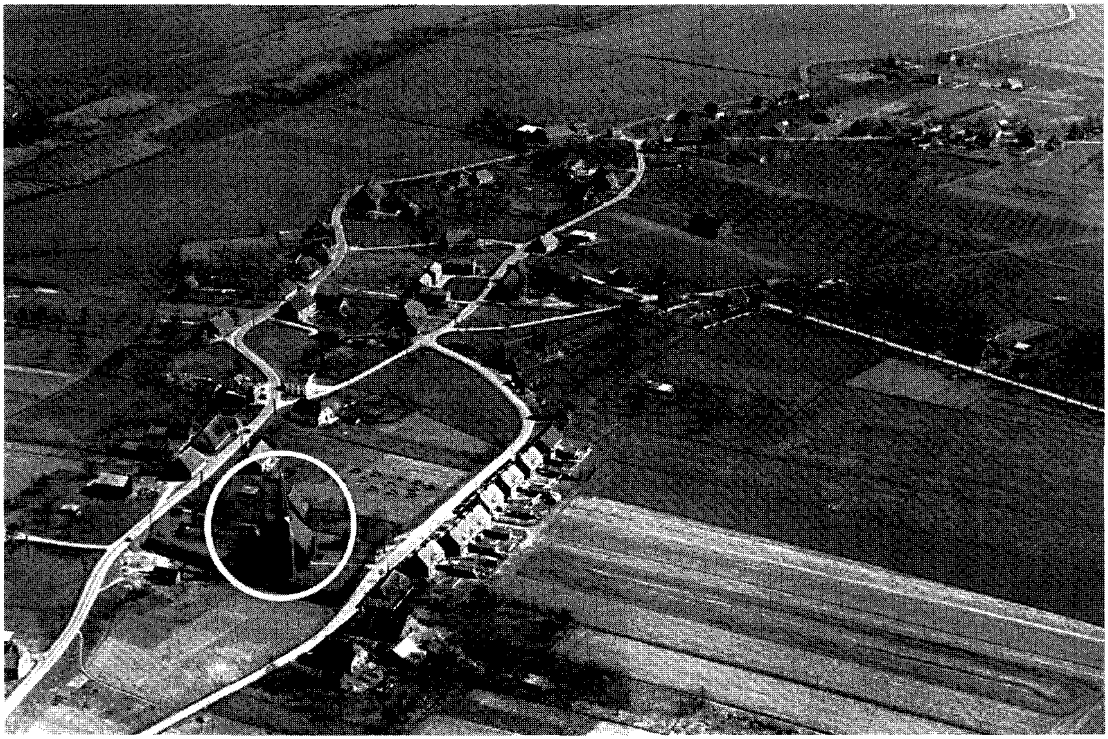


Fig. 13. Traditional home range of the Barn Owl in river landscape in Liemers. The picture shows the village of Aerdt with many farmsteads situated on a natural levee along an old branch of the Rhine. Near the village orchards and complexes of arable fields are found. Nearby (top left) a fen landscape with reed-beds and adjoining grassland-complexes can be seen. The Barn Owl used to breed in the village church (see circle). Photo KLM-Aerocarto.

Plateau landscape. This region has a very long occupancy history both of men and owls, living together in traditional farms. These are loosely nucleated or still more dispersed (often along the borders of small valleys). The owls can find much prey around the farmsteads. Favourite foraging habitats in the surrounding countryside are complexes of arable fields (type 2.2), areas with mixed farming and many trees (2.6) and grassland-complexes with hedges (2.4), the last type being situated in the stream valleys and in adjoining moor-reclamations. Home ranges in the plateau landscape usually show a larger proportion of woodland (types 3.3 and 3.4) than those in the cover-sand region.

Semi-natural landscapes. No Barn Owls are breeding at all in the fen landscape, on the wooded moraine ridge and in the moor landscape in the study area. Occasionally observations were made of Barn Owls searching for prey along the edges of large woods and along the margins of marshes and moorland.

5.3 Review of the main habitat requirements

Considering the habitats favoured by Barn Owls we can discern a number of basic essentials which apparently define the ecological requirements of this species:

1. The occurrence of old buildings accessible to owls, preferably surrounded by somewhat untidy places with old trees (e.g. farmyard, churchyard, castle park, standard orchard).
2. A relative openness of the habitat (characteristic of most types of farmland) in combination with the presence of many small landscape elements such as pools, swamps,

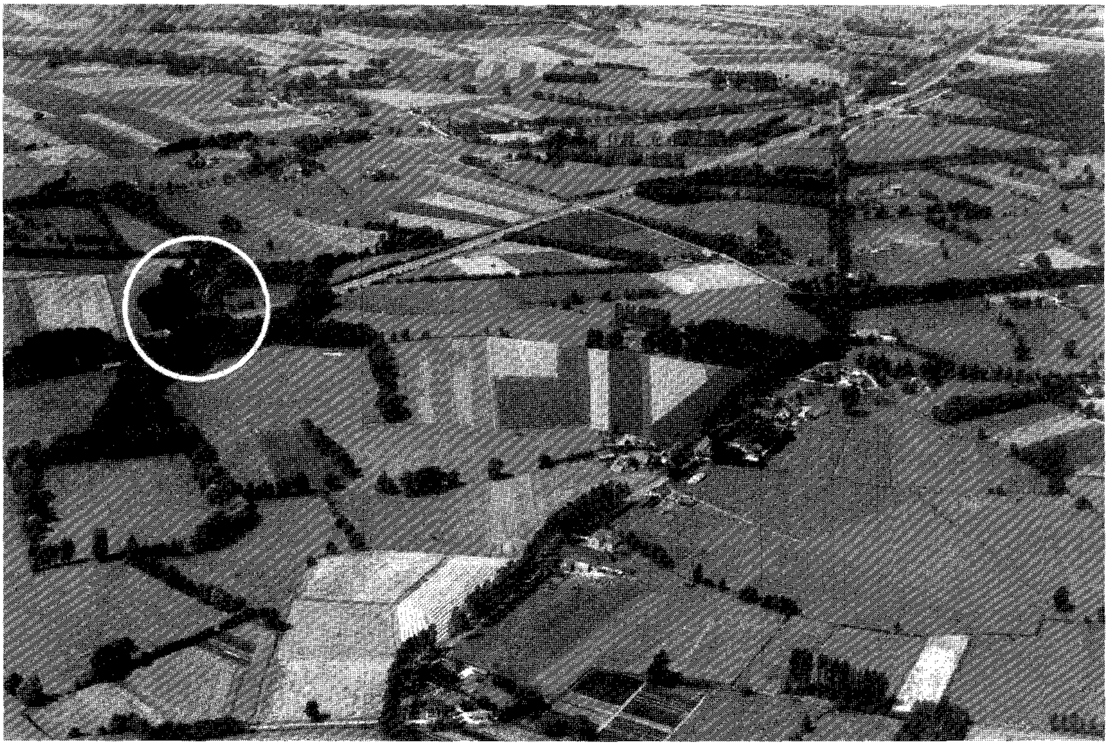


Fig. 14. Traditional home range of the Barn Owl in cover-sand landscape in Achterhoek. The picture shows the hamlet of Barlo with many loosely nucleated farmsteads. It depicts a small-scale landscape with many copses, lines of trees and wooded banks bordering complexes of arable fields (on cover-sand ridges) and grassland complexes (on lower intervening grounds). Furthermore (top right) a moor reclamation landscape with forest plantations and grassland complexes can be seen. The Barn Owl traditionally breeds in an old farmstead surrounded by trees (see circle). Photo KLM-Aerocarto.

rows of trees, old standard orchards, hedges and small woodlots (as especially well represented in the types 2.4, 2.5 and 2.6 of Table 6). Such small landscape elements have to show a scattered pattern over the home range rather than being concentrated in large complexes.

3. The occurrence of relief in landscape (high-low pattern) proves to be a common factor in many traditional Barn Owl home ranges. Relief causes differences in ground water level and soil, and therefore variation in land use and vegetation, bringing about diverse small mammal habitats favoured by hunting Barn Owls. The need for relief is fulfilled by some specific habitat-complexes (particularly the types 2.3, 2.5 and 2.6 in Table 6), but also within some landscape types as a whole (complex of natural levees and valleys in the river landscape, complex of ridges and depressions in the cover-sand region, complex of plateau remnants and stream valleys in the plateau landscape).
4. And finally, Barn Owls favour patches of more or less open land which are not too intensively tended by man, such as rough pastures, hay-fields, damp grasslands or wetlands, coarse ditches and roadside verges, grassy slopes, young plantations, waste and other marginal land, fringes of hedgerows and edges of woodland etc.

Most of these basic conditions are described in one or another form in the detailed records of habitat choice of *Tyto alba* in its western and central European range (e.g. Honer 1963, Glue 1967, Sparks & Soper 1970, Schneider 1977, von Knorre & Barnikow 1981, Epple & Hölzinger 1987). For, the conditions outlined above provide Barn Owl pairs with enough shelter and food for themselves and for their young throughout the seasons and in successive years. Suchlike prime Barn Owl habitats are pictured in Figures 15 and 16.

6. PREY STOCK AND OWL'S DIET

Barn Owls are mainly nocturnal feeders, usually searching for small mammals by way of hunting flights at a height of 1-3 meter. Apparently most prey are located by sound (Cramp 1985). Its long and broad wings enables the Barn Owl to fly slowly and silently over open habitats, along hedgerows and woodland edges and so on. It often follows regular hunting beats, in which field boundaries such as hedges, wooded banks and ditches are favoured flight lines. Such searching flights are sometimes alternated by short periods of hovering above a particular spot before dropping to the ground to strike a rodent. Another foraging method is performed from fence posts or other perches; this is the manner in which Barn Owls hunt within buildings also. Details concerning hunting techniques can be found in Sparks & Soper (1970) and Bunn *et al.* (1982). The Barn Owl feeds almost exclusively on small mammals in every part of its European range. Members of the three mammal families *Microtidae* (voles), *Muridae* (mice and rats) and *Soricidae* (shrews) formed 86-99% of the total number of prey identified from pellet analyses in seven European countries (Mikkola 1983). The same applies to the Dutch situation and, more particularly, to the study area in Liemers and Achterhoek, where small mammals constituted 96.5% of the total number of prey items (n= 10160) identified by pellet analyses, as against birds 2.9%, amphibians 0.5% and insects 0.1% (de Bruijn 1979).

6.1 Occurrence of prey species in various landscape types

For a reasonable understanding of the prey selection of the Barn Owl, basic knowledge of the prey stock is essential, especially with regard to the occurrence and habitats of the main prey species. In this we will focus on the group of small mammals which form the staple food of the Barn Owl. Much information on the occurrence and the habitat selection of small mammals in the Netherlands can be found in Wammes (1979), van der Reest (1989) and Broekhuizen *et al.* (1992). There is a fair amount of information available on the occurrence of small mammals (*Microtidae*, *Soricidae*, *Muridae*) in the study area, from unpublished field work both in Liemers and Achterhoek, in which various habitats were sampled with Longworth live-traps. Table 7 compiles all available information on the occurrence of small mammals in the study area. This global scheme demonstrates the distribution and relative abundance of this group of prey species in the landscape types where Barn Owls are found.

It appears from Table 7, that two (or maybe three) potential prey species are widely distributed and abundant in all five landscape types concerned: the Common Vole *Microtus arvalis* (Syn.: Continental Vole) and the Common Shrew. In the past it was generally accepted that all Common Shrews in The Netherlands belong to the species *Sorex araneus* but recent zoological research has shown that another species, *Sorex coronatus*, occurs. In former studies no distinction was made between *S. araneus* and *S. coronatus* and this applies to the author's work, too; therefore both taxa are taken together as *S. araneus/coronatus*. There are indications, that *S. coronatus* drives out *S. araneus* towards the wetter habitats in NW Europe (Mys *et al.* 1985). Recent pellet examinations have shown that both species indeed occur in the study region in Liemers as well as in Achterhoek (M. La Haye, pers. comm.).

Common Voles live in farmland which is not too intensively tended; on more cultivated farm-

Table 7. Occurrence of small mammals in various landscape types in study area. Distribution and status are indicated as follows: ⬤ = widely distributed, abundant; ● = rather local, but common in suitable habitats; • = widely distributed, but in small numbers; · = local, small numbers; + = of incidental occurrence; - = absent.

Prey species	Polders	Reclaimed Moors	River landscape	Cover-sand landscape	Plateau landscape
SORICIDAE:					
Sorex araneus/coronatus	⬤	⬤	⬤	⬤	⬤
Sorex minutus	–	·	·	•	•
Crocidura russula	+	·	⬤	●	⬤
Neomys fodiens	+	–	+	–	·
MICROTIDAE:					
Microtus arvalis	⬤	⬤	⬤	⬤	⬤
Microtus agrestis	+	●	•	•	●
Clethrionomys glareolus	–	+	●	⬤	⬤
Arvicola terrestris	•	•	●	•	•
MURIDAE:					
Apodemus sylvaticus	•	●	⬤	⬤	⬤
Mus musculus	●	•	⬤	⬤	⬤
Micromys minutus	·	–	●	·	●
Rattus norvegicus	·	·	•	•	•
Total number of species	7-10	9-10	11-12	11	12
- category ⬤	2	2	5	5	6
- category ●	1	2	3	1	2
- category •	2	2	2	4	3
- category ·	2	3	1	1	1

land they are found along parcel boundaries and in hedgerows and wooded banks fringed with rough grassy vegetation, in road verges, on coarse dike slopes etc. They can be very numerous in polder and riverine areas, especially in large plains of sparsely used pastures and hayfields: so-called 'vole plague areas' (van Wijngaarden 1957). *Microtus arvalis* has an enormous reproductive capacity, resulting in strongly increasing numbers during summer and autumn. On the other hand Common Vole populations can sustain severe losses in the winter season, especially during periods of unfavourable weather, e.g. hard frost or prolonged heavy precipitation (rain, snow). Common Vole populations fluctuate violently, typically reaching peak numbers every 3 or 4 years. This phenomenon is most strongly developed in real vole plague areas. However, such areas are getting increasingly scarce as a result of intensification of farming practices; this process was recognised by van Wijngaarden (1957) as early as the mid 1950s. During the present survey, vole plague areas were still found in a number of polders and riverine areas in Liemers and in one or two moor-reclamations in Achterhoek. The vole population cycles could be reconstructed thanks to statements of farmers on vole abundance, by means of rough estimates of the density of fresh vole burrows (occupied runs) and through regu-

Fig. 15. Mixed farmland in western Achterhoek (cover-sand landscape). Between the cornfield on a ridge and the lower-lying grassland, a herbaceous strip with brambles and bushes is present. Many invertebrates and small mammals (shrews, voles, mice) live in such marginal edges. Habitat of the Barn Owl, Stonechat *Saxicola torquata* and Yellowhammer *Emberiza citrinella*. Photo Onno de Bruijn.

lar counts of numbers of vole-eating raptors (Kestrels *Falco tinnunculus* and Buzzards *Buteo buteo*) which annually visited a vole plague study area (see de Bruijn 1979). The results are compiled in Table 8. The combined information allows the identification of vole cycles (period 1965-85) in the study area as well as the troughs in vole abundance and the real peak vole years.

Common Shrews are also widespread and abundant over the whole study region. *Sorex araneus/coronatus* appear to be very common in widely divergent landscape types all over the study area. They haunt habitats with rough grassy vegetation: coarse grasslands, verges of roadsides and ditches, fringes of hedges and wooded banks, edges of woodland, coppices, orchards and gardens. Populations of Common Shrews do not fluctuate violently in numbers as do vole populations, but seem to be rather stable in time (Croin Michielsen 1966).

Of the remaining shrews (*Soricidae*), only the White-toothed Shrew *Crocidura russula* is widely distributed and at least locally abundant in the study area. More than other shrews, it lives around farmyards, but this species can also be common on arable fields and in wooded banks. Real concentrations ('hot-beds') of White-toothed Shrews are locally found in the river landscape and in the sandy districts, while in contrast they are nearly completely absent in the polders and in the moor-reclamations. The other two shrews are only locally distributed and occur in small numbers. The Pygmy Shrew *Sorex minutus* occurs mainly in the sandy regions, the fine Water Shrew *Neomys fodiens* is nowadays only

Fig. 16. Mixed farmland in northern Liemers (river landscape). Due to the presence of many small landscape elements and habitat diversity, about 10 small-mammal species (shrews, mice, voles) live here. The presence of micro-relief brings about sheltered niches where owls can catch prey in winters with snow cover. Habitat of the Barn Owl, Little Owl *Athene noctua* and Grey Partridge *Perdix perdix*. Photo Dick Langwerden.

regularly found along the beautiful brooks of the Winterswijk plateau.

Of the remaining voles (*Microtidae*), none is anywhere near as numerous as the Common Vole. Only the Bank Vole *Clethrionomys glareolus* is abundant in the well-wooded landscapes, inhabiting forestry and horticultural plantations, coppices, wooded banks and various types of woodland. The Field Vole *Microtus agrestis* (Syn.: Short-tailed Vole) appears to be not so abundant in the study area, residing in long grassy vegetations in various habitats, farmland as well as moorland and woodland. The Water Vole *Arvicola terrestris* is widely distributed in wet habitats but is not numerous.

Finally, the group of mice and rats (*Muridae*) must be reviewed. The Wood Mouse *Apodemus sylvaticus* is generally distributed and is common (particularly in Achterhoek), inhabiting scrub, hedgerows, wooded banks, fringes of woodland and adjacent rough grassland. The House Mouse *Mus musculus* prefers to live in the neighbourhood of human habitation, probably in rather variable numbers (sometimes forming real 'family-swarms'). The pygmy Harvest Mouse *Micromys minutus* is rather scarce and has no substantial importance as a prey species for the owls. The Brown Rat *Rattus norvegicus* is widely distributed, but not really numerous except on a local and temporary basis.

6.2 Review of the prey stock

Reviewing the prey stock in different landscape types, the following conclusions can be drawn (Table 7):

1. Three landscape types in the study area have

Table 8. Population level of the Common Vole *Microtus arvalis* and reconstruction of the vole cycle in study area in two consecutive periods (1967-75 and 1976-84). For each year the density of voles is indicated in brackets. Key: 1 = very scarce (trough), 2 = moderate, 3 = abundant, 4 = very abundant (peak year).

	Period 1967-75	Period 1976-84
Poor vole years (1-2)	1969 (1), 1970 (2), 1973 (1)	1976 (1), 1979 (1), 1980 (2)
Good vole years (3-4)	1967 (4), 1968 (3), 1971 (4) 1972 (3), 1974 (4), 1975 (3)	1977 (3), 1978 (3), 1981 (4) 1982 (3), 1983 (3), 1984 (4)
Reconstruction of the vole cycle	(1966)-1968 1969 -1972 1973 -1975	1976-1978 1979-1984

NOTE. Methods used for establishing the vole population level in the study area are described in de Bruijn (1979). The intervals between successive numbers on the ordinal scale do not necessarily correspond to equal difference in densities of the voles.

a relatively wide spectrum of small mammals (11-12 potential prey species): the river landscape, the cover-sand landscape and the plateau landscape. These are likewise the landscapes with a complex geomorphological structure (see legend to Fig. 2), with the most variation in habitat-complexes (Table 6) and landscapes which are favoured by Barn Owls (Table 2)! In contrast, the uniform polders and the moor-reclamation landscape have a relatively narrow prey spectrum (7-10 potential prey species).

2. The Common Vole *Microtus arvalis* and Common Shrews *Sorex araneus/coronatus* are widely distributed and abundant in all landscape types harbouring Barn Owls in the study area. Besides these, some other species are widely distributed and abundant in the areas with the greatest habitat diversity (river, cover-sand and plateau landscape), viz. the White-toothed Shrew *Crocidura russula*, the Bank Vole *Clethrionomys glareolus*, the Wood Mouse *Apodemus sylvaticus* and the House Mouse *Mus musculus*. In the polders and moor-reclamations only Common Voles and Common Shrews have this general status.
3. Besides the species mentioned above, all other small mammals are found in considerable numbers only locally or temporarily in the study area, as shown in Table 7.

These conclusions concerning the prey stock hold the key to a good understanding of the feeding ecology of the Barn Owl. In the past much work has been dedicated to the diet of the Barn Owl in Liemers and Achterhoek by making extensive pellet examinations (de Bruijn 1979). The localities where pellets collections have been made are shown in Figure 3. In the present study, only the essentials of the relations between the Barn Owl and its prey are outlined. Figure 17 shows the prey spectra of the Barn Owl in Liemers and Achterhoek, with a subdivision in relation to vole density (diet in good and poor years of the Common Vole) and in relation to season (summer and winter diet). In the prey spectra of Figure 17, the contributions of the main prey species of the Barn Owl are expressed in terms of weight. The complete underlying data of prey occurrence have been recorded in Appendix 3.

6.3 Barn Owl diet in Liemers

In Liemers the Barn Owl diet reflects the vole cycle as it follows the peaks and troughs in the population of the Common Vole *Microtus*

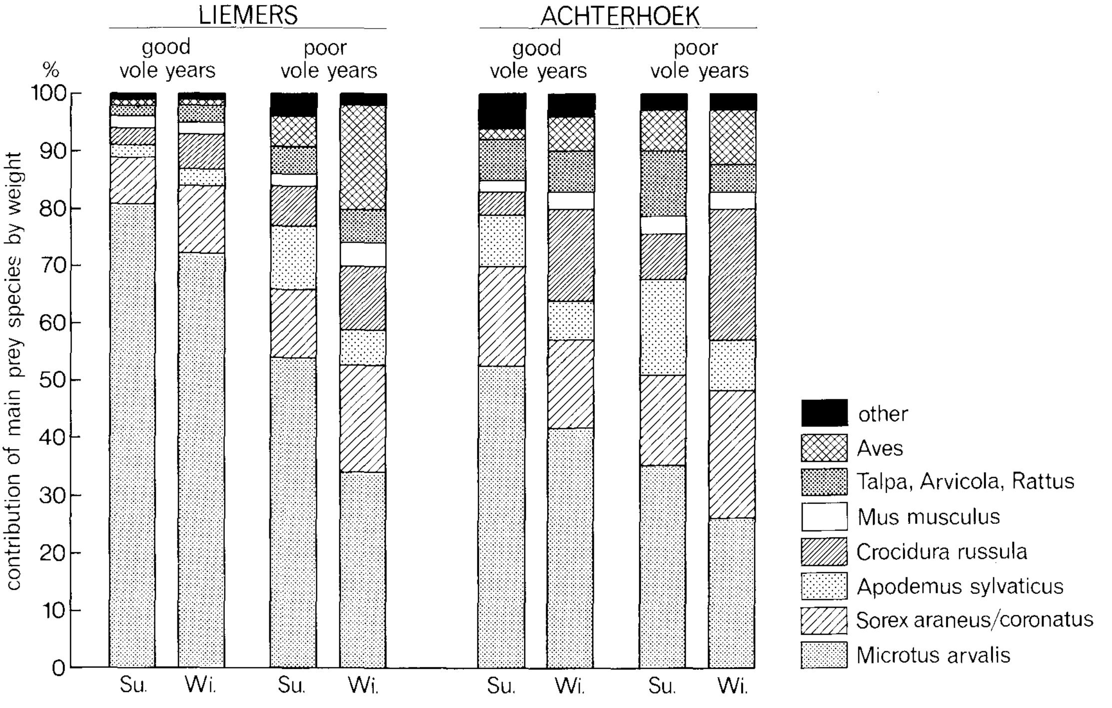


Fig. 17. Food spectra of the Barn Owl in Liemers and Achterhoek in relation to vole population level and to season (Su = May-October, Wi = November-April). The contribution of the main prey species by weight is given based on pellet analyses. Basic data regarding number of prey items taken are given in Appendix 3.

arvalis. The numbers of Common Shrews *Sorex araneus/coronatus* fall and rise in inverse proportion to the numbers of voles taken. In peak years the Common Vole generally constitutes 70% or more of the prey-weight throughout the year (see Fig. 17); in 'vole plague areas' in the polder and river landscape the voles generally contribute as much as 90-100% to the Barn Owl diet (de Bruijn 1979). In years with intermediate or low vole density, shrews are taken in some numbers (particularly in winter when vole mortality is high). In uniform landscapes such as most polders or after ambitious land consolidation operations, the alternative prey is insufficient: generally only Common Shrews are available which on an average have barely half the weight of a Common Vole. Even in poor vole years, as commonest secondary prey species the Common Shrew contributes on average only 15-20% of the prey weight. Therefore Barn Owls are forced to leave uniform landscapes at times of vole scarcity, as any birds remaining are virtually doomed to starve. Locally in the river landscape and in the cover-sand regions in N. Liemers, alternative prey can be found: especially Wood Mice *Apodemus sylvaticus* along hedgerows and at the edges of woodland. Furthermore in winter another prey species can figure importantly in these areas, viz. the White-toothed Shrew *Crocidura russula* (which is nearly completely absent in the polder landscape and in the moor-reclamations). The greatest proportion of White-toothed Shrews (more than 10% by weight) in the diet of Barn Owls is characteristically found in the winter season, reflecting a shift in preferred foraging areas of the owls at that time: from the fields in summer to the surroundings (and the interior!) of buildings in winter. To some extent the same applies to the House Mouse *Mus musculus* as a prey species. In periods with vole scarcity, Barn Owls are inclined to hunt other small terrestrial prey. Where no alternative mammal prey is available, some Barn Owls in Liemers manage to survive by specialising on bird prey (mainly on House Sparrows *Passer domesticus*). Otherwise Barn Owls vanish out of uniform landscapes at times of vole scarcity. In this respect, however, the Barn Owl is not nearly so flexible as the nomadic Long-eared Owl *Asio otus* which in winter often concentrates on communally roosting birds in suburbs, preying upon local sources of small mammals and House Sparrows (Smeenk 1972, Wijnandts 1984).

6.4 Barn Owl diet in Achterhoek

In Achterhoek in general more diversity of habitats types is found with a richer mammal fauna, particularly in the cover-sand and the plateau region (see Table 7). Real vole plagues hardly occur in Achterhoek, but still the vole cycle makes itself felt in the prey spectrum (see Fig. 17). In good vole years the contribution of the Common Vole *Microtus arvalis* averages about 45-50% of the prey-weight. Besides the vole, some other species form the staple food in such years: Common Shrews *S. araneus/coronatus* (about 15% by weight), the White-toothed Shrew *Crocidura russula* (5-15%) and the Wood Mouse *Apodemus sylvaticus* (5-10%). In years of vole scarcity, the food supply is much better buffered in Achterhoek than in Liemers due to the greater landscape diversity of the cover-sand area and the Winterswijk plateau with so many woodlots, hedgerows, wooded banks, remains of moorland and small brook valleys. As a consequence, the smaller proportion of *Microtus arvalis* in the food (25-35% of the prey-weight) can be compensated by an increased contribution of *Sorex araneus/coronatus* (15-20% by weight), *Crocidura russula* (up to 20% in winter) and *Apodemus sylvaticus* (10-15%), supplemented with Water Voles *Arvicola terrestris* and Brown Rats *Rattus norvegicus*. It is a remarkable phenomenon that the Bank Vole *Clethrionomys glareolus* is hardly found as Barn Owl prey (Appendix 3), although it is very common in the well-wooded Achterhoek. Probably the Bank Vole, due to its habitat-selection, is not so vulnerable to predation by the Barn Owl as distinct from the Tawny Owl *Strix aluco* (Mikkola 1983). During periods of vole scarcity, shrews and mice constitute the main secondary prey of the Barn Owl. In this respect the Barn Owl differs from the sedentary Tawny Owl which is less dependent on small mammals and can easily resort to bird prey and medium-sized mammals (Smeenk 1972, Voous 1988). In Achterhoek, however, the great landscape diversity with many small-mammal prey species is in general highly supportive, allowing Barn Owls not only to survive but even to raise young in poor vole years.

7. REPRODUCTION IN RELATION TO FOOD SUPPLY

In western and continental Europe, the usual three or four year cycle of the Common Vole *Microtus arvalis* has a strong effect on the breeding performance of the Barn Owl (see Fig. 18). The vole cycle influences the annual occupancy rate of Barn Owl territories, the average clutch size and the fledging success (Schönfeld & Girbig 1975, Baudvin 1975, Braaksma & de Bruijn 1976, Kaus 1977, de Bruijn 1979). In the present study, the vole population cycles could be reconstructed for the period 1965-85 (Table 8). Low vole densities were found in 1966, 1969-70, 1973, 1976 and 1979-80. In the remaining years, the vole population level was intermediate to high, with 1967, 1971, 1974, 1981 and 1984 as real peak vole years.

7.1 Non-breeders and the breeding segment in the population

It is a well-known fact that Barn Owl territories (even the most traditional ones) are not occupied every year by a breeding pair of owls.

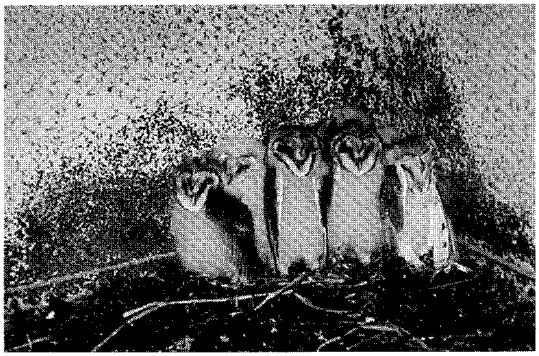


Fig. 18. Every 3 or 4 years, peak numbers of the Common Vole *Microtus arvalis* occur in 'vole plague areas'. These pictures were taken near Netterden (Liemers) in 1967. About 10 fresh vole burrows can be seen in an area of only 2 m^2. The local Barn Owls bred twice and successfully raised 8 young in their second brood. Photos Onno de Bruijn.

The occupancy rate seems to be primarily related to the food supply, especially to the vole population level. Secondly, weather conditions (particularly in the preceding winter) could play a part in controlling Barn Owl populations. The resultant of both is clearly reflected in the occupancy history of single Barn Owl territories (see de Bruijn 1979: 136) and in the frequency and duration in occupancy of breeding sites (see Table 5). The pattern of abandonment and re-occupation of Barn Owl territories has been studied in detail by Schönfeld *et al.* (1977) by systematic ringing of adult birds in an eastern German population. At most traditional nest sites, the females were replaced every two or three year; the turnover in males seemed to be even higher. These rapid changes in individual birds are not caused by outmigration but by the short life of Barn Owls (see also Chapter 9). After a harsh winter and certainly in trough vole years, many territories fall vacant, to be gradually re-occupied by other individuals in better times. These can be taken over by immigrants as well as by non-breeding owls which form a surplus within the population. The patterns of immigration and emigration in the study area are dealt with in Chapter 8 whereas the existence and the size of a non-breeding segment in the Barn Owl population is discussed below.

During the population surveys, we came across non-breeding Barn Owls in the intensively censused plots nearly every year (see Chapter 3). These were single birds as well as couples for which no nest could be found even after thorough searching of all potential breeding sites. The annual size of this non-breeding segment can be taken from the basic survey data in Appendix 2. These data are summarized in Table 9 for both Liemers and Achterhoek for the whole study period. The over-all share of non-breeding owls in the population averaged 19% in Liemers and 13% in Achterhoek; this difference between the two regions proved to be statistically significant (χ^2 test, $p < 0.05$). Most of the non-breeding owls were single birds, but couples and even triplets showed up within the population, contributing 4% and 1% to the numbers of owls, as given in Table 9.

The non-breeding element is necessary to fill gaps caused by mortality in the breeding population in order to maintain the annual balance in numbers. Unpaired birds were regularly established in traditional territories; usually the following year a breeding pair put in an appearance again. Non-breeders were also encountered in more marginal habitats in the study region in which Barn Owls rarely or never bred. Genuine non-breeding (territory holding by paired non-

Table 9. Size and composition of the non-breeding segment of the Barn Owl population in Liemers and Achterhoek (study period 1967-84).

	Liemers		Achterhoek	
	n	total of individuals	*n*	total of individuals
Non-breeding elements:				
– 1 owl present	38	38 (14%)	44	44 (8%)
– 2 owls present	5	10 (4%)	12	24 (4%)
– 3 owls present	1	3 (1%)	1	3 (1%)
Total number of non-breeding owls		51 (19%)		71 (13%)
Breeding pairs	108	216 (81%)	238	476 (87%)
Total number of owls		267 (100%)		547 (100%)
Non-breeding segment		51 (19%)		71 (13%)
Breeding segment		216 (81%)		476 (87%)

NOTE. Data refer to the five census plots which were intensively monitored over the whole study period (see Appendix 2 for the annual survey results).

breeders) was relatively rare (see Table 9), which is in agreement with the findings of Bühler (1964). Non-breeding triplets with intensified courtship activities in spring were once encountered in Liemers (at Gendringen in 1978) and once in Achterhoek (at Winterswijk in 1978).

The size of the breeding segment (percentage of owls involved in reproduction) proved to fluctuate from year to year in the study region. Most extreme values were found in 1969 and 1979 (both minimum years in vole density) when no breeding owls were present in the census plots in Liemers but some unpaired birds were noticed. In contrast, in 1981 in Liemers and in 1982 in Achterhoek (both years with a high vole abundance) all Barn Owls present in the census plots were paired birds with confirmed broods (Appendix 2). The breeding segment of the population thus showed its maximum possible range (0-100%) during this study.

Table 10 shows the size of the breeding segment in relation to the vole population level in two consecutive periods. More owls were involved in breeding in good vole years than in poor vole years (Wilcoxon test, $p < 0.05$). Statistically there is an indication that in Liemers in the first period (1967-75) the breeding segment was lower than in the second period (1976-84), but no causal explanation supported by scientific evidence could be found for this.

In the whole study period (1967-84), the relationship between the breeding occurrence of the Barn Owl and the vole population level was evident. This appears clearly from the annual occupancy rate of Barn Owl territories (expressed as percentage of the traditional territories which are occupied by actually breeding pairs) as shown in Table 11. For both Liemers and Achterhoek the occupancy rate is higher in good than in poor vole years (Wilcoxon test, both $p < 0.005$).

So the occupancy rate of Barn Owls territories is connected with the prey stock which in turn is linked with the state of the environment. It is very interesting to trace whether there have been changes in the occupancy rate of Barn Owl territories over the last decades. This can put us on the track of recent habitat changes influenc-

Table 10. Size of the breeding segment of the Barn Owl population in Liemers and Achterhoek in relation to vole population level in two consecutive periods (1967-75 and 1976-84). Breeding segment = % of owls involved in reproduction.

District	Vole population level	Breeding segment of the population			
		period 1967-75		period 1976-84	
Liemers	poor vole years	64%	(0-75%)	76%	(0-86%)
Liemers	good vole years	80%	(76-84%)	90%	(80-100%)
Achterhoek	poor vole years	81%	(67-85%)	84%	(76-90%)
Achterhoek	good vole years	87%	(80-92%)	89%	(78-100%)
Liemers	all years	77%	(0-84%)	87%	(0-100%)
Achterhoek	all years	86%	(67-92%)	88%	(76-100%)

NOTES. A review of the poor vole years and the good vole years is given in Table 8. The size of the breeding segment over the whole study period (1967-84) averaged 81% in Liemers and 87% in Achterhoek.

ing Barn Owl populations. Therefore the occupancy rates of Barn Owl territories in Liemers and Achterhoek have been calculated for the two consecutive periods 1967-75 and 1976-84. These two periods can be compared well, because both comprise the same numbers of poor and good vole years, see Table 8. In this analysis all territories were examined which have been occupied at least once by breeding Barn Owls in both census periods.

Firstly we will consider the developments in Liemers. In poor vole years, the mean annual occupancy rate of Barn Owl territories showed no statistical differences, averaging 18% and 14% respectively when the two periods are compared. In good vole years, however, the mean occupancy rate in Liemers dropped from 51% (period 1967-75) to 35% (period 1976-84) and this proved to be a significant decline (one-sided *t* test, $p < 0.005$). These results can be explained as follows. As a consequence of intensification of agriculture over the last decades, vole numbers have seriously decreased in the well-managed grassland areas of Liemers. At present, most remaining Barn Owls pairs have taken refuge in the small-scale areas with many hedgerows and woodlots in Northern Liemers, where they are less dependent on Common Voles for their staple food; most of them even breed in poor vole years. From such stations of survival, temporarily good foraging grounds (vole plague areas) could be populated in peak vole years in former days. At present, alas, the Barn Owl breeding population in Liemers can no longer benefit from good vole years to such an extent, while many vole plague areas have been lost. In the polders and riverine areas, many former territories have been completely deserted or are only occupied in extreme peak years of the Common Vole (cf. Figure 6). Most deserted territories are situated in areas where large-scale land consolidation operations have been carried out aimed at a strong intensification of agriculture.

In Achterhoek the occupancy rate of Barn Owl breeding territories remained rather stable in the last decades, both in the poor vole years (at 28% and 26% in succession) and in the good vole years (48% and 46% respectively) when the two periods are compared. As of old, the Barn Owl population is less dependent on *Microtus arvalis* for its staple food in this district (see Chapter 6). Although vole populations in Achterhoek have decreased to some extent, the food supply has apparently not yet become a key

Table 11. Mean occupancy rate of Barn Owl territories in Liemers and Achterhoek in relation to vole population level in two consecutive periods (1967-75 and 1976-84). Occupancy rate is expressed as percentage of traditional Barn Owl territories occupied by pairs which were actually breeding (clutch laid).

District	Vole population level	Mean occupancy rate of territories			
		period 1967-75		period 1976-84	
Liemers	poor vole years	18%	(0-29%)	14%	(0-29%)
Liemers	good vole years	51%	(41-59%)	35%	(29-53%)
Achterhoek	poor vole years	28%	(15-37%)	26%	(22-30%)
Achterhoek	good vole years	48%	(37-67%)	46%	(37-59%)
Liemers	all years	40%	(0-59%)	28%	(0-53%)
Achterhoek	all years	42%	(15-67%)	39%	(22-59%)

NOTE. A review of the good and the poor vole years is given in Table 6. Data in this table are based on monitoring of 17 traditional territories in Liemers and 27 traditional territories in Achterhoek. These were all territories which have been occupied at least once by a breeding pair of Barn Owls in both 9-year census periods.

limiting factor for the breeding occurrence of the Barn Owl in this district, as it is nowadays in large parts of Liemers.

7.2 Fledging success in Liemers and Achterhoek

In any year, the breeding performance of a Barn Owl population is not only determined by the occupancy rate of traditional territories by breeding pairs, but also by the average clutch size and the fledging success. In the study area, we have not systematically collected data on clutch size of Barn Owls in order to avoid disturbance as much as possible during the normal incubation period. However, the relation between the average clutch size and the vole population level has clearly been demonstrated in former Dutch studies (Braaksma & de Bruijn 1976, de Jong 1983) as well as in studies from other European countries (Schönfeld & Girbig 1975, Baudvin 1975). Breeding performance can be evaluated comprehensively by the number of young which are reared. This parameter ('fledging success') includes factors such as clutch size and hatching success.

Figure 19 shows the fledged brood size for good and for poor vole years. Both in Liemers and in Achterhoek, more young were raised in good vole years than in poor vole years (one-sided t-test, both $p < 0.05$). In single years, in Liemers the mean fledged brood size ranged between 2.7 (n=3) in 1973 and 5.7 (n=4) in 1983. In Achterhoek, the extreme values ranged between 2.0 (n=5) in 1970 and 4.0 (n=12) in 1974. In both districts, broods of 6 or more young were successfully raised only in good vole years. In the peak year 1967, a Barn Owl pair in a vole plague area at Gendringen (Liemers) successfully reared a second brood with 8 young. In the peak year 1981, a male Barn Owl paired with two females (bigamy!), and these birds raised at least 8 young in a nestbox at Breedenbroek (Achterhoek).

For the purpose of this study, it is once more interesting to check whether there are trends in breeding performance. In Table 12, data concerning fledging success in Liemers and Achterhoek are arranged for two consecutive periods and also in relation to vole density. A variance analysis has been performed on the basic data in order to test variation in fledging success in relation to space (Liemers versus Achterhoek), time (period 1967-75 versus 1976-84) and vole

Table 12. Breeding performance of the Barn Owl in Liemers and Achterhoek in relation to vole population level in two consecutive periods (1967-75 and 1976-84). Breeding performance is expressed as mean brood size at fledging (completely failed broods included). Sample size (*n*) refers to the total number of broods examined.

District	Vole population level	Mean brood size at fledging			
		period 1967-75		period 1976-84	
Liemers	poor vole years	2.8	(*n*=6)	3.0	(*n*=8)
Liemers	good vole years	4.3	(*n*=23)	3.6	(*n*=36)
Achterhoek	poor vole years	2.6	(*n*=11)	2.9	(*n*=32)
Achterhoek	good vole years	3.4	(*n*=52)	3.1	(*n*=105)
Liemers	all years	4.0	(*n*=29)	3.5	(*n*=44)
Achterhoek	all years	3.3	(*n*=63)	3.0	(*n*=137)

NOTE. The over-all fledging rates (period 1967-84) averaged 3.7 (*n*=73) in Liemers and 3.1 (*n*=200) in Achterhoek.

abundance (good vole years against poor vole years). Over the whole period, more young per brood were raised in Liemers than in Achterhoek, averaging 3.7 and 3.1 respectively ($p < 0.005$). Further, more young were raised in good vole years than in poor vole years, averaging 3.4 and 2.9 respectively ($p < 0.05$). There is indication of a decrease in the number of fledged young over time, averaging 3.5 for the first period and 3.1 for the second period ($0.10 < p < 0.05$). No two-way or three-way interactions were observed.

In Liemers, in poor vole years the mean fledging success averaged 2.8 and 3.0 respectively when the two periods are compared. In these trough years Barn Owls nowadays only breed in small-scale landscapes (with a well-buffered food supply); today suchlike strongholds are still found in Northern Liemers. In good vole years the average number of fledglings in Liemers dropped significantly from 4.3 to 3.6 (one-sided t test, $p < 0.05$). Here again the effect of the disappearance of real vole plagues manifests itself: such flourishing food supplies (once leading to many large Barn Owl broods in Liemers) are becoming increasingly rare in recent times. However, there proved to be no statistically significant trend in the over-all reproduction rates in Liemers, which averaged 4.0 and 3.5 fledglings per brood in the two consecutive periods (one-sided t test, $p > 0.15$).

In Achterhoek in poor vole years, the mean fledging success averaged 2.6 to 2.9 young for the two consecutive periods as against 3.4 and 3.1 respectively in good vole years. Statistically these figures indicate no significant changes in breeding performance in Achterhoek over time.

The stable occupancy rate and breeding performance in the small-scale landscapes of Northern Liemers and Achterhoek (with its well-buffered food stock) is advanced by the supplying of optimal nestboxes (also placed far from busy roads where many Barn Owl are killed). The impact of the relationships of these complexly interwoven factors will be elaborated in Chapter 10.

7.3 Second broods

Occupancy rate of territories and fledging success are closely linked with prey abundance, and so is the incidence of Barn Owl pairs which breed twice within a single year. We had about a dozen (unconfirmed) reports of second Barn Owls broods in the study area as regards the period 1956-66, for the greatest part origining from Liemers. In the intensive study period 1967-

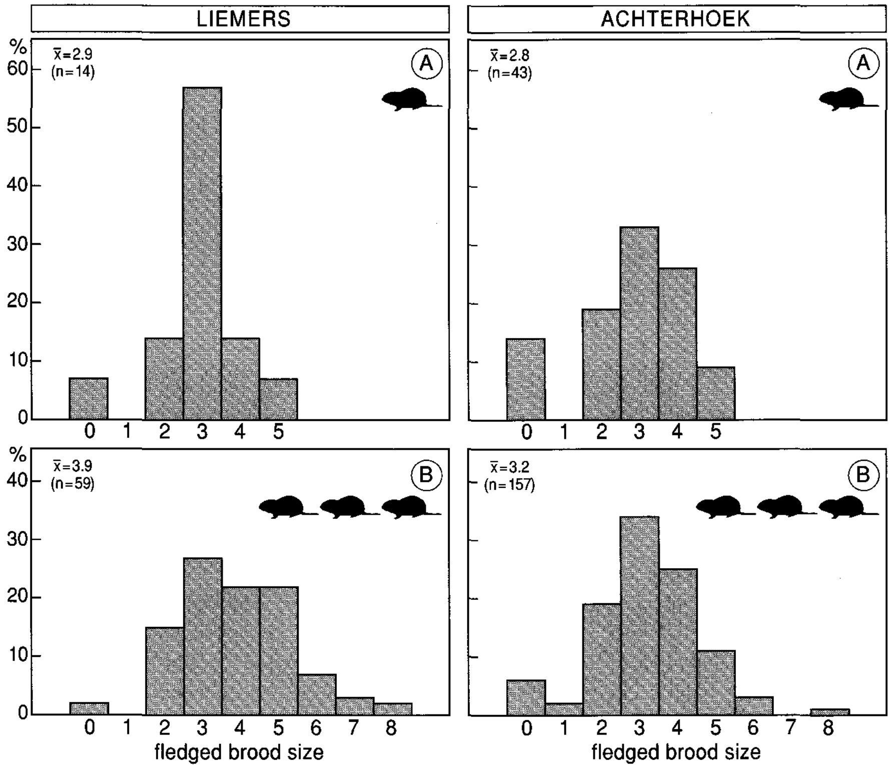


Fig. 19. Breeding performance of the Barn Owl in Liemers and Achterhoek in relation to vole population level (a: poor vole years, b: good vole years). Figures show the distribution of brood size at fledging in the period 1967-84. Both in Liemers and Achterhoek, significantly more young were raised in good vole years than in poor vole years (both $p < 0.05$).

84, we succeeded only five times in establishing the incidence of second broods with certainty: once in each of the peak vole years 1967, 1971, 1974, 1977 and 1984, in a Barn Owl population numbering 19-29 (mean 23) breeding pairs. All of them took place in breeding territories located in Liemers or on the border of Liemers and Achterhoek.

Viewed nation-wide, in the 1970s the percentage of Dutch Barn Owl pairs with second broods amounted to 3-5% in good vole years, with 1974 as a striking exception: then 15 out of 138 recorded Barn Owl pairs produced second broods (=11%), according to the national survey (S. Braaksma, pers. comm.). In Britain, where the Common Vole *Microtus arvalis* is replaced by the Field Vole *M. agrestis*, second Barn Owl broods are even more rare than in The Netherlands nowadays. The 'Atlantic' weather conditions in NW Europe seem to preclude the occurrence of successful second broods except in unusually favourable years (Bunn *et al.* 1982). Furthermore, in countries with modern farming practices (as in The Netherlands) second clutches are uncommon owing to the fact that in well-managed farmland areas the vole population is suppressed and prevented from reaching peak levels (van Wijngaarden 1957).

This differs markedly from the situation in a number of central European countries, where second Barn Owl broods were frequently observed in several Barn Owl population studies carried out in the period 1967-75: in peak years of the Common Vole, in a western German population 29-49% of the Barn Owl pairs produced second broods (Kaus 1977), as against 56-65% in an eastern German population (Schönfeld & Girbig 1975) and 52-58% of a breeding Barn Owl population in the eastern part of France (Baudvin 1979). The contribution of second broods to the reproduction rate must not be underestimated, as appears from the studies of Schönfeld and fellow-workers of a Barn Owl population in eastern Germany (former GDR). In two years with low vole densities (1969 and 1973), the mean number of fledged young amounted to 3.1 per breeding pair; in these years, no second broods were produced at all. In two peak vole years (1971 and 1974), the mean fledging success of the first broods amounted to 3.8 young. These reproduction rates are still in the same order as the values found in the Dutch study population. However, in the two peak vole years on an average 62% of the German population produced second broods with a mean fledging success of 5.3 young. When the second broods are apportioned among the whole breeding population, the mean fledging success leaps up to 7.1 fledged young per breeding pair in the peak vole years! Such an astonishingly high productivity -which in former days might also have occurred in Liemers when periodic vole plagues were common- can compensate for high mortality rates, such as occur in uniform landscapes in winters with minimum vole densities.

8. DISPERSAL PATTERNS

A lot of the Barn Owl's life is concealed from humans. Many aspects of the owl's life story cannot be observed directly because of its crepuscular and elusive nature. However, by way of ringing records one can gain a deeper understanding of the movements, the span of life and the mortality of Barn Owls. Therefore a ringing programme has been set up in Liemers and Achterhoek. In order to limit disturbance, only nestlings were systematically ringed. Adult Barn Owls were only very incidentally caught (24, of which 6 have been recovered).

In the period 1967-84, a total of 663 nestlings in the study area (Liemers: 157, Achterhoek: 506) were marked with rings. Through The Netherlands Bird Ringing Centre ('Vogeltrekstation Arnhem' at Heteren), we got a selection of 133 ringing returns (Liemers: 34, Achterhoek: 99) for further analysis as accounted for in section 3.2.

8.1 Post-fledging dispersal and other movements

In Europe, Barn Owl populations are basically resident. However, young birds especially make dispersals which are more extensive in some years than others. After fledging, juveniles remain dependent on their parents for about 1-2 months. After achieving independence, they gradually leave their native grounds (Bunn *et al.* 1982, Cramp 1985). In the study area, a remarkable case of post-fledging dispersal was shown by an owlet ringed as a nestling (ringmark: Arnhem-5032478) early in June 1975 near Aalten (Achterhoek): 52 days later it was encountered in good health in a nestbox at Neede 23 km north of its birthplace amongst a brood of nearly fledged congeners! Most movements of Barn Owls (both in terms of numbers and of distances moved) occur in the period September-November, though some movements can continue throughout the first winter. The region which is reached by wandering Barn Owls in late autumn or early winter usually seems to become the prospective breeding area. Here they can fill vacant territories. Remigration back to the natal area is not known in this species (Glutz von Blotzheim & Bauer 1980).

Especially interesting is the life history of the Barn Owls which were recorded more than twice after ringing. One female was ringed as a nestling (mark 6044713) in June 1980 near Sinderen (Achterhoek) and reported with a brood of young in June 1982 as well as in June 1983 in the same nestbox in Dale at 9 km from her birthplace; she died as a traffic victim near her place of settlement in December 1983. Another female had a very remarkable life story: (A) she was ringed (Arnhem-6044724) in June 1981 as a member of a 'super brood' (at least 8 young) at Breedenbroek; (B) in March 1982 she collided with a window at Beltrum (23 km north of A), but could fortunately be rehabilitated and given back her freedom; (C) then we controlled her in June 1982 as a breeding bird in a nestbox near Corle (14 km south of B), where she was confronted with the demolition of the breeding place (an old barn) in the winter 1982/83; (D) thereupon she emerged in June 1984 with a brood in a nestbox (7 km NW of C) near Lievelde; (E) in June 1986 we encountered this famous bird again in a nestbox near Barlo (6 km south of D) with a couple of young and very much alive at an age of 5 years! At that time she lived about 13 km NE of her birthplace.

Figure 20 shows the dispersal patterns of Barn Owls ringed as nestlings in Liemers (triangles) and Achterhoek (squares). A distinction is made between owls found dead within one year after ringing (open symbols) and owls which were found subsequently (closed symbols). Regarding the juvenile population (n=91), about 45% of the young Barn Owls were recovered within 25 km of their birthplace and another 15% within 25-50 km. As regards direction, a random dispersal pattern is manifest. For a species suffering from periodic mass mortality (as occurred in 1961/62, 1962/63, 1968/69, 1978/79 and 1984/85), such random dispersal seems to be a very good mechanism to occupy vacant territories. Only a small part of the juvenile population had moved far away: 18% of the nestlings were recorded in their first year over 100 km away from their birthplace. A few were reported more than 500 km away: one in the German Democratic Republic at 560 km NE (ringmark 5125342) and two in France at 805 km SW (mark 6041164) and at 925 km SSW (mark 5147265). Another bird (mark 5184120) was recovered at 780 km SW in France five months after ringing, while one of its siblings (mark 5184119) was recorded 1½ years after ringing as a road victim only 5 km from their birthplace near Winterswijk.

The closed symbols in Figure 20 give a review of the nestlings which were recovered more than one year after ringing. In this population, the movements show the same pattern with regard to distance as is found in the juvenile population: 64% of the older birds (n=42) settled within 50 km of their birthplaces. A fair number of them had apparently spent their whole life not far away from their natal area, as instanced by the two birds mentioned above. About 24% of the older birds ringed as nestlings in the study area were recovered between 50-100 km away. One adult owl was reported dead 2½ years after ringing in France at 860 km SW (mark 6039372); of course, the long-distance travel could have taken place in the first year of its life. Compared with the juvenile population, the dispersal pattern of the older birds seems to show irregularity with regard to direction: no less than 45% of them were ultimately recovered in the N to E sector (0°-90°), but statistically this divergence in the dispersal pattern proved to be dubious (χ^2 test, df=3, $0.10 < p < 0.05$). However, it is remarkable that precisely in the N and NE part of The Netherlands a considerable recovery of the Barn Owl population has occurred since 1980 thanks to an intensive conservation campaign, following up the pioneer work in Liemers and Achterhoek.

Adult Barn Owls are generally sedentary, though they can still wander (especially in winter) within a rather restricted area. We had six returns of Barn Owls which were ringed in the study area as adult birds: all of them were recovered within 15 km of the ringing place (1-19 months after ringing). Barn Owls can and do sometimes move further away in later life as proved by a Barn Owl ringed as a nestling (mark 5147216) in Dale (Achterhoek) in June 1981. This owl collided with a car in November 1983 in the Northern Achterhoek; after rehabilitation it was released here. In February 1985, however, it was found dead near Groningen about 140 km to

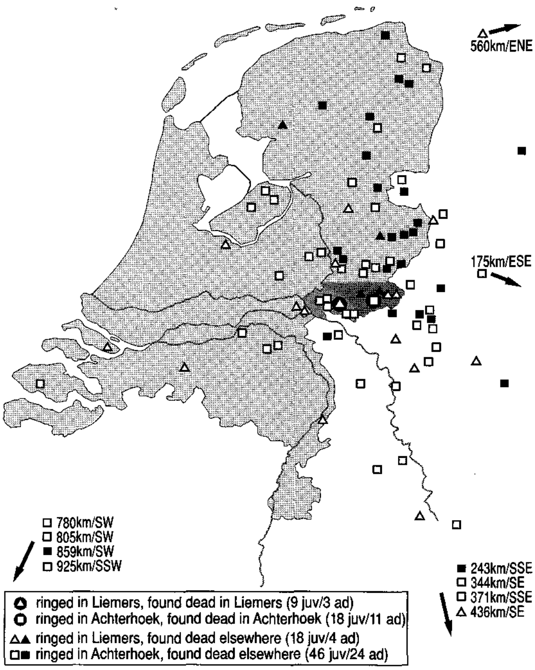


Fig. 20. Dispersal of Barn Owls ringed as nestlings in Liemers (triangles) and Achterhoek (squares). Open figures refer to birds recovered within one year after ringing, solid figures refer to birds recovered subsequently. Achterhoek functions as a 'source area' (see also Fig. 21 and Table 14).

the north! We assume that prey scarcity in the snowy winter 1984/85 induced this bird to leave its native grounds in later life just as many owls did in the harsh winter of 1978/79 (Braaksma 1981, 1988).

It is interesting to check whether there are trends in dispersal patterns. Therefore the movements of Barn Owls ringed in Liemers and Achterhoek in two consecutive periods (1967-75 and 1976-84) have been analysed (see Table 13). No differences in dispersal distances could be noted between owlets ringed in Liemers and owlets ringed in Achterhoek. Equally no trends over time (period 1967-75 compared with 1976-84) could be established, either by testing the movements according to distance category (Kolmogorov-Smirnov test, $p > 0.15$) or by testing the exact distances moved (Wilcoxon test, $p > 0.15$). In analysing the British ringing database, Percival (1990) also found neither regional nor temporal trends in Barn Owl dispersal distances.

In certain years, Barn Owl movements show an eruptive nature in western and central Europe. In these mass movements it is chiefly first-year birds that move, but some adults can also be involved. In this respect the Barn Owl is more or less intermediate between the nomadic Short-eared Owl *Asio flammeus* and the strictly sedentary Tawny Owl *Strix aluco* (Lack 1966, Voous 1988). Large-scale movements happen in particular autumns with a high density of the Barn Owl population and it might be a prey-related phenomenon connected with crashing vole populations. Such eruptive dispersals are often combined with increased Barn Owl mortality which will be brought about by a reduced prey supply; this effect can be heightened by adverse weather conditions (Sauter 1956, Honer

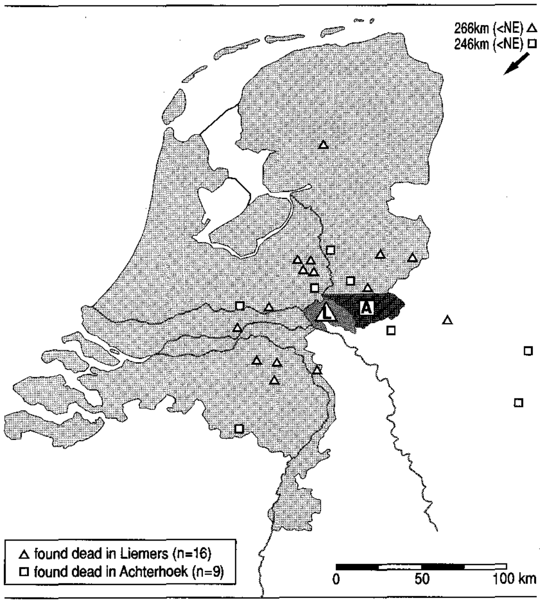


Fig. 21. Origin of owls ringed as nestlings outside the study region and found dead in Liemers (triangles) and in Achterhoek (squares). Liemers functions as a 'sink area' (see also Fig. 20 and Table 14).

Table 13. Dispersal of Barn Owls ringed as nestlings in Liemers and Achterhoek in two consecutive periods (1967-75 and 1976-84). Figures refer to number of owls found dead.

Distance moved (km)	ringed in Liemers		ringed in Achterhoek	
	period 1967-75	period 1976-84	period 1967-75	period 1976-84
0-2	2	3	2	3
3-25	5	5	10	23
26-50	4	1	8	12
51-100	3	5	8	15
101-250	2	2	5	7
251-500	-	1	1	1
> 500	-	1	1	3
Total	16	18	35	64

1963, Glutz von Blotzheim & Bauer 1980, Cramp 1985, Bairlein 1985). The process outlined above shows complex relationships between movements, weather conditions, prey-availability and mortality in Barn Owls. Distances moved but also the habitat capacities and the structure of the owl's population in the areas reached, will determine the place of settlement of wandering owls.

8.2 The balance between immigration and emigration: sink and source areas

Owls not only move out of the study region, they also move in. Figure 21 shows the origin of owls ringed as nestlings outside the study region which have been recovered in Liemers (n=16) and in Achterhoek (n=9). 56% of these owls were ringed as nestlings less than 50 km away and another 24% was born within a distance of 50-100 km from the study region. Two immigrants were ringed about 250 km away in NE direction (Germany). One of the two was ringed as nestling and found dead four months later in Liemers (Helgoland-3065285). The other bird was ringed as adult in April 1979 near Rotenburg/Wümme; in June 1982 this owl (Helgoland-4032358) was controlled as a breeding bird in a nestbox near Aalten (Achterhoek). Next winter it was found dead in a barn about 3 km away from the breeding place. There proved to be no statistical difference in the origin and distances moved, between immigrants found in the first year after ringing and birds found subsequently, so these categories are taken together.

However, there proved to be a remarkable distinction as regards the origin of the birds found in Liemers and the birds found in Achterhoek, as shown in Table 14. The records are divided into two categories, viz. 'born locally' (ringing district = finding district) and 'immigrants' (born outside the finding district). From a total of 42 findings in Achterhoek, 13 (=31%) were immigrants (4 from Liemers and 9 from elsewhere); 69% of the recoveries in Achterhoek were locally born birds. In contrast, in Liemers only 36% of the findings concerned locally born birds whereas no less than 21 out of the 33 recoveries (=64%) were immigrants (5 from Achterhoek and 16 from elsewhere). Testing showed that this difference in origin between owls found in Liemers and owls found in Achterhoek is statistically significant (χ^2 test, $p < 0.01$).

This result gives valuable information about the balance between immigrants and emigrants in Liemers and Achterhoek, respectively. The

Table 14. Origin of Barn Owls ringed as nestlings (1967-84) and found dead within the study districts (Liemers and Achterhoek).

Origin	Found dead in Liemers		Found dead in Achterhoek	
	n	(%)	n	(%)
Born locally	12	(36)	29	(69)
Immigrants	21	(64)	13	(31)
Total recovered	33	(100)	42	(100)

NOTE. Category 'born locally' comprises owls ringed in the district where they were found dead later on. Category 'immigrants' comprises owls ringed outside the district where they were found dead.

interesting conclusion can be drawn that the population structure of Liemers is dominated by immigrants (either from Achterhoek or from elsewhere). This region functions as a 'sink area' (net import of owls), in which gaps caused by mortality are filled up by incomers. In contrast, most owls of the Achterhoek population are born locally. This region functions as a 'source area' (net export of owls), in which a population surplus emigrates to compensate losses caused by mortality elsewhere (cf. Woolfenden & Fitzpatrick in Perrins *et al.* 1991).

9. MORTALITY AND CAUSES OF DEATH

From the 133 returns of owls ringed as nestlings in the study area, 91 (68%) were recovered during the first year after ringing whereas 42 (32%) were recovered subsequently. The juvenile population of the Barn Owl differs in many aspects of its biology (including mortality rate) from the adult population. So first year recoveries and subsequent recoveries (more than one year after ringing) are analysed separately.

9.1 Seasonal recovery pattern

Figure 22 shows the monthly recovery pattern based on recoveries of owls which were ringed in the study area in the period 1967-84. A distinction is made between first year recoveries and records of older birds. Both in the juvenile and in the adult population, about 75% of the birds died in autumn and winter (September up to and including February). In first-year owls, 44% of the birds was found dead in the period September-November and 33% was found in the period December-February. The high mortality in the first period can be related to the many risks which the inexperienced owls have to face during the post-fledging dispersal. Death reports of juveniles in autumn show a relatively high proportion of traffic victims and of owls which have collided with other obstacles. The mortality in winter (December-February) must apparently be attributed to reduced prey supply (vole scarcity) whether or not this is interwoven with adverse weather conditions. In this period starvation is often mentioned in single death reports (especially in the winters 1968/69 and 1978/79). A post-fledgal and a winter peak in juvenile mortality have been noticed in a number of Barn Owl populations (Glutz von Blotzheim & Bauer 1980); they are also observed in some populations of the Little Owl *Athene noctua*, e.g. in Germany (Exo & Hennes 1980).

In the adult Barn Owl population the mortality in autumn (period September-November) was relatively low at 19% of the total findings, in contrast to the juvenile population. The adult

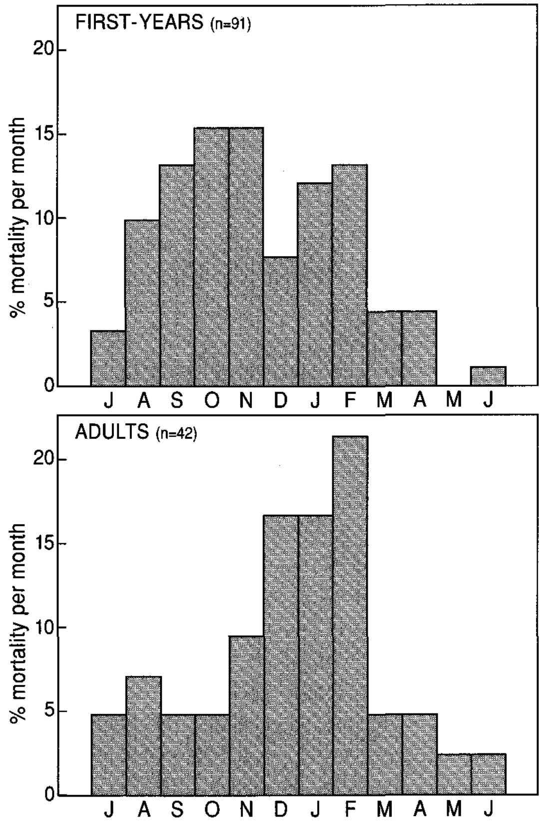


Fig. 22. Monthly mortality pattern of first-year and adult Barn Owls based on ringing recoveries. Figures refer to birds ringed as nestlings in Liemers and Achterhoek in the period 1967-84 and found dead both inside and outside the study region.

mortality shows one marked peak during the months December-February with no less than 55% of all findings. Again reduced prey-availability lies at the root of most of the deaths in these months, as can be concluded from the starvation weights of winter victims (de Jong 1983). The decline in landscape diversity is also to blame in this regard, an aspect which will be dealt with in Chapter 10. Also many traffic victims are recorded in winter. The same seasonal distribution in adult mortality with one marked winter peak was noticed in Switzerland (Schifferli 1957, Güttinger 1965). A second mortality peak of adult Barn Owls (viz. in the breeding season) which has been claimed in some other studies (see Glutz von Blotzheim & Bauer 1980) could not be established in the present study nor in a former Dutch one (Braaksma & de Bruijn 1976). Such a peak in adult mortality during the breeding season is however known in Little Owl populations, including the Dutch one (Exo & Hennes 1980).

Our findings agree with Newton *et al.* (1991), which found the same marked seasonal pattern in Barn Owl deaths in Britain, with peaks in autumn (due mainly to juveniles) and in late winter (due to both adults and juveniles).

Table 15. Annual mortality (%) of Barn Owls based on ringing data. Numbers refer to owls ringed as nestlings in the whole study area (period 1967-84) and found dead both inside and outside this area (up to 1-1-1990). The mean length of life after ringing was 398 days (n=133).

Year of life	Number alive at beginning of year	Number dying over the year	Annual mortality
1.	133	91	68%
2.	42	21	50%
3.	21	9	43%
4.	12	5	42%
5.	7	4	57%
6.	3	2	66%
7.	1	1	100%

NOTE. The mean annual mortality of adults amounted to 49% from second year onwards and 48% from third year of life onwards (method of calculation after Schifferli 1957).

9.2 Annual mortality and life-expectation

How long do Barn Owl live and how is mortality distributed over the consecutive year-classes? To answer these questions Table 15 was composed. In the study region, the mean term of life since ringing amounted to a scanty 400 days. Out of a total of 133 owls ringed as nestlings and found dead afterwards, no less than 91 died in their first year of life and another 21 in the second year. This means that only 16% of the owls (21 out of 133) were still alive after two years. These birds are very important in preserving the Barn Owl population, the more so since their further survival chances are relatively good in the third and fourth year of life (see below). But only 7 out of 133 birds (5%) reached an age of five or more. The age-distribution outlined above fits the general Dutch pattern (Braaksma & de Bruijn 1976). The oldest recorded Barn Owl in the study area was ringed in June 1981 near Aalten (Achterhoek) and died as a road victim in July 1987 at 13 km NW of its birthplace. This bird (mark 5147245) reached an age of six. It is possible that an even older bird will be found after completion of this review, as out of 680 Dutch ringing recoveries, 7 Barn Owls were reported at ages of between 7-12 year (de Jong 1983)[1].

The annual mortality of Barn Owls ringed in the study area is demonstrated in Table 15. The mortality in first year owls averaged 68% and

[1]Indeed a much older Barn Owl was later reported from the study region. This bird was ringed (Arnhem-5032457) as nestling near Meddo (Achterhoek) in June 1974 and found freshly dead in October 1991 in Haarlo about 15 km away from its birth place. With its age of 17 year and 4 months it is one of the five oldest Barn Owls ever recorded in The Netherlands (R.D. Wassenaar, pers. comm.).

Table 16. Annual mortality (%) and life expectation of Barn Owl populations based on ringing data. Calculations are based on recoveries of owls which were ringed as nestlings (*n* = number of recoveries). Mortality (%) is calculated for first and second year (1., 2.) and from third year onwards (≥ 3.). Life expectation (in years) is calculated from first, second and third year onwards (≥ 1., ≥ 2., ≥ 3.). The methods of calculation are after Schifferli (1957).

Nation	Census period	*n*	Mortality (%)			Life expectation (years)			Source
			1.	2.	≥ 3.	≥ 1.	≥ 2.	≥ 3.	
CH	up to 1950	330	64	54	39	1.3	1.7	2.1	Schifferli (1957)
CH	up to 1970	866	68	51	43	1.2	1.6	1.8	Glutz & Bauer (1980)
GDR	1968-1973	138	69	56		1.3	1.8		Schönfeld (1974)
NL	1967-1984	133	68	50	48	1.1	1.5	1.7	this study (see note)

NOTE. Dutch data refer to owls ringed as nestlings in Liemers and Achterhoek (period 1967-84).

proved to be significantly higher than in adult birds in which it averaged 49% (χ^2 test, $p < 0.05$). The high juvenile mortality is easily accounted for by the many risks which the inexperienced birds have to face during the post-fledging dispersal (death on roads, being locked up, starvation). The massacre is still larger in the event of an eruptive dispersal (Sauter 1956) and there is also a relationship between mortality and vole population level: a juvenile mortality up to 95-100% has been observed for vole trough years (Schönfeld *et al.* 1977, Taylor 1989). In contrast to the high juvenile mortality, a substantially lower adult mortality is characteristic. According to the data in Table 15, the annual mortality descends to 50% in the second year of life and it amounts to 42-43% in the third and fourth year of life. After this it rises rapidly in the higher year-classes. If a Barn Owl manages to survive its first year of life, its survival chances are thus relatively good: its life experience is enlarged and it probably will also have succeeded in finding a suitable domain. For the Barn Owl study population, the mean annual mortality in adults can be computed to be 49% from the second year of life onwards and 48% from the third year of life onwards (calculated after the manner of Schifferli 1957).

A similar pattern in mortality rate has been established in other European Barn Owl populations as shown in Table 16. This indicates a growing life expectation during the first three years of life. At the time of ringing as nestlings, the expected mean life-time is only 1.1 years for Barn Owls born in Liemers and Achterhoek. However, one-year old birds have a mean life expectation of 1.5 years (from the second year of life onwards), also reaching an age of 2.5 year on average. Two-year old birds even have a mean life expectation of 1.7 years, also reaching an age of 3.7 years on average (calculations after Schifferli *loc. cit.*). Nevertheless, adult owls seldom reach a longevity of over five years. The prospects for a longer life seem to be not so good for Barn Owls in the affluent modern human society with its intensive land use. In this respect the trend of declining life expectations of the Barn Owl in Switzerland might be a bad omen (see Table 16). The annual mortality figures of the Dutch study population are somewhat higher (and the figures of life-expectation thus somewhat smaller) in comparison with the Barn Owl population in Germany and Switzerland. Analysis of Swiss and German ringing recovery data revealed interesting differences in mortality (and thus in life-expectation) between *Tyto alba*, *Asio otus* and *Strix aluco*. First-year mortality and adult mortality in *Tyto* was 68% and 43% (resulting in life expectations of 1.2 years and 1.8 years respectively) whereas these mortality rates in *Asio* amounted to 52% and 31% (life-expectations 1.4 and 3.3 years respectively) and

Table 17. Annual mortality of Barn Owls in Liemers and Achterhoek in two consecutive periods (1967-75 and 1976-84). Numbers refer to owls ringed as nestlings and found dead both inside and outside the ringing districts. Data concern recoveries up to 1-1-1990.

Ringing district	Period	Total number of recoveries	Recovered in first year of life	Recovered in subsequent years						Mean term of life since ringing
				2.	3.	4.	5.	6.	7.	
Liemers	1967-75	16	11 (69%)	1	2	1	1	-	-	450 days
Liemers	1976-84	18	16 (89%)	1	1	-	-	-	-	183 days
Achterhoek	1967-75	35	23 (66%)	6	2	2	2	-	-	420 days
Achterhoek	1976-84	64	41 (63%)	13	4	2	1	2	1	440 days

NOTE. The over-all first-year mortality (period 1967-84) amounted to 79% in Liemers and 65% in Achterhoek, whereas the over-all mean adult mortality (from 2nd year of life onwards) amounted to 47% in Liemers and 49% in Achterhoek. These values were computed from the data in the table above (method of calculation after Schifferli 1957).

in *Strix* to 49% and 25% (corresponding to life-expectations of 2.6 years and 3.6 years). Barn Owl populations can compensate the relatively high mortality figures due to the species' reproduction capacity which is higher than in *Asio* and *Strix* (Schifferli 1957, Glutz von Blotzheim & Bauer 1980).

During the Dutch study we observed decreasing Barn Owl populations in Liemers whereas the Achterhoek population increased in the period 1967-84. Therefore it is interesting to check trends in mortality rate between these districts. In Table 17 the annual mortality of Barn Owls ringed in Liemers and Achterhoek has been examined for two consecutive periods (1967-75 and 1976-84). In Liemers an increase in first-year mortality was found, from 69% to 89%. Such a trend was not found in Achterhoek (66% and 63%, respectively). Testing the exact ages, the survival in Liemers in the second period (1976-84) proved to be significantly lower than in the first period in Liemers and in either periods in Achterhoek (Wilcoxon test, $p < 0.005$): the mean term of life (days) after ringing averaged in Liemers only 183 days in the period 1976-84 compared with 435 days on average in the other categories (cf. Table 17).

The over-all first-year mortality (period 1967-84) amounted to 79% in Liemers and 65% in Achterhoek. The very high first-year mortality in Liemers appears to be a driving factor behind the decrease of the Barn Owl in this region in the period 1967-84 (see further Chapter 10).

The over-all adult mortality (from second year of life onwards) averaged 47% in Liemers and 49% in Achterhoek. No over-all trend over time could be found by testing the exact ages of adult birds, neither in Liemers nor in Achterhoek (Wilcoxon test, both $p > 0.15$). For detailed investigation of age- en time-specific variation in mortality, it would be advisable to analyse the total comprehensive Dutch ringing database using advanced statistical techniques (see section 3.2).

There is a problem in interpreting the results of the data of Table 17 as these refer to owls found dead both inside and outside the respective ringing districts. Therefore we made a selection of the ringing recovery data in the following way: for both Liemers and Achterhoek, the recoveries were selected applying to owls which have been found dead in the same district in which they were ringed as nestlings. The recovery data were arranged according to year-classes: see Table 18. Consequent conclusions about differences in mortality between the two districts can only be made by assuming that the owls have not left their 'life district' in the span of time

Table 18. Mortality of Barn Owls in Liemers and Achterhoek, according to recoveries of owls ringed as nestlings in the period 1967-84. Figures show numbers of owls which were recovered within the ringing districts (up to 1-1-1990).

Ringing district	Recoveries within ringing district	Recovered in first year of life	Recovered in subsequent years						Mean term of life since ringing
			2.	3.	4.	5.	6.	7.	
Liemers	12	9 (75%)	1	1	1	-	-	-	302 days
Achterhoek	29	18 (62%)	5	2	1	1	1	1	482 days

NOTE. The mean annual mortality of adults (from 2nd year of life onwards) amounted 50% in Liemers and 41% in Achterhoek on the basis of the data in the table above (calculated after Schifferli 1957).

between ringing and day of death. This assumption seems to be realistic in the light of the preceding analysis of movements. According to the data in Table 18, the mortality of first year Barn Owls living in Liemers amounted to 75% as opposed to 62% in Achterhoek. The annual mortality rate of adult Barn Owls averaged 50% in Liemers as against 41% in Achterhoek. The mean term of life in Liemers was only 302 days as against 441 days in Achterhoek. As far as can be concluded from the available information, Barn Owls apparently have to face more life risks in Liemers than in Achterhoek.

9.3 Causes of death of Barn Owls in the study area

At the end of this chapter, we will deal with the causes of death of Barn Owls. During our research in the period 1967-84, we received information about 140 Barn Owls found dead in the study area (nestlings not included). In 90 birds the death cause or detailed recovery circumstances were known, 48 of them from ringing returns and 42 from other sources. These data revealed surprisingly different ratios between the various causes of death dependent on the recovery source (see discussion in section 3.3). In Appendix 4 a systematic separation is made between ringing recoveries (reported to The Netherlands Bird Ringing Centre) and other checked information (own finds and reliable reports to the author or other members of the Achterhoek-Liemers Working Group for Barn Owl Protection). The main causes of death are arranged according to recovery source in Table 19. The data based on ringing recoveries suggest one mortality cause being of outstanding importance: 56% of the ringed owls were reported as road victims. Starvation in hard winters (15%), being locked up unintentionally (8%) and collisions with obstacles (6%) were mentioned as secondary mortality causes in the ringing recovery reports. The recoveries from other sources report a proportion of 'only' 24% road victims, and besides this, starvation in hard winters as the main cause of death (19%). Against the much

Table 19. Causes of death of Barn Owls in Liemers and Achterhoek arranged according to recovery source: A = ringing recoveries; B = other checked information.

Cause of death	A (n=48)	B (n=42)
Road victim	56%	24%
Starved in hard winters	15%	19%
Locked up unintentionally	8%	12%
Collided with obstacles	6%	12%
Killed deliberately	2%	12%
Pesticides	-	10%
Others	13%	11%

NOTE. Source A comprises ringing recoveries stored in the Dutch ringing databases (Ringing Centre at Heteren). Source B covers information gathered by the author and fellow-workers of the Liemers-Achterhoek Society for Barn Owl Protection. Basic data are shown in Appendix 4.

Table 20. Causes of death of Barn Owls in Liemers and Achterhoek in two consecutive periods (1967-75 and 1976-84). Figures show numbers of full-grown owls found dead (percentages are given in brackets).

Cause of death	Liemers			Achterhoek			Total study area		
	Period 1967-75	Period 1976-84	Total numbers period 1967-84	Period 1967-75	Period 1976-84	Total numbers period 1967-84	Period 1967-75	Period 1976-84	Total numbers period 1967-84
Starved in hard winters	3	3	6 (15.4)	3	6	9 (17.6)	6 (14.6)	9 (18.4)	15 (16.7)
Road victim	6	14	20 (51.3)	5	12	17 (33.3)	11 (26.8)	26 (53.1)	37 (41.1)
Railway victim	1	1	2 (5.1)	1	1	2 (3.9)	2 (4.9)	2 (4.1)	4 (4.4)
Killed deliberately	3	-	3 (7.7)	2	1	3 (5.9)	5 (12.2)	1 (2.0)	6 (6.7)
Locked up unintentionally	3	2	5 (12.8)	2	2	4 (7.8)	5 (12.2)	4 (8.2)	9 (10.0)
Collided with obstacles	1	1	2 (5.1)	3	3	6 (11.8)	4 (9.8)	4 (8.2)	8 (8.9)
Drowned	-	-	- (-)	4	2	6 (11.8)	4 (9.8)	2 (4.1)	6 (6.7)
Pesticides	1	-	1 (2.6)	3	-	3 (5.9)	4 (9.8)	- (-)	4 (4.4)
Taken by (avian) predator	-	-	- (-)	-	1	1 (2.0)	- (-)	1 (2.0)	1 (1.1)
Total	18	21	39 (100%)	23	28	51 (100%)	41 (100%)	49 (100%)	90 (100%)

NOTES. Figures comprise ringing recoveries as well as all other checked sources (cf. Appendix 4). In addition to the above-mentioned records, the following numbers of dead Barn Owls were reported without detailed data about the cause of death: Liemers - 20 (period 1967-75: 11, period 1976-84: 9), Achterhoek - 29 (period 1967-75: 14, period 1976-84: 15), total study area - 49 (period 1967-75: 25, period 1976-84: 24).

lower proportion of road victims, a number of other mortality causes were reported to us relatively often (each of them contributing 10-12% of the known causes of death): being locked up, collisions with all sorts of obstacles, deliberate killings by humans and poisoning by pesticides.

As a result of searching conversations with finders of ringed Barn Owls, it has become clear to us that a number of mortality causes are apparently under-represented in the ringing statistics. The reason for this is dual: (1) The cause of death is not so conspicuous and therefore often not mentioned by the finder or not clearly recorded in the ringing statistics (winter victims, pesticides); (2) The cause of death is intentionally kept concealed in the finder's report: this is clearly applicable in most cases of deliberate killings (which still occur in spite of the complete legal protection of the Barn Owl in The Netherlands). On the other hand, the cause of mortality is easily recognizable in traffic victims; these are therefore recorded relatively often as such in the ringing recovery reports. Moreover, road victims are comparatively easily found. Finally, a number of Barn Owls were calculatedly reported as road victims by the finder, although on closer investigation on our part, it proved they had been deliberately killed (for instance to be stuffed). So we must conclude that road victims are over-represented in the ringing statistics, at the expense of a number of other causes of death. Testing of the proportion of road victims in the ringing statistics (56%) against the rate obtained from other checked information (24%) showed that this difference according to source was statistically very significant (test in 2x2-contingency tables, $p < 0.001$). Such an over-representation of road victims in ringing statistics at the expense of other causes of death was also noticed by Illner (1992). It probably also holds for the percentage distribution of death causes as published earlier for the whole Dutch Barn Owl population (Braaksma & de Bruijn 1976: 159, de Jong 1983: 55), because the mortality figures in these studies are based mainly on ringing records. In the present study, the quantitative analysis of the various causes of death is based on all available recovery sources (both ringing recoveries and other checked information) in order to limit the bias.

According to the review in Table 20, there are seven main causes of death of Barn Owls in the study region: 1. Death on roads (41%); 2. Starvation in hard winters (17%); 3. Locked up unintentionally in buildings (10%); 4. Collisions with obstacles (9%); 5. Deliberate killings by humans (7%); 6. Drowning (7%); 7. Pesticides (4%). Altogether, these factors are nowadays responsible for about 95% of all known causes of death. By far the majority of mortality cases are plainly caused by direct or indirect human activities. We think that in modern societies fairly few Barn Owls die from natural causes: this can be concluded from the relatively short life times in the study region (see Table 15-18) compared with the longevity data recorded for Barn Owls in central Europe (up to 12-17 years: Glutz von Blotzheim & Bauer 1980). In order to trace trends in the mortality pattern, the recovery data from the study region are subdivided according to finding district (Liemers versus Achterhoek) and to finding period (1967-75 versus 1976-84) in Table 20. The main causes of death will then be discussed according to importance.

Death on roads. Nowadays death on roads (Fig. 23) is the main cause of mortality of Dutch Barn Owls and the same applies to the study area where it averages 41% of all known causes of death. In The Netherlands an increase in the proportion of road victims was already noticed in the period 1950-75 (Braaksma & de Bruijn 1976). Since then this trend has continued as shown in Table 20: in the study area the mean percentage of road victims increased significantly from 27% in the period 1967-75 to 53% in the period 1976-84 (test in 2x2-contingency tables, $p < 0.01$). Several reasons are responsible for this dreadful development which was observed both in Liemers and Achterhoek. First of all the number of vehicles has sharply in-

Fig. 23. Road traffic mortality forms the main cause of death of the Barn Owl in The Netherlands. Photo J. de Jong.

creased during the past decades and the same applies to the motorized movements due to evening outings of the local people. Many new roads were built or improved in favour of fast traffic. Also roadside verges nowadays harbour relatively more voles and mice owing to the kind of verge management (only occasional mowing, no use of pesticides) which has been practised more and more since the end of the 1970s, particularly along the national motorways. Nowadays, the Common Vole favours low-intensively managed road verges above other habitats and can be very numerous here (van der Reest 1992). Such a rich prey supply entices Barn Owls (and other vole predators, such as the Polecat *Putorius putorius*), to hunt rather along roadsides than in the intensively managed hinterland, with the result that many of them die as traffic victims (see also Uhlenhaut 1976, Kaus 1977, Bunn *et al.* 1982, Illner 1992). The proportion of Barn Owls which died on roads is considerably higher in Liemers than in Achterhoek (51% and 33%, respectively) which is a significant difference (test in 2x2-contingency tables, $p < 0.05$). The relatively unfavourable situation in Liemers compared with Achterhoek must be mainly attributed to: (1) a denser network of motorways and main roads in Liemers, and (2) a smaller proportion of woodlots and hedgerows, particularly in W. and E. Liemers. Along such landscape elements Barn Owls can hunt much more safely than along the roadsides! The impact of these aspects will be further discussed in Chapter 10.

Starvation in hard winters. In the study region, winter victims constituted about 17% of the dead Barn Owls with known recovery circumstances. A lot of Barn Owls die in harsh winters, particularly during periods of prolonged deep snow cover when it becomes increasingly difficult to find prey outside: when no alternative food resources are available, Barn Owls get into serious trouble within 1-2 weeks (Honer 1963, Glutz van Blotzheim & Bauer 1980, de Jong 1983). Primarily, food shortage seems to be responsible for the death of Barn Owls; only extreme snowy winters (such as 1962/63 and 1978/79) result in population declines caused by abnormally high mortality, as already suggested by Güttinger (1965) and recently demonstrated by Taylor (1989). The high winter mortality by starvation in central European Barn Owls must be attributed to the relatively very small fat reserves of *Tyto alba.* After expenditure of its reserve fat, the Barn Owl can only tolerate a relatively small loss of weight. Its hunger resistance (expressed in the percentage difference between normal net body weight and starvation weight) is smaller than in the other owl species, which averages 20-21% in *Tyto* as against 32-33% in *Asio* and 32-37% in *Strix* (Piechocki 1960).

In the study area, the percentage of emaciated winter victims was 15%-18% of all deaths of Barn Owls (Table 20). Here 1968/69 and 1978/79 proved to be the critical winters with the most reports of starved owls. The occupancy history of many traditional Barn Owl territories in the study area abruptly ended in these winters as reflected in sharply decreasing breeding numbers (see Figure 7!). In both winters the vole population level was low (Table 8) whereas the duration of lasting snow cover (5-10 cm) amounted to 13 days and 23 days respectively. In contrast, in the winter 1981/82 a period of 15 days snow cover (7-10 cm) brought no reports of starvation in Barn Owls but in this winter the vole abundance was high. In Achterhoek, a number of Barn Owl pairs succeeded in surviving the adverse poor vole winters of 1968/69 and 1978/79 thanks to the well buffered prey stock in this region. Recovery of the Barn Owl population took only a few years in the well-preserved Achterhoek landscape. In Liemers, these vole troughs were associated with a complete disaster in the Barn Owl population. The recovery took longer than in Achterhoek and, what is more, the former population was not reached again in most of Liemers, particularly in regions with devastated landscape diversity (W. and E. Liemers).

In former days (up into the 1950s), Barn Owls could find alternative prey in adverse times near corn ricks and chaff heaps (when grain was threshed through the winter), as well as in granaries and in other farm buildings. These food resources are hardly available nowadays since the combine harvesting of cereals. Moreover, the harvest is centrally stored in modern well-sealed grain elevators. On a local basis, waste grain dumps have been provided to attract wild prey and Barn Owls have been supplementarily fed with laboratory mice and dead young chickens during critical winter periods: this has proved successful in the study region as well as elsewhere in The Netherlands (Bottema 1982, de Jong 1983). Without such artificial measures, however, the best survival chances for Barn Owls in inclement winters with reduced vole availability are in landscapes with many sheltered micro-niches rich in small-mammal species which can be caught by hunting owls (see Figure 15 and 16). They are particularly found in mixed farmland with many hedgerows and woodlots.

Locked up unintentionally. About 10% of the owls died because they were trapped in buildings. This fate befell a number of owls which had flown into buildings where windows had been opened temporarily; these owls died of starvation when the windows were later closed. In 1968 a brood of 3 young woefully died in a castle in Liemers, when both their parents were locked up in an attic through an oversight. Some owls starved when they were locked up in churches of which the louver-holes and other entrance-holes were fenced in. Also in this category fall bird which got trapped in chimneys and ventilation-shafts.

Collided with obstacles. Another 9% of the owls died as a consequence of a collision with all sorts of obstacles (other than motorized road traffic and trains), e.g. walls, windows, electric power cables and barbed wire.

Killed deliberately. In spite of legal protection, a number of Barn Owls were deliberately killed by man, accounting for about 7% of all known causes of death in the whole study period (1967-84). This emerged not from the ringing recovery data but from our own checked information (see Appendix 4). A number of reasons was given in excuse for the killings: 'owls give me the creeps', 'the owls made such horrible noises', 'the owl made a mess' and 'the owl had killed chickens'. Some owls turned out to have been killed because of the demand for stuffed birds: in The Netherlands the Barn Owl appears to be the most commonly stuffed bird species (see Braaksma & de Bruijn 1976)! Thanks to an extensive and sustained enlightenment campaign, deliberately killing of Barn Owls hardly occurs any more in the study region (only one reported case in the period 1975-84).

Drowning was the cause of death in 7% of the recovered owls in the study region. Drowning

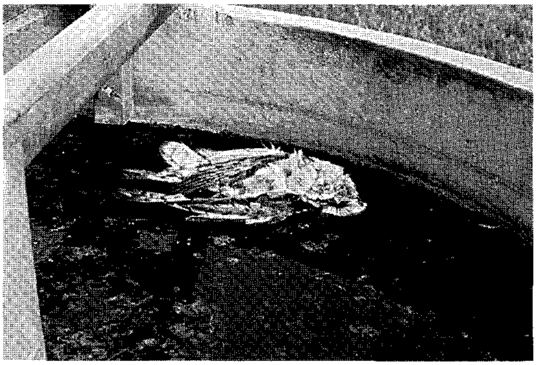


Fig. 24. Drowned Barn Owl. Photo A. Liosi.

(Fig. 24) is also well-known from other Barn Owl populations both in The Netherlands and abroad (e.g. Shawyer 1987). It is not clear whether drowned owls had wanted to drink or to bathe; it is also possible that they were attracted by their own reflections in the water (see Bunn *et al.* 1982). In the study period, all known drowning casualties of Barn Owls were recorded from Achterhoek: many of them refer to just-fledged owls which drowned in steep-sided water butts and cattle troughs. These are generally used in this relatively dry and sandy region. Recently in Liemers, however, some drowning accidents have been reported in storage basins of liquid manure.

Pesticides. All remaining causes of death were reported less frequently than 5%. One of them still deserves special attention: death due to toxic chemicals contained in pesticides. As in all European countries, in The Netherlands many species of raptors and owls were seriously threatened by the unbridled use of pesticides in the post-war decades (Mörzer Bruijns & van Genderen 1966, Koeman *et al.* 1968, 1969). In the period 1955-1970, some organochlorine insecticides (DDT, Dieldrin, Aldrin) and fungicidal seed-dressings (methyl-mercury compounds) used in agriculture proved to be especially catastrophic, because these chemicals combine toxicity with persistence; the same applies to PCB's (polychlorinated biphenyls) from various industrial products. After a partial ban on the most dangerous insecticides, the mean residues of organochlorines (DDE, HCB, Dieldrin) decreased considerably in Dutch Barn Owls found dead in the period 1968-1978 (Fuchs *et al.* 1972, Fuchs & Thissen 1981) and to a lesser extent this applies to PCB's. In the study region we had a number of convincing reports of poisoned Barn Owls in the period 1967-75 but none thereafter. We still think that the widespread use of persistent toxic chemicals in agriculture played a part in the failure of the Barn Owl population to recover from the losses in the disastrous winters of 1961/62 and 1962/63 (see also Braaksma & de Bruijn 1976). After the progressive ban on the most dangerous pesticides and restricted use of some other toxic chemicals in the late 1960s and early 1970s, a number of raptor species has shown a remarkable revival in The Netherlands (as well as in other countries), for example Sparrowhawk *Accipiter nisus* and Buzzard *Buteo buteo* (Teixeira 1979, SOVON 1987, O'Connor & Shrubb 1986, Bijlsma 1993). However, in the Dutch Barn Owl population such a remarkable revival did not happen in the period up to 1980. In Britain, Newton *et al.* 1991 reported a marked decline in aldrin-dieldrin poisoning in the intensively farmed areas in eastern England in the period 1987-89 compared with the 1960s and 1970s. They assume that for a period of 20 years or more, these pesticides have reduced the Barn Owl population in those areas to below the level that the contemporary landscape could support. It seems likely that the same process has played part in The Netherlands, because pesticide usage and population trends of raptors and owls run largely parallel in Britain and The Netherlands. In the period 1980-89 poisoning by toxic chemicals was only rarely found in Barn Owls examined in the Central Veterinary Institute at Lelystad (Th. Smit, pers. comm.). Indeed, the Dutch Barn Owl population has recovered since the 1980s to some extent in a number of parts of The Netherlands (de Jong 1989, van der Hut *et al.* 1992) while a recent recovery in Britain has been presumed by Percival (1990) on the base of increased breeding performance and survival since the mid 1970s. Hopefully this improving trend will continue, although a number of restricting factors (such as suburbanisation, expansion of road networks in combination with increased traffic density, and the lessening of landscape diversity) will probably prevent *Tyto alba* from fully regaining its former areal distribution and attaining the high numbers in which it was found before 1963. Continuation of intensive regional research on Barn Owl populations is urgently needed in combination with environmental monitoring (including checks on residue levels of PCB's and toxic second-generation rodenticides).

10. POPULATION PERFORMANCE AND UNDERLYING ENVIRONMENTAL FACTORS

In the previous chapters, the ecology and the population dynamics of the Barn Owl in Liemers and Achterhoek over the last few decades have been described. In this chapter, a summary review will be given of the relationships between population changes in the two regions and trends in the main demographic features (reproduction, dispersal, mortality). For both Liemers and Achterhoek, the values for single demographic parameters will be integrated in a scheme to achieve an over-all picture of the balance in numbers on population level. So the relative importance of reproduction, mortality, immigration and emigration on the annual balance-sheet in numbers can be analysed. The observed population patterns will be considered in relation to external (environmental) factors, particularly winter weather conditions, food supply, and availability of suitable nesting sites. Also habitat changes caused by suburbanisation and expansion of road networks will be analysed. In connection with this, changes in farmland and in farming practices will be considered and the possible effects of these on the Barn Owl population. Such an approach is important, because knowledge of the environmental limiting factors is essential for effective conservation measures and population management.

10.1 Review of the population performance of the Barn Owl in Liemers and Achterhoek in the period 1967-84

A number of tables have been presented to analyse trends in population levels and in the main demographic parameters in Liemers and Achterhoek by comparison of two consecutive periods (1967-75 and 1976-84). The most important data are summarized in Table 21.

The numbers of breeding Barn Owls have definitely declined in Liemers while in Achterhoek they have increased. A linear regression analysis was made of the annual numbers of Barn Owl (both breeding and non-breeding birds) over the period 1967-84, based on the data in Appendix 2. This analysis showed a significant decrease in Liemers ($p < 0.05$) and a significant increase in Achterhoek ($p < 0.005$). The mean annual numbers of owls per 100 km2 in Liemers and Achterhoek (period 1967-75 compared with 1976-84) are given in Table 21. The decline in Liemers can mostly be accounted for by the serious decreases in W. and E. Liemers. The increase in Achterhoek occurred all over this region (see Fig. 8).

In Liemers, a lower proportion of owls was involved in breeding than in Achterhoek, averaging 81% and 87% respectively ($p < 0.05$). More traditional breeding places were occupied by breeding pairs of Barn Owls in good vole years than in poor vole years and this applied to Liemers as well as Achterhoek (both $p < 0.005$). However, in Liemers in good vole years the occupancy rate decreased from 51% (1967-75) to 35% (1976-84), and this decline proved to be statistically significant ($p < 0.005$). Many of the traditional territories in Liemers became permanently abandoned, especially in the former 'vole plague areas' which were located in W. and E. Liemers. Moreover, in good vole years in Liemers the reproduction rate dropped from 4.3

Table 21. Review of the population performance of the Barn Owl in Liemers and Achterhoek.

Population parameter	Liemers			Achterhoek		
	period 1967-75	period 1976-84	period 1967-84	period 1967-75	period 1976-84	period 1967-84
Population level (mean annual number of owls per 100 km^2)	7.7	4.2	5.9	10.7	13.6	12.2
Breeding segment (mean percentage of owls involved in reproduction)	77%	87%	81%	86%	88%	87%
Reproduction performance (mean number of fledged young per breeding pair)	4.0	3.5	3.7	3.3	3.0	3.1
Mean mortality of first-year owls	69%	89%	75-79%	66%	63%	62-65%
Mean annual mortality of adult owls			47-50%			41-49%
Critical productivity (mean number of fledged young per pair required for population equilibrium)			4.9-5.5			2.5-3.2

NOTES. Compilation of data from Appendix 2 (population level), Table 10 (breeding segment), Table 12 (reproduction) and Tables 17 & 18 (mortality). Critical productivity is calculated from the values of the breeding segment and the mortality rates of first-year and adult owls (see text).

fledglings (1967-75) to 3.6 (1976-84), which was a significant decline ($p < 0.05$). In poor vole years the reproduction rates remained stable (averaging 2.8 and 3.0 fledglings per brood, respectively) due to the pairs breeding in the small-scale prime habitats in Northern Liemers. As a result, there proved to be no statistically significant trend in the over-all reproduction rate in Liemers (averaging 4.0 and 3.5 fledglings per nest in the two consecutive periods). In Achterhoek the corresponding occupancy rates and fledging rates stayed rather stable (see Tables 11 and 12), showing no significant trends when the two periods were compared. The same applies to the over-all fledging rate, which averaged 3.3 (1967-75) and 3.0 (1976-84), respectively.

Analysis of the dispersal patterns showed no clear trends either in time (period 1967-75 compared with 1976-84) or in space (Liemers versus Achterhoek), as discussed in section 8.1. However, a remarkable general difference was noted between Liemers and Achterhoek. Analysis of the origin of owls found dead showed that Liemers functions as a 'sink area' and Achterhoek as a 'source area' (cf. Table 14, Figures 20 and 21). A source area is where reproduction exceeds mortality, and a sink is where reproduction is insufficient to balance mortality, so that persistence depends on immigration (Newton in Perrins *et al.* 1991). The effects of these processes in our study region will be demonstrated in the next section.

An analysis of the mortality of first-year and adult owls shows a significantly higher mortality rate among first-year owls (average 68%) than among adult owls (on average, 49% annual mortality from second year of life), as given in Table 15 ($p < 0.05$). The mortality of first-year owls in Liemers was 69% in the first period (1967-75) but as high as 89% in the second period (1976-84); this can also be seen in the average span of life which fell from 450 days to 183 days (Table 17). In Achterhoek these rates were 66% (420 days) in 1967-75 and 63% (440 days) in 1976-84. Testing the exact ages, the mortality in Liemers in the second period proved to be significantly higher than in the first period in Liemers and in both periods in Achterhoek ($p < 0.005$). No statistically significant trend over time could be observed in adult mortality, either in Liemers or in Achterhoek.

To summarize, the only significant trend in demographic parameters was found in a higher first-year mortality in Liemers in the second period, compared to the first period and to both periods in Achterhoek. This factor seems to be the primary explanator for the observed decline in the Liemers population, as no clear trends in breeding performance, dispersal pattern or in adult mortality rate could be established. Further research at national level would be required to clarify this matter more in detail, through analysing the comprehensive Dutch ringing databases using advanced statistical techniques.

Percival (1990) used a key factor analysis on all the ringing data available in England to determine which population parameter had the greatest influence on Barn Owl population balance. In this, first-year mortality was identified as the key factor. Relatively small changes in this led to large changes in over-all population size. This supports the findings in the study region as stated above.

10.2 Critical productivity in Liemers and Achterhoek

The combined effects of apparently small changes in reproduction and mortality rates can bring about major changes in population balance. Exo & Hennes (1980) provide the following formula in which first-year mortality (q) and adult mortality (m) are used to calculate the number of fledglings (f) which would be necessary to keep the population in balance:

$$f = \frac{2m}{1-q}$$

This calculation assumes an equilibrium between emigration and immigration. It applies for species that breed in their first year, such as the Little Owl and the Barn Owl (Glutz & Bauer 1980). A further assumption in the equation above is that all full-grown birds take part in reproduction. In Barn Owls, however, this appears to be not valid: there proved to be a rather small but not negligible non-breeding element both in the Liemers and the Achterhoek population, as discussed in section 7.1 of this paper. Therefore, the formula for calculating the critical productivity has to be adapted as follows:

$$f = \frac{2m}{1-q} x \frac{1}{b}$$

in which b is the proportion of breeders (breeding segment) in the population.

For calculating the critical productivity according this formula, the following values were used. The proportion of breeders (b) amounted to 0.81 (Liemers) and 0.87 (Achterhoek), according to Table 9. As regards the mortality of first-year owls (q) and adult owls (m), both data sets of Table 17 and Table 18 were used. These were: Liemers (q=0.79, m=0.47 and q=0.75, m=0.50), and Achterhoek (q=0.65, m=0.49 and q=0.62, m=0.41), respectively. Using these two data sets, the following ranges in critical productivity (f) were calculated: Liemers 4.9-5.5 and Achterhoek 2.5-3.2. These values are thus the average number of fledged young per brood which have to be produced for achieving population balance (at a supposed equilibrium of immigration and emigration).

In Liemers, the critical value calculated above was not achieved; in reality it amounted to 3.7 fledglings per brood. Without net imports of Barn Owls this population cannot maintain itself, as appears to be the case. It is only because of net imports of owls to this 'sink area' that the Liemers population still persists. In Achterhoek, the calculated critical productivity was reached: the observed value was 3.1 fledglings per brood. In fact, some overproduction must have taken place, as this region functions as a 'source area' (see above).

To summarize, the combination of the observed reproduction and mortality rates provide an explanation both of the decrease of the Barn Owl population in Liemers and of the increase in Achterhoek. In any case it is obvious that the extremely high first-year mortality rate in Liemers must be reduced to make this region less dependent on source areas such as Achterhoek. An increased reproduction rate would further help to restore the population balance in Liemers. In Achterhoek the Barn Owl population proves to be self-maintaining, because here reproduction compensates local mortality; more than that, this region even functions as a net export area for Barn Owls. The relative importance of all these population parameters will be reviewed in the next section.

10.3 Integration of demographic parameters on population level: the annual balance in numbers

In Figure 25 all demographic features are combined in a scheme using the values for single population parameters as observed in Liemers and Achterhoek. The scheme starts with a supposed population level of 25 owls for both Liemers and Achterhoek. This in good agreement with the real numbers at the start of this study (1967-68), when the Barn Owl populations of the census plots in Liemers and Achterhoek were of the same order of 25-30 owls (breeders as well as non-breeders). At the start of the breeding season, a defined proportion of the population takes part in the breeding process (on average, 81% in Liemers and 87% in Achterhoek). The breeders produce a known number of young (on average, 3.7 fledglings per pair in Liemers and 3.1 in Achterhoek). The total population (non-breeders, breeding adults and juveniles) are exposed on mortality. In Liemers, the mean annual mortality is 50% in adults and 75% in juveniles, in Achterhoek the corresponding rates are 41% and 62%. The scheme shows the number of surviving owls after inserting all of these observed values: there should be 22 owls in Liemers and 28 in Achterhoek. Starting from a population size of 25 owls, this should mean a decrease of 3 individuals (= -12%) per year in the Liemers population and an increase of 3 individuals (= +12%) per year in the Achterhoek population. However, these values are not in agreement with the population changes observed in reality: the Liemers population should then have become extinct within 10 years (what did not happen) and in Achterhoek a much lower rate of increase was observed. The real rates of decline and growth can be calculated from the data in Appendix 2. The Liemers population averaged 30 individuals in 1967-68 and 12 individuals in 1983-84, which means an average decrease of about 1 owl (= -4%) per year. The Achterhoek population averaged 26 individuals in 1967-68 and 43 individuals in 1983-84, which means an average increase of about 1 owl (= +4%) per year. Starting from a population level of 25 owls (year n), this leads to a population size of 24 owls in Liemers and 26 owls in Achterhoek one year later (year n+1); these closing values are inserted in the scheme. The gap between the values of the population sizes as calculated before (Liemers: 22, Achterhoek: 28) and the 'real' values after one year (Liemers: 24, Achterhoek: 26) must be accounted for by the only missing population parameter in this scheme, viz. dispersal. This means that there must have been an average import of 2 owls per year in Liemers (net immigration) and an average export of 2 owls per year from Achterhoek (net emigration) to complete the annual balance-sheet in numbers. These conclusions are in

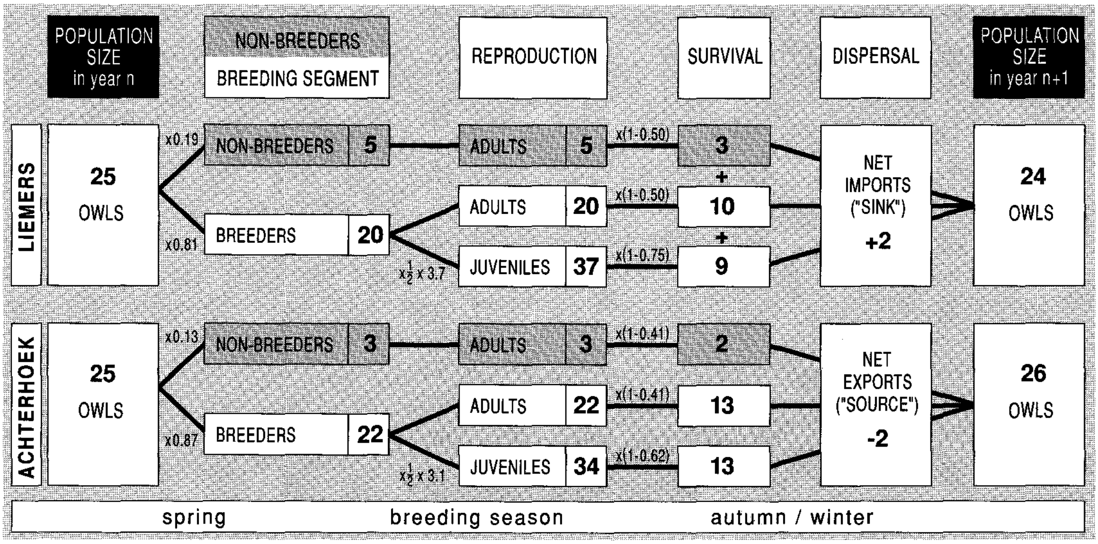


Fig. 25. The relative importance of various demographic parameters on the population size of the Barn Owl in Liemers and Achterhoek. Values for single parameters are based on the mean data established for the period 1967-84 as compiled in Table 21. Liemers functions as a 'sink area' and Achterhoek as a 'source area' (see text for further details).

striking agreement with the observed phenomenon that Liemers is a sink area (net imports of owls) while Achterhoek is a source area (net exports of owls)! In this way Figure 25 shows the relative importance of all demographic parameters. Although it concerns 'mean values', it gives an interesting quantitative review of a population in decline (Liemers) and a growing population (Achterhoek) based on field observations.

Two final remarks can be made in connection with the conclusions found in the foregoing sections. Firstly, in Liemers the high juvenile mortality forms the limiting bottle-neck in the annual population cycle. Secondly, only the proximity of source areas (such as Achterhoek) has enabled the Liemers population to persist (cf. Pulliam 1988).

10.4 External factors affecting Barn Owl populations

The main factors which can negatively affect the Barn Owl population size can be divided into five groups (see also Braaksma & de Bruijn 1976, Glutz von Blotzheim & Bauer 1980, Bauer & Thielcke 1982, Shawyer 1987, Epple & Hölzinger 1987, Batten *et al.* 1990, Percival 1991):

1. Deaths caused by human intervention (persecution, road mortality, pesticides).
2. Unfavourable weather conditions (severe frost, deep snow, persistent heavy rain).
3. Reduced food supply (low vole density, narrow diversity in prey species).
4. Habitat changes on farmland (resulting in loss of prey-rich foraging habitats) and urbanisation of rural areas.
5. Reduced availability of breeding places and suitable nest sites.

In this chapter we will discuss the importance of these environmental factors on the Barn Owl population in the study region and, finally, we will review the primary external factors which limit the Barn Owl numbers in Liemers and Achterhoek.

Road victims, persecution, pesticides. The main causes of death the Barn Owl in the study area are road traffic, starvation (see next subsection) and deaths by human intervention (both accidental and deliberate), as shown in Table 20. The importance of different factors varies according to the origin of the reports: ringing data as opposed to checked information gathered by members of the Achterhoek-Liemers Working Group for Barn Owl Protection (see Table 19). The ringing data show a percentage of road traffic victims which is twice as high as that found in the other reports (56% as opposed to 24%); this difference is statistically significant ($p < 0.001$). The over-representation of road victims in the ringing data has been discussed in section 9.3. In the analysis both sources of data were used, each contributing about half of the total cases.

The trend in causes of death for the periods 1967-75 and 1976-84 shows a significant increase ($p < 0.01$) in the number of traffic victims from 27% to 53%. This increase was observed both in Liemers and in Achterhoek. Altogether, road victims formed 51% (Liemers) and 33% (Achterhoek) of the total deaths recorded. An increase in road victims since 1960 is known from the whole of The Netherlands (Braaksma & de Bruijn 1976, de Jong 1983) and also from Britain (Shawyer 1987, Newton *et al.* 1991). Recently, a study on road traffic victims in birds in The Netherlands has been carried out (van den Tempel 1993). The Barn Owl proved to be one of the most vulnerable bird species as regards road traffic. Road mortality was estimated to cause about 10-20% annual mortality in the Dutch Barn Owl population. It was concluded that increased mortality due to road traffic may have an impact on the population balance of the species. Most Barn Owls were found dead along the national motorways with its vole-rich road verges due to low-intensity management. In The Netherlands, the total length of motorways increased from 350 to 2000 km in the period 1960-85 and the number of motorized vehicles grew from 450.000 to 4.500.000 in the same period, according to national statistics (CBS/Rijswijk).

In the study region, the present high proportion of traffic deaths in Liemers (33%-67%, depending on recovery source) is unfavourable. Many recovery reports of ringed owls concern juvenile birds found dead in autumn and early winter (during the post-fledging dispersal) along the E-36 motorway and other main roads. As far as we could examine these birds, they generally showed no starvation weights; so it involves probably healthy birds enticed by the prey-richness of the road verges. The conclusion can be drawn that such heavy losses due to road mortality in Liemers (which are significantly higher than in Achterhoek: $p < 0.05$) will contribute substantially to the very high mortality in this region. It must be realized that a reduction of the extremely high juvenile mortality in Liemers (75-80%) to the level of the annual juvenile mortality in Achterhoek (60-65%) should allow this species to maintain itself on its own in Liemers, as can be assessed with the scheme of Figure 25. Today Liemers with its dense network of main roads forms a sink area in which only continuous imports from source areas can compensate heavy losses such as caused by high road mortality.

In the most recent period Barn Owls have rarely been deliberately killed, thanks to an intensive public awareness campaign at the regional and the national level (Braaksma 1970, Braaksma & de Bruijn 1974, de Jong 1983, de Bruijn 1987, de Jong 1989). Persecution by trapping or shooting is nowadays only a secondary factor and not a threat to survival.

Pesticides are nowadays only rarely reported as a cause of death. The latter has been true since 1975, both for the study area and for The Netherlands in general (pers. comm. Th. Smit, CDI/Lelystad). In the discussion under section 9.3 it has already been noted that this development parallels the partial ban on the most persistent and lethal agrochemicals (DDT, Lindane, methyl-mercury compounds) in The Netherlands. It is likely that through the more selective use of chemicals in The Netherlands (just as in areas of intensive agriculture in England: Newton *et al.* 1991), pesticides have not been a limiting factor for Barn Owls since the mid 1970s.

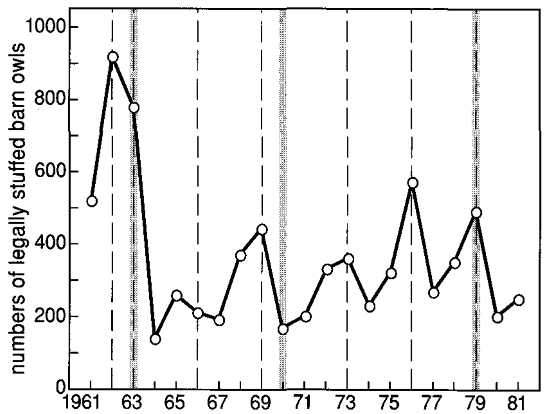


Fig. 26. Annual numbers of legally stuffed Barn Owls in The Netherlands (period 1961-81) in relation to minima in the Common Vole density (dotted lines) and excessive snow years (grey bars). Peaks in mortality correspond to minima in vole density. Redrawn from van der Hut *et al.* 1992.

However, alertness is necessary as regards the potential risk of PCB's and toxic second-generation rodenticides (cf. Batten *et al.* 1990).

Effects of harsh winters. In the study area, the percentage of starved winter victims was 15%-18% of all deaths of Barn Owls (Table 20). Here 1968/69 and 1978/79 proved to be the critical winters with the most reports of emaciated owls.

Barn Owls probably die more from shortage of food than from cold. It is likely that only very severe and snowy winters (such as 1962/63 and 1978/79) have an effect on the number of breeding pairs through increased mortality (Güttinger 1965, Braaksma & de Bruijn 1976, Braaksma 1981, Taylor 1989). The importance of sufficient food supply was demonstrated in the harsh snowy winter of 1978/79, when a number of Barn Owls in Liemers and Achterhoek survived due to supplementary feeding (see section 9.3), while many unfed congeners died. Figure 26 shows extreme external conditions (snow-rich years and vole troughs) in relation to Barn Owl mortality, as expressed in the annual number of legally stuffed Barn Owls in The Netherlands in the period 1961-81 (data after van der Hut *et al.* 1992, re-analysed). The correlation between the vole troughs and mortality is obvious, the relationship between extreme snow years and mortality less. Six out of seven vole troughs coincided with (relative) peaks in Barn Owl mortality. A stepwise multiple regression analysis showed a significant, negative, correlation between the numbers of stuffed owls and the vole population level ($p < 0.01$, R^2=0.30). When the annual duration of snow cover or annual indices of winter severity was brought into this model, no significant relationship with the number of stuffed owls could be shown. A direct relationship between vole population and frost/snow could also not be demonstrated. So the vole abundance appears to be the proximate factor as regards Barn Owl mortality.

In this study we could not find a relationship between particular winter conditions (weather data provided by KNMI/De Bilt) and the breeding performance of the Barn Owl. Neither the number of snowy days nor the severity of the winter (as measured by the Hellman or IJnsen index) showed significant relationships with the breeding numbers or the brood success in the following breeding season.

In England, Percival (1990) analysed the BTO nest records and ringing databases, and tested reproduction, dispersal and mortality statistically against weather factors. Weather appeared to have a greater effect on Barn Owl survival than on its breeding performance. Winter frost and summer rain were positively related to first-year Barn Owl mortality rate, and winter rain and low temperature in spring to the adult mortality rate. These factors explained however only a limited proportion of the over-all variation in mortality, so there must be other influencing factors too. It would be desirable to examine the Dutch ringing database (which is comprehensive enough to estimate annual mortality rates) to obtain further clarification on this. To unravel these complex relationships, simultaneous analysis of the food supply situation would be advisable.

Effects of vole abundance. The Common vole *Microtus arvalis* is the most important prey species of the Barn Owl in The Netherlands (de Bruijn 1979) and this holds both in Liemers and Achterhoek. The dominant position of the Common Vole in the food spectrum of the Barn Owl in the study area is shown in Figure 17. There appears to be a statistically significant correlation between the number of breeding pairs of Barn Owls and the vole population. Based on the annual variation in the vole numbers, see Table 8, a linear regression analysis shows that fluctuations in vole population can account for 51% and 73% of the variance in the numbers of breeding pairs in Liemers and Achterhoek, respectively ($p < 0.01$ and $p < 0.001$). Another regression analysis showed the positive correlation between vole population and breeding performance of the Barn Owl (average annual number of fledglings) in the study area ($p < 0.05$, R^2=0.36). In good vole years, the owls raised on average 3.4 young per pair as against only 2.9 young in poor vole years ($p < 0.05$). A relationship between vole density and owl mortality could not be shown for

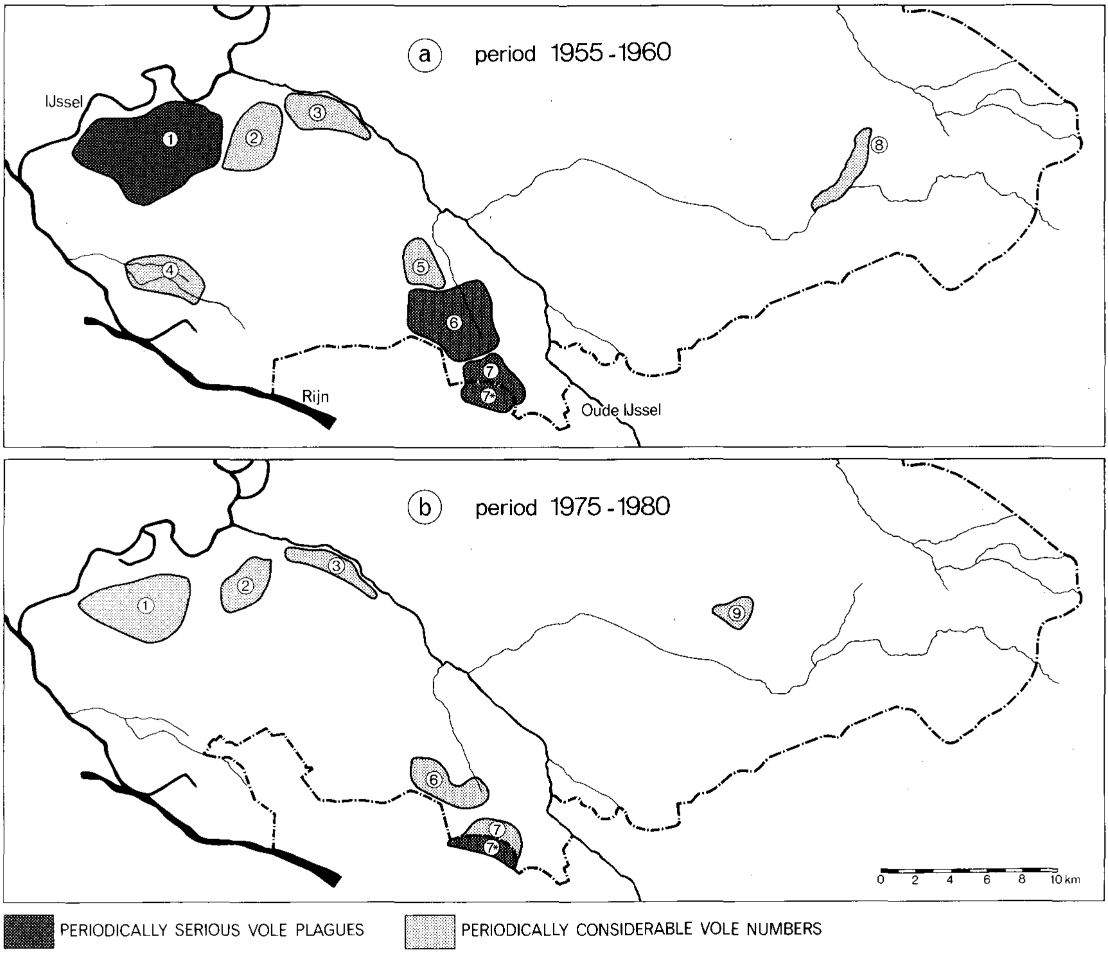


Fig. 27. Changes in the occurrence of vole plague areas in the study region: period 1955-60 compared with 1975-80.

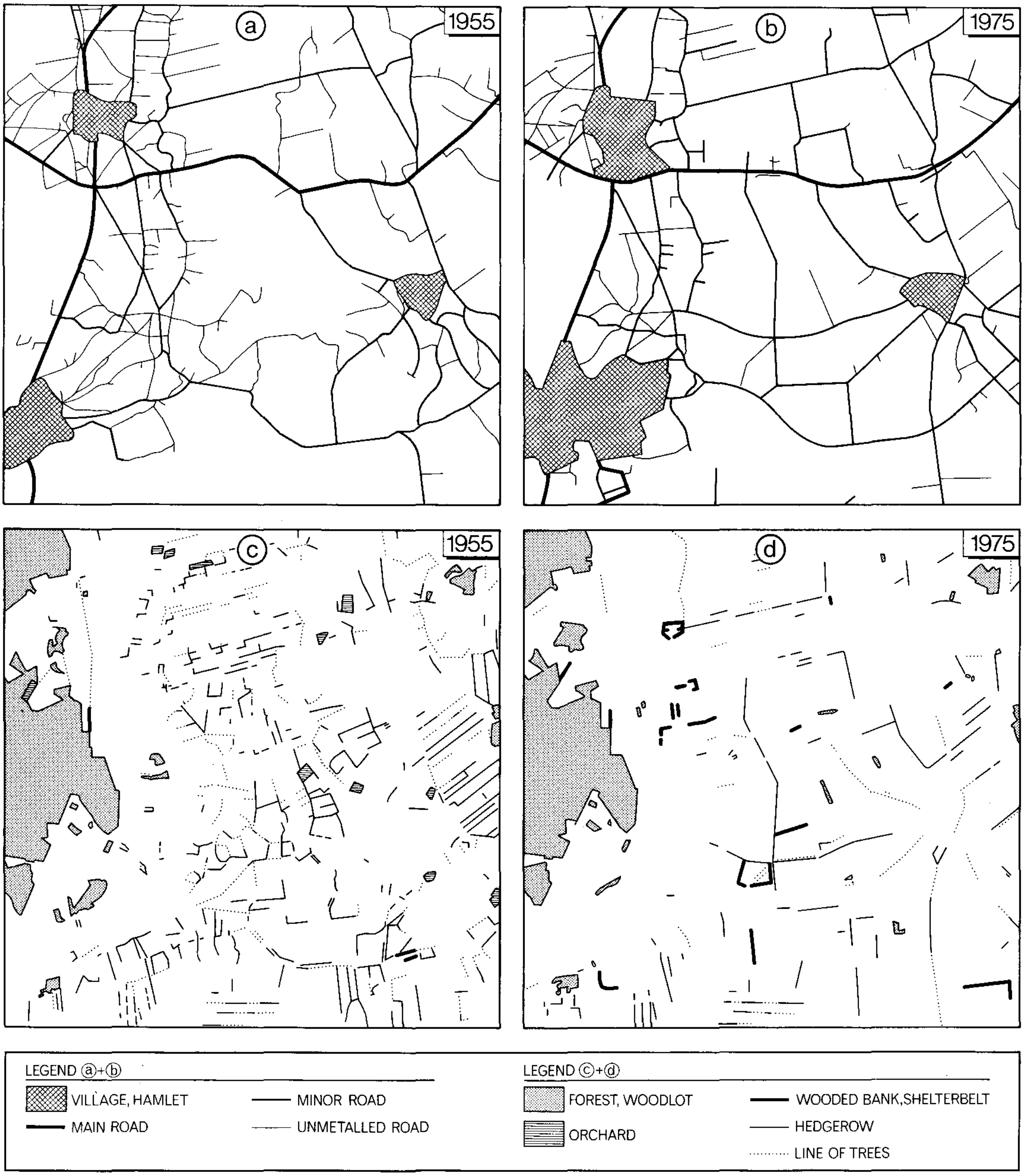


Fig. 28. Changes in landscape features in eastern Liemers: situation circa 1955 compared with situation circa 1975. Figures show suburbanisation and road-system (upper part) and the pattern of woodlots and the network of hedgerows (lower part) in an area of 5 by 5 km (plot 2a). Note the expansion of the villages, the increase in metalled roads and associated loss of dirt roads, and the enormous reduction of hedgerows due to large-scale land consolidations at the end of the 1960's. In this part of Liemers the Barn Owl population decreased seriously in the period 1955-75.

the study area, because we could not make annual mortality estimations. However, such a (negative) correlation between vole density and mortality could be demonstrated for the Dutch Barn Owl population as a whole (see the last subsection and Figure 26).

In connection with this, it may be interesting to note the recent research by Taylor *c.s.* (1989, 1992) in Scotland. Here the Field Vole *Microtus agrestis* is the main prey species of the Barn Owl; this vole is subject to fluctuations on a 3-4 year cycle which are similar to the cycles of the Common Vole on the Continent. The vole population density in Scotland affects both the reproduction and the mortality rates of the Barn Owl. The mortality rate appears to be the most important factor in determining the annual variations in the number of breeding pairs.

Anyhow, it is clear that the vole population level has a strong effect on the Barn Owl population by influencing both the breeding performance and the survival. Therefore it is important to check the environmental factors which act on the size of vole populations. The major factor in this is the agricultural land use (van Wijngaarden 1957).

Habitat changes on farmland. The Netherlands has a largely agricultural landscape. Variations in topography combined with relatively stable and extensive farming practices over centuries had resulted in an enormous diversity of landscape types with a very rich flora and fauna until the first half of the 20th century. During the course of the last 50 years much of this natural richness has alas been lost as a result of industrialisation, urbanisation of rural areas and intensification of agriculture land use (de Molenaar 1980).

In the first half of the century new technical developments led to large-scale reclamation of wetlands and moors. A number of wetland species have suffered severe losses from these developments. A small number of bird species, including some grassland waders (e.g. the Black-tailed Godwit *Limosa limosa*), the White Stork *Ciconia ciconia* as well as the Barn Owl were initially able to benefit from this (Rooth 1957, de Bruijn 1982, de Molenaar 1983). After the Second World War there was a strong trend towards intensification in agriculture, characterized by rationalisation and mechanisation (replacement of horse power and labour by machines), improvement of the external conditions of production (drainage, consolidation of land holdings, large-scale removal of hedgerows), changing crop management (increasing use of fertilizers and pesticides), change of crops grown (maize instead of wheat and rye) and the cultivation of marginal land. Up until the 1960s there were small-scale, low-intensity mixed farms everywhere in Liemers and Achterhoek. Throughout this farmland numerous hedges and copses were intermingled together with pieces of semi-natural habitats such as woods, marshes and bogs. As a consequence of this diversity throughout the countryside, this region had a very rich flora and fauna including 135 species of breeding birds.

Along with the Common Agricultural Policy developments in the European Community (now the European Union), these traditional low-intensity mixed farms were very rapidly converted into large-scale specialized dairy farms with high stocking rates and very intensive land use from 1970 onwards. The effects of the rationalisation and intensification of agriculture can be summarized as follows (Harms *et al.* 1984):

a. Deterioration of the abiotic components of the environment (soil, water and air pollution);
b. Damage to the historic-cultural and scenery elements (old buildings, hedgerows, coppices etc.);
c. Reduction of the biotic diversity (flora and fauna).

The results of these developments on birdlife of farmland habitats have been both very deep and far-reaching (Bezzel 1982, O'Connor & Shrubb 1986). In this section, discussion is limited to the effects of changing farming practices on the Barn Owl habitat in Liemers and Achterhoek.

In the 1950s the use of grasslands was relatively extensive, particularly in the large expansive areas of the polders, riverine areas and in

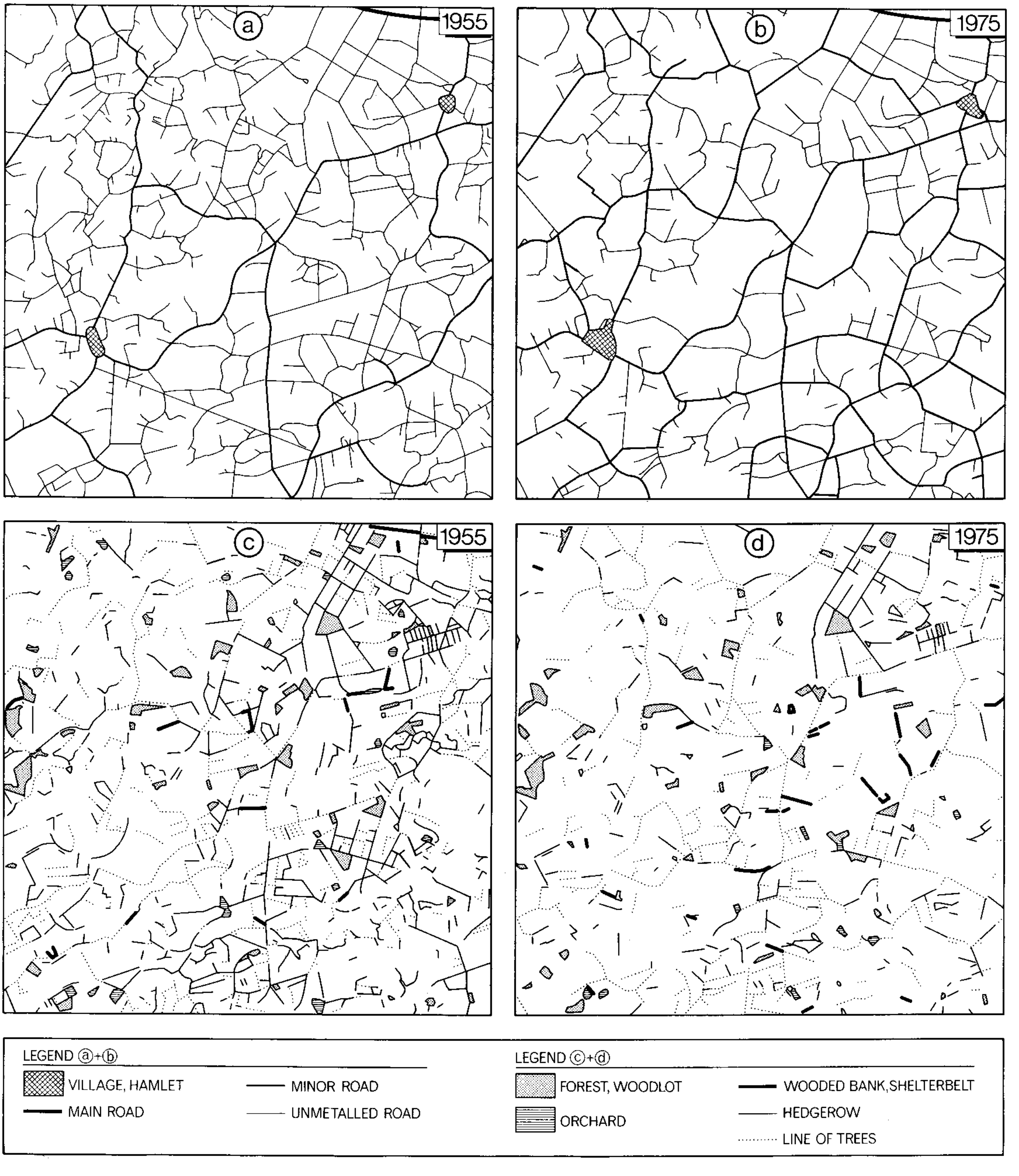


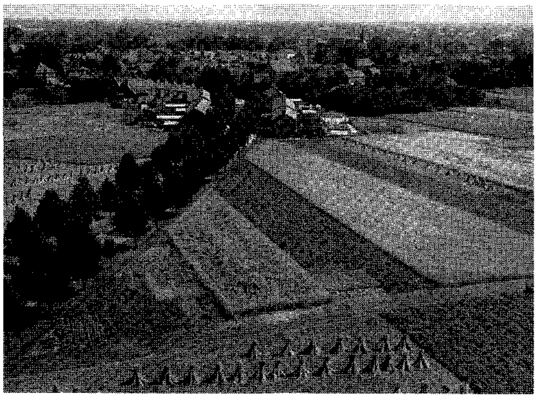
Fig. 29. Changes in landscape features in western Achterhoek: situation circa 1955 compared with situation circa 1975. Figures show suburbanisation and road-system (upper part) and the pattern of woodlots and the network of hedgerows and wooded banks (lower part) in an area of 5 by 5 km (plot 4a). In this area only a slight expansion of the villages can be noted and many roads are still unmetalled. A reduction of hedgerows and wooded banks has taken place, but a rather dense network of linear woody landscape elements still exists over the whole area. In this part of Achterhoek the Barn Owl population has increased in the period 1955-75.

moor-reclamations. This kind of remote grassland area was used for growing hay or as summer pasture and lends itself to periodic vole plagues (van Wijngaarden 1957). Interviews with many farmers were used to map these (see Fig. 27). In the mid 1950s in Liemers real vole plagues occurred periodically on as much as 4000 ha and in addition there were 2500 ha of herbaceous grasslands where relatively large numbers of voles were found. These formed rich food resources for many pairs of Barn Owls which produced large clutches and sometimes even two broods in peak vole years (de Bruijn 1979). By the mid 1970s land consolidation and intensification of grassland management (shift from hay to silage, pasture improvement, increased stocking rates) had reduced the real plague zone to one area of 350 ha while the remaining grasslands with relatively large vole populations were estimated at 3000 ha (see Fig. 27). This process continued in the 1980s. In this way a large area of suitable Barn Owl habitat has disappeared in Liemers. The owl's breeding population decreased by 60% between 1955 and 1975 (see Table 1). The decrease in vole numbers is reflected in lower occupancy rate of Barn Owl territories and decreasing reproduction rates in peak vole years (see Tables 11 and 12). It is quite possible that this process has also led to increased mortality among Barn Owls in Liemers

Table 22. Changes in habitat features on farmland plots in Liemers and Achterhoek: situation circa 1955 compared to situation circa 1975. Figures concern sum total (area/length) of habitat variables per 100 km^2 (based on data in Appendix 5).

	Liemers			Achterhoek		
	1955	1975	Change (%)	1955	1975	Change (%)
Orchards (ha)	471	143	-70%	47	24	-49%
Small marshlands (ha)	96	50	-48%	-	-	
Vole-rich grassland complexes (ha)	2000	1100	-45%	100	100	
Villages (ha)	520	1242	+139%	92	192	+108%
Woodlands (ha)	292	352	+21%	710	695	-2%
Dual highway (hm)	-	62	++	-	-	
Metalled roads (hm)	1655	1928	+16%	891	1817	+104%
Unmetalled roads (hm)	1755	826	-53%	4426	2836	-36%
Hedgerows and wooded banks (hm)	1170	605	-48%	2665	1716	-36%
Lines of trees without underlying hedges (hm)	651	521	-20%	1391	1517	+9%
Edges of woodland (hm)	372	543	+46%	1715	1700	-1%
Edges of marshland (hm)	163	69	-58%	-	-	
Rough field slopes (hm)	233	129	-45%	1880	1234	-34%
Banks of dikes (hm)	186	163	-13%	-	-	

NOTE. Figures concern total sum of habitat features in following census plots (see Figure 3): Liemers = plots 1A/1B/2A/2B (total sum 100 km^2); Achterhoek = plots 4A/4B/5A/5B (total sum 100 km^2).



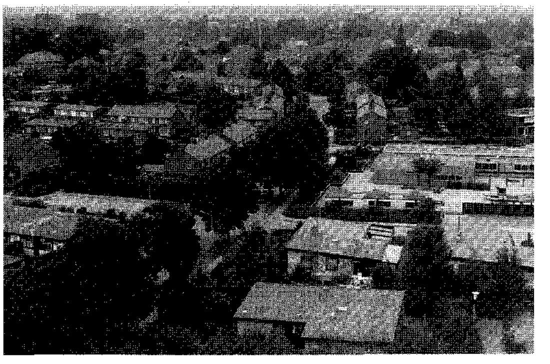


Fig. 30. Up until the 1960's, most villages and small cities in the study region harboured a breeding pair of Barn Owls. They usually bred in the centre in a church or other old building. Their hunting grounds were at the outskirts of the village where small-scale farming was practised as shown in the picture taken at Aalten (Achterhoek) in 1956 (Photo Wim K. Steffen). During the last decades, most villages have been expanded substantially and the former hunting grounds have been built over as shown in the picture taken in 1986 (Photo Maaike de Bruijn-Feldbrugge). By the end of the 1980's no Barn Owls were breeding within the villages in the study region any longer. Today they all breed in farms situated in the countryside.

(cf. Figure 26). In Achterhoek, the Common Vole plays a less dominant role; the greater landscape diversity (with its mixture of open fields, hedgerows and copses) gives the owls here a wider choice of prey species (cf. Figs. 7 and 17). In Achterhoek there are no indications of lower reproduction rates or higher mortality in the period 1967-84 (Table 21).

In the context of this study detailed research was made into the loss of Barn Owl habitat from 1955 to 1975. In this regard a selection of habitat features which are of real importance for this species was made, based on the owl's habitat requirements (see section 5.3). Changes in the quantity of these landscape elements were measured from topographic maps in ten plots each of 25 km^2 spread over Liemers and Achterhoek (Fig. 3), using a digital computer. The results of this analysis can be found in Appendix 5.

The data have been aggregated into two 100 km^2 samples (one for Liemers and one for Achterhoek), see Table 22. In Liemers mainly polder and riverine landscapes are involved, whereas the Achterhoek plots consist of cover-sand, plateau and moor-reclamation landscapes. The numbers in Table 22 refer to length (in hm) or area (in ha) per 100 km^2. The landscape changes are illustrated for one of the base plots in Liemers and one in Achterhoek, see Figures 28 and 29.

In Liemers a number of developments unfavourable to the Barn Owl came to light through this exercise:

- loss of a large area of old orchards and extensively managed (vole-rich) grassland;
- expansion of villages and suburbanisation;
- the construction of a motorway and the building of metalled roads to replace dirt roads (which are relatively safer for Barn Owls: Illner 1992);
- a great reduction in the length of hedgerows, tree lines, rough field slopes and marsh edges where Barn Owls prefer to hunt.

In Achterhoek there were also some unfavourable developments in the period 1955-1975, but these were not so dramatic as those observed in Liemers (cf. Fig. 28 and 29):

- orchards and vole-rich grasslands had never played such an important role, so reduction in their areas has not been so serious for the Barn Owl here;

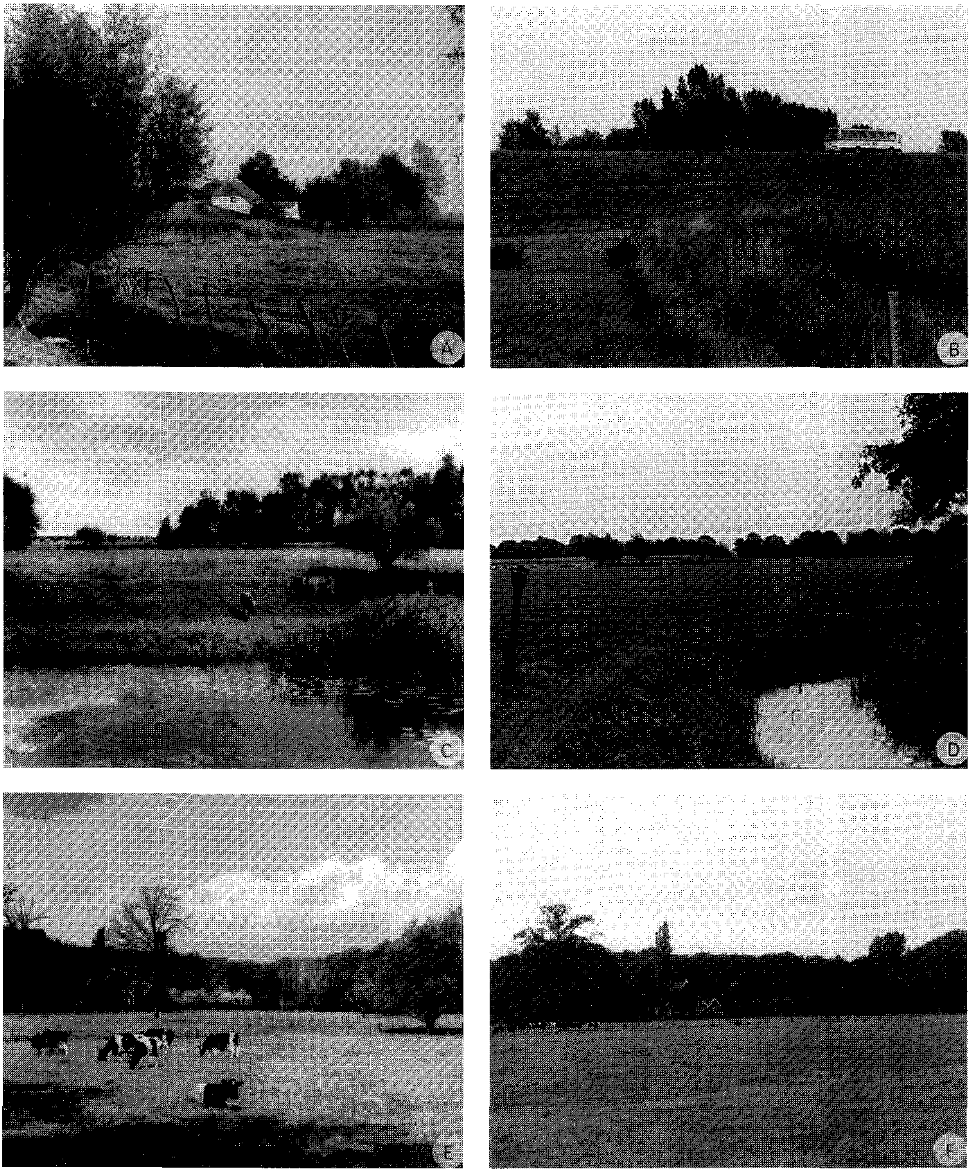


Fig. 31. Changes in landscape features and land use in the study region. A. River landscape near Herwen (W. Liemers) in 1964. Photo J.G.J Frentrop. B. The same spot in 1986. A new road on a dike has been built. The pollard-willows have been removed. Maize cropping has taken the place of extensively managed grassland. Photo Maaike de Bruijn-Feldbrugge. C. River landscape near Laag-Keppel (N. Liemers) in 1958. Notice the rough grassland associated with low stocking rates. Photo Archives Staring Institute. D. The same spot in 1986. The pool has been filled in, a drainage ditch has been dug. The grassland parcels have been enlarged in combination with levelling down of the relief, leading to more intensive grassland management. Photo Maaike de Bruijn-Feldbrugge. E. Plateau landscape near Winterswijk (E. Achterhoek) in 1966. Photo Archives Natuurmonumenten. F. The same spot in 1986. The grassland parcels have been enlarged and solitary trees have been removed. Photo Maaike de Bruijn-Feldbrugge.

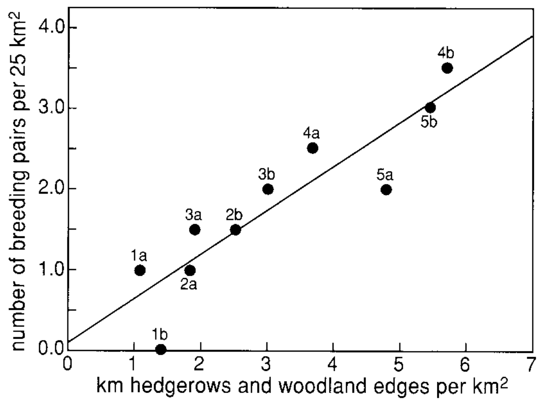


Fig. 32. Barn Owl breeding density in relation to the total length of hedgerows, wooded banks, lines of trees and woodland edges. The fitted line as computed using linear regression analysis shows the highly positive correlation ($p < 0.001$) for the ten census plots situated in Liemers and Achterhoek (Fig. 3). In this basic model, the total length of the landscape variables explained 79% of the variance in the number of breeding pairs of the Barn Owl.

there has been little increase in the size of villages;

- there has been an increase in metalled roads but there are still many dirt roads;
- there has been less reduction in the length of hedgerows, shelterbelts and tree lines; in fact, the total remaining length of these is three times higher in Achterhoek than in Liemers.

Figure 30 depicts suburbanisation and Figure 31 illustrates changes in landscape and intensification of farming in the study region, showing pictures taken at the same spot at intervals of 20-30 years. The captions for these pictures describe the most important changes which have taken place. The radical changes in land use during the 1970s and 1980s have eliminated small mammals in farmland. As a consequence, herbaceous road verges as well as tree lines and hedgerows have become crucial for the Barn Owl, because small mammals in farmland are nowadays concentrated in such landscape elements or the rough strips along them (van der Reest 1989). A reduction in these woody linear elements has negative consequences for all the prey species of the Barn Owl (Wammes 1986). Up until 1960, high Barn Owl densities were also found in more open polder and riverine areas in The Netherlands, when real plagues of Common Voles still occurred in these landscapes (see van Wijngaarden 1957 and Honer 1963).

In the present study a positive relationship was found between the Barn Owl population and the total length of hedgerows, wooded banks, tree lines and woodland edges. This is true for both Liemers and Achterhoek. Figure 32 shows the length of these linear elements versus Barn Owl breeding density in 1974-75 in the 10 plots. A linear regression analyses showed a statistically very significant relationship ($p < 0.001$, R^2=0.79). The number of breeding pairs is thus directly proportional to the length of hedges, tree lines and wood edges!

A number of factors together form the causal explanation for this relationship. As noted above, the value of these landscape elements for Barn Owls is determined by the presence of many small mammals, both in the woody elements themselves and in the small strips of extensively managed rough grassland which are usually found along these linear elements. In general, small-scale landscapes appear to have an over-all lower farming intensity than 'rationalized' landscapes. The diversity of mixed farmland guarantees a varied prey spectrum, which forms a buffer for Barn Owls in times of vole scarcity. Furthermore, most hedges and wooded bank are situated along parcel boundaries; hunting flights along these stretches, as well as along woodland edges, keep Barn Owls off the dangerous roadsides. And where high hedges flank roads, owls are forced to cross roads on safe heights which restricts the number of road traffic victims (M.F. Mörzer Bruijns, pers. comm.). This could also form the explanation for the significantly lower proportion of road deaths of Barn Owls in Achterhoek than in Liemers (Table 20), as the remaining length of hedges, wooded banks and lines of trees in Achterhoek is three times higher than in Liemers (Table 22).

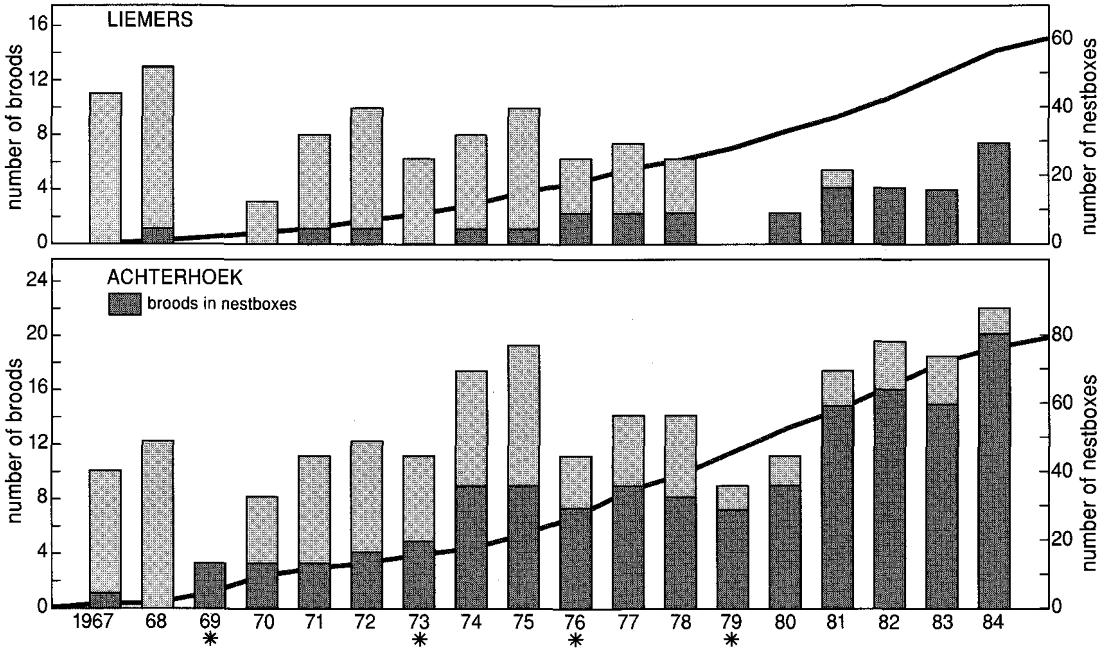


Fig. 33. Annual number of broods and the proportion of broods in nestboxes (darkgrey shaded) in the Barn Owl population in Liemers and Achterhoek in the period 1967-84. Asterisks indicate minima in the Barn Owl population corresponding with troughs in the vole cycle. Lines show the number of nestboxes available.

From the point of view of nature conservation, an important question is what total length of such elements is necessary to support a viable population of Barn Owls. Shawyer (1987) suggests a density of 0-2.5 breeding pairs per 100 km^2 as 'critical' and a population of 2.6-4.0 pairs per 100 km^2 as 'vulnerable'. This standard is applicable to the Dutch situation (see Chapter 4). Using this, it can be seen from Figure 32 that where there is less than 2 km of these linear elements per km^2 left on average, the habitat situation becomes critical for the Barn Owl. This was in fact the case for the Liemers plots as given Table 22. Around 1975 the average length of woody linear landscape elements was 1.7 km per km^2 and there were on average 3.5 breeding pairs of Barn Owls per 100 km^2 (3 in 1974 and 4 in 1975). The situation in the Achterhoek plots was much more positive: here the average length of linear elements was 5.1 km per km^2 in 1975 and there were as many as 11 pairs of breeding Barn Owls per 100 km^2 (10 in 1974 and 12 in 1975).

Given the current production pressure on farmland, which eliminates the small mammals, an minimum average length of hedges, tree lines and wood edges of 3-5 km per km^2 is advisable for Barn Owls populations in the future. In Barn Owl strongholds a length of over 5 km per km^2 is desirable to keep up 'source' owl populations. These values fall in the same range as those proposed by Shawyer (1987) and Taylor (1989) for Britain. The importance of hedgerows and woodland edges for small mammals can greatly be increased by the creation and adequate management of small grassland margins and herbaceous field edges (ideally 3-6 meter wide) along these landscape elements and along water courses. An alternative could be the creation of scattered small woodlots fringed with broad (10-

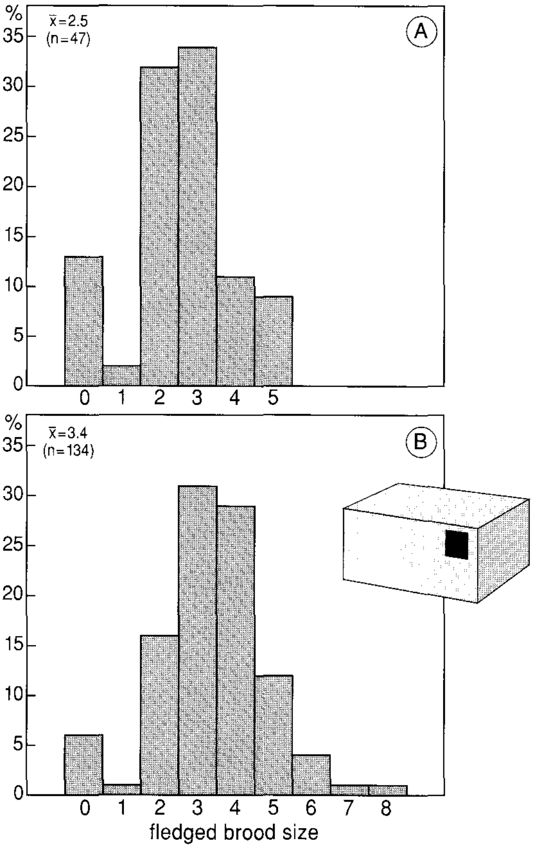


Fig. 34. Brood performance of the Barn Owl in nestboxes (lower part) compared with brood performance in other nest sites (upper part). Figures show the distribution of brood size at fledging in the period 1976-84. The brood success in nestboxes proved to be significantly higher than in the other nest sites ($p < 0.001$).

15 m wide) rough grassy strips which are extensively managed (Wagenvoort 1989).

Availability of nest sites (including nestboxes). In the early years of the study period, a negative trend became apparent regarding the availability of nest sites. At least 30 of the 95 known breeding sites (31%) were lost in the period 1956-84. The loss in Liemers was particularly great (18 out of the 39 known breeding places, i.e. 46%). This involved churches (6 former breeding places were closed off, because the louver-holes were fenced in), farm buildings (8 breeding places lost by demolition or rebuilding), castles (2 cases of entrance holes being closed off) and houses (2 cases of renovation). In Achterhoek, the loss was not so great (12 out of 56 known breeding places, i.e. 21%): this involved 2 churches, 9 farms and 1 windmill.

To offset this negative trend, a major campaign to protect existing breeding places (opening flight passages) and to create new nest sites was initiated in 1967. Over 200 nestboxes have been placed all over Liemers and Achterhoek in the period 1967-84 (see Fig. 12). The campaign started with safeguarding of the traditional breeding sites and through concentrating nestboxes in the prime habitats. Then a network of boxes all over the study region was completed.

The success of this long campaign has been great. A steadily increasing percentage of Barn Owls is resorting to these nestboxes (Figure 33). During the initial stage of the nestbox scheme (period 1967-75), about 23% (39 out of 172) of the known Barn Owl broods in the intensively monitored plots were established in nestboxes. In the next period (1976-84), about 76% of the recorded Barn Owl broods (133 out of 175) were situated in nestboxes. Both in Liemers and Achterhoek, nearly all Barn Owls have taken refuge in the nestboxes. In connection with a steadily growing number of these artificial nest sites, at least 90% of the Barn Owl pairs in Liemers and Achterhoek used such nestboxes for breeding by 1990. In small-scale landscapes of Achterhoek and Northern Liemers, in six plots of 10 by 10 km, very high Barn Owl densities (11-13 breeding pairs per 100 km^2) have been noticed recently (1990). Nearly all of these were nesting in the boxes provided, and the brood successes were very good (on average, 3.9 fledged young per brood; n=70). Before 1980 the availability of suitable nest sites was much lower. Such high Barn Owl densities can be only attributed to the ample availability of nestboxes in good breeding places (10-20 nestboxes per

25 km² in the core areas around 1990). So the nestbox campaign has proved to be an important weapon in the struggle for the conservation of the Barn Owl population.

During the course of our nestbox campaign, we gained a number of experiences regarding the optimal type of nestbox and the ideal locations for placing them. The positive effect of nestboxes was probably enhanced by placing them in buildings of 'Barn Owl friendly' people in 'Barn Owl fitting' areas and usually far from dangerous roads, to achieve positive impacts on reproduction and survival. The brood success in nestboxes was tested after completion of a random distribution pattern of the boxes over the various habitats all over the study region. Figure 34 shows the breeding performance (numbers of fledged young per brood) in nestboxes compared with that in 'free' nest sites in buildings (under roofs, on lofts and rafters, amongst bales of hay) in the period 1976-84. The number of fledged young in nestboxes averaged 3.4 as against only 2.5 in other nest sites, and this difference proved to be statistically significant (test of homogeneity against trend, $p < 0.001$). It can be noticed that the first value exceeds the critical productivity in Achterhoek (2.5-3.2 young per brood) in contrast to the second value! For Liemers, the mean fledged brood size in nestboxes is still too low to compensate the current mortality rates (cf. Table 21).

In Britain, Glue (1992) also found a positive impact of nestboxes on reproduction. This emphasizes the importance of the nestboxes, particularly in areas where the species is threatened by a number of developments such as nowadays occur in large parts of western Europe: suburbanisation, expansion of road networks and increasing traffic density, and intensification and rationalisation of agriculture.

10.5 Environmental limiting factors in Barn Owl populations of Liemers and Achterhoek

At the end of this chapter, we will review the main environmental factors which have influenced the size of the Barn Owl populations in Liemers and Achterhoek. Distinction will be made between the 1960s, the 1970s and the 1980s.

In the beginning of the **1960s**, a very strong decrease was found in the Barn Owl breeding populations. This started with two successive poor vole years (1961 and 1962), which effect was strengthened by mass-mortality in the very extreme winter of 1962/63. Normally, Barn Owl populations recover within six years, but at the end of the 1960s the Dutch population had restored itself only partially (Braaksma & de Bruijn 1976). The same applied to the populations of Liemers and Achterhoek (see Table 1). There were indications of lessening landscape diversity, decreasing nest site availability and increasing road mortality, but probably the key limiting factor was formed by toxic pesticides which prevented the Barn Owl reaching numbers which the food-resource level and the contemporary landscape could support (just as in eastern Britain: Newton *et al.* 1991). Toxic pesticides act negatively both on reproduction and survival.

In the **1970s**, Barn Owl numbers in Liemers further decreased, but in Achterhoek a revival took place (Table 1). A partially ban on some persistent agrochemicals led to significant lower residue levels of the most toxic chemicals (Fuchs & Thissen 1981). In those years, large-scale changes in agriculture occurred, in combination with removal of hedges and wooded banks, and road improvement and expansion. The negative implications were larger in Liemers than in Achterhoek (this study). On the other hand, the nestbox campaign got going and proved to be successful. The reduced impact of pesticides and the improved nest site availability, however, led to population growth only in the better preserved landscapes of Achterhoek. In Liemers these improving external factors could not stop the population decline which must be attributed to the intensification and rationalisation of agriculture (leading to the disappearance of vole-rich areas and large-scale reduction of hedgerows). The Barn Owl breeding density in farmland appeared to be determined by the length of the remaining hedgerows, wooded banks and woodland edges.

In the **1980s**, the decline was going on in western and eastern Liemers, as a result of a continuation of the processes mentioned before. An increase in first-year mortality was established, for which also the very high proportion of road victims accounted. Fortunately, the Liemers population is supported by a net immigration of Barn Owls from source areas (such as Achterhoek) where productivity exceeds mortality. In the small-scale landscapes of northern Liemers, the Barn Owl population stabilized and recently high breeding densities were recorded in the nestbox network in this area. In Achterhoek, the population also grew in parallel with the increased supply of nestboxes, which supports evidence that nest site availability was the environmental limiting factor in these well-preserved landscapes with an buffered food supply.

The relationships between the most important external (environmental) factors and the main internal (demographic) features, as found in this study for the 1980s, is shown in Figure 35. In this diagram, the landscape and human land use occupies a central place. It determines the available food resources, both quantitative (population sizes of small mammals) and qualitative (diversity of the prey spectrum). This influences breeding performance as well as survival of the Barn Owl. With the contemporary intensive agriculture, the total length of hedgerows, lines of trees and woodland edges (with its adjoining rough grassland strips) determines the owl's population sizes in farmland areas.

Two main factors act upon the internal population balance of the Barn Owl. On the positive side, the reproduction can be improved by offer-

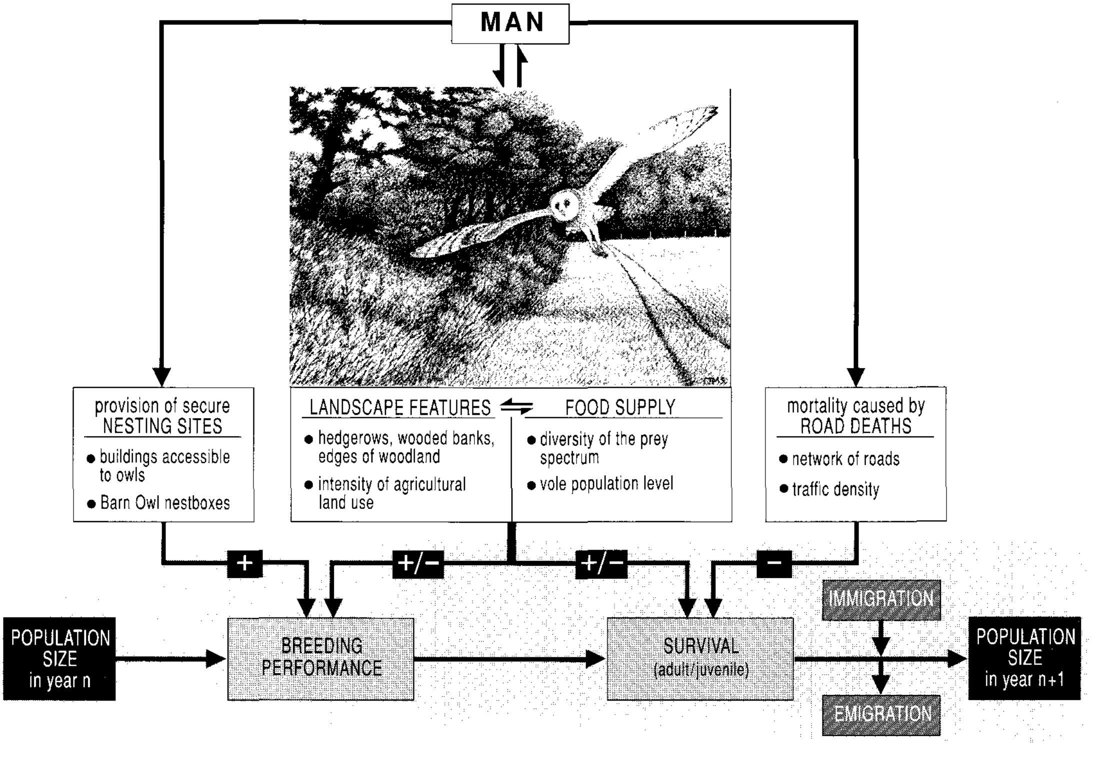


Fig. 35. The relationship between external (environmental) factors and internal (demographic) parameters in the Barn Owl population in the study region. The diagram shows the relationships as found in this study for the 1980s. Illustration Frits-Jan Maas.

Table 23. Changes in breeding occurrence of birds in Liemers and Achterhoek in the period 1963-1982 in relation to habitat preference and migratory behaviour. The selection of species which have increased and the species which have decreased in breeding numbers is based on data in Appendix 6. The species are sub-divided into two groups according to their habitat preference in study area (semi-natural landscapes versus mixed farmland). The migratory behaviour of the species in The Netherlands is indicated as follows: E = resident or wintering in Europe, A = wintering in Africa.

Breeding species with main occurrence in semi-natural landscapes		Breeding species with main occurrence in mixed farmland	
Population increase	Population decrease	Population increase	Population decrease
E Podiceps cristatus	A Ixobrychus minutus *	E Buteo buteo	A Anas querquedula *
E Ardea cinerea	A Sterna hirundo **	E Turdus pilaris	A Crex crex *
E Anas strepera	A Chlidonias niger *	E Corvus frugilegus	A/E Tringa totanus *
E Aythya ferina	A Jynx torquilla **		E Lullula arborea *
E Aythya fuligula	A Caprimulgus europaeus *		A Saxicola rubetra *
E Accipiter gentilis	A Riparia riparia *		E Saxicola torquata **
E Accipiter nisus	A Luscinia svevica *		E Miliaria calandra **
E Loxia curvirostra	A Acroceph. schoenobaenus *		A Emberiza hortulana *
	A Acroceph. arundinaceus *		

NOTE. Species indicated by an * are listed as endangered and characteristic species in The Netherlands (Osieck 1986). Species indicated by ** were later enlisted as endangered birds in The Netherlands (Osieck & Hustings 1994).

ing optimal nestboxes. On the negative side, in urbanised areas with dense networks of main roads the mortality is very high and the population balance is negative. In such sink areas, Barn Owl populations can only persist thanks to continual imports from source areas. In the study region, such Barn Owl sources are formed by: (1) mixed farmland areas with a high density of hedgerows, wooded banks and coppices, (2) a rather low density network of main roads, and (3) a large supply of safe nesting sites, as now provided by intensive nestbox campaigns.

11. THE FUTURE OF THE BARN OWL AND OTHER BIRDS IN MIXED FARMLAND

The developments described in the previous chapter have an impact not only on the Barn Owl but also on many other bird species. Therefore the population trends of 50 other scarce bird species which are characteristic of the region were also monitored over the period 1965-80. Many of these birds, like the Barn Owl, were later listed in the Dutch 'red list' of endangered species (Osieck 1986, Osieck & Hustings 1994). A number of conclusions regarding how the Barn Owl and other scarce bird species could be more effectively protected in mixed farmland can be drawn from the relationships identified. Barn Owl protection can in this way be broadened to an action programme covering groups of bird species and other conservation interests.

11.1 Changes in bird populations in the period 1965-1980 in relation to habitat choice and migratory habits

Methods regarding the selection and census techniques of 50 breeding birds in the study region were discussed in section 3.3 of this paper. A list of the species included in this study will be found in Appendix 6, where the numbers of breeding pairs are compared between the

Fig. 36. Male Corncrake *Crex crex* photographed in a herbaceous strip along a cornfield at Beltrumsche Veld (Achterhoek) in July 1978. The Corncrake is a species which is threatened world-wide (Collar & Andrew 1988). Threats to survival include replacement of cornfields by maize cropping, loss of hay meadows, earlier harvesting dates, loss of herb vegetation at field margins and the hazards of migration across the Sahara and Sahel (Batten *et al.* 1990). Species of this kind run double risks as a result of their migratory habits and their habitat selection. Photo Jos Korenromp.

periods 1963-67 and 1978-82. Those species which show the most obvious changes in numbers were selected for further analysis. This concerned 17 species (34%) with a marked decrease and 11 species (22%) with a marked increase in the study area. Two further criteria were used to categorize these birds species in Table 23:

- habitat choice: birds breeding mainly in mixed farmland versus birds breeding mainly in semi-natural habitats (marshland, moorland, woodland) in the study region;
- migratory habits: those that winter in Europe versus those that migrate to Africa (source: Speek & Speek 1984).

From the scheme in Table 23 a number of patterns can clearly be seen:

1. In semi-natural habitats there is an equilibrium between the number of species which have increased and the number of species which have decreased. All species which have increased are non-migratory or winter in Europe. These are species mainly from eutrophic waters and artificial lakes (e.g. Great Crested Grebe *Podiceps cristatus*, Tufted Duck *Aythya fuligula*, Pochard *Aythya ferina*, Gadwall *Anas strepera*) and from the coniferous woods (Sparrowhawk *Accipiter nisus*, Goshawk *Accipiter gentilis*, Crossbill *Loxia curvirostra*). All species that live in semi-natural habitats and which have decreased are Africa migrants. This includes many wetland species (Little Bittern *Ixobry-*

chus minutus, Common Tern *Sterna hirundo*, Black Tern *Chlidonias niger*, Sand Martin *Riparia riparia*, Bluethroat *Luscinia svevica*, Great Reed Warbler *Acrocephalus arundinaceus*, Sedge Warbler *A. schoenobaenus*) and to a lesser extent birds of open woodlands and heathlands (Wryneck *Jynx torquilla*, Nightjar *Caprimulgus europaeus*).

2. In mixed farmland habitats the species which have decreased outnumber by far species which have increased. The few species which are found in farmland and have increased are, as before, exclusively non-migratory birds. These are species which live in mixed farmland with small woodlots (Buzzard *Buteo buteo*, Rook *Corvus frugilegus*, Fieldfare *Turdus pilaris*). The many species that live in mixed farmland and which have suffered large decreases in numbers are not uniform with regard to their migratory habits. They include both Africa-migrants as well as non-migrants and birds which winter in Europe. They concern species of the damp hay fields (Garganey *Anas querquedula*, Corncrake *Crex crex*, Redshank *Tringa totanus*, Whinchat *Saxicola rubetra*, Corn Bunting *Miliaria calandra*) and the small-scale farmland with hedgerows, wooded banks and copses (Stonechat *Saxicola torquata*, Woodlark *Lullula arborea*, Ortolan Bunting *Emberiza hortulana*).

These patterns give rise to a number of interesting conclusions. All the species which have increased in numbers are non-migratory or have only limited dispersals. These are primarily species of semi-natural habitats, mostly water birds, which have benefited from waste water treatment in the last few decades, from eutrophication of water resources and from the digging of sand and gravel pits (e.g. Great Crested Grebe, Tufted Duck, Pochard). There are also woodland birds which have increased, particularly from the ageing coniferous plantations (Crossbill) and into this category come also the birds of prey (Buzzard, Sparrowhawk, Goshawk). These, like the Rook, have in addition benefited from better protection and from the gradual change towards less environmentally damaging agrochemicals over the study period.

Many of the species which have decreased are Africa-migrants. This includes a number of marsh birds (such as the Little Bittern and the Sedge Warbler) and birds of river banks and sand pits (such as the Sand Martin and the Common Tern) which have probably decreased for reasons which lie beyond the breeding area, viz. in the overwintering range in Africa (cf. Winstanley *et al.* 1974, Braaksma 1977, Marchant *et al.* 1990). Other species which have decreased breed in the extensively managed farmland, and this includes not only Africa-migrants (Garganey, Whinchat, Ortolan Bunting and Corncrake: Fig. 36) but also some which winter in Europe (Woodlark, Corn Bunting and Stonechat: Fig. 37). The conclusion is valid that these species, like the Barn Owl, have been affected by rationalisation and intensification in agriculture (cf. Vogelwerkgroep ZO-Achterhoek 1985, Hustings *et al.* 1990, Lensink & Vogelwerkgroep Arnhem 1993).

From the point of view of nature conservancy, the conclusion seems to be that species from semi-natural habitats (marshland, moorland, woodland) are relatively safe if they are non-migratory or winter in Europe. In contrast, Africa-migrants run much higher risks and intercontinental conservation measures need to be taken.

Many species breeding in mixed farmland are endangered regardless of their migratory habit. The reduced diversity of farmland and the intensification of agricultural practices seems primarily responsible nowadays, as has been demonstrated for the case of the Barn Owl. Species breeding in mixed farmland and migrating to Africa are particularly threatened. Dramatic examples in the study area are the Garganey *Anas querquedula* (numbers decreased from 90-125 pairs in around 1965 to 8-16 pairs in around 1980) and the Ortolan Bunting *Emberiza hortulana* (falling from 120-150 pairs to 12-15). There are better prospects for farmland birds with limited dispersals, such as the Barn Owl,

Fig. 37. Male Stonechat *Saxicola torquata* photographed on a fence post between a meadow and a strip of marginal land near Lievelde (Achterhoek) in July 1980. In the 1960's the Stonechat was a rather common breeding bird both in Liemers and Achterhoek. However, during the 1970's and 1980's this fine bird completely vanished out of farmland habitats in the eastern part of The Netherlands; here only a small population remained in semi-natural habitats (heaths and moorland), particularly in well-managed nature reserves. During the 1970's and early 1980's the species did not have to face severe winters in its southern European wintering quarters. However, since 1970 serious losses have been caused by the scaling up of Dutch agriculture, the intensification of grassland management, the destruction of hedgerows, burning of ditch slopes in the breeding season and the cultivation of pieces of marginal land in farmland areas (Hustings 1986). Photo Jos Korenromp.

the Little Owl *Athene noctua*, the Grey Partridge *Perdix perdix* and the Corn Bunting *Miliaria calandra*. Conservation measures regarding the local habitat (increasing the diversity in farmland environments) certainly offer an opportunity for maintaining and increasing their breeding populations within a relatively short period of time (10-15 years).

11.2 Conservation measures for the Barn Owl and other characteristic bird species in mixed farmland

At the end of this study, a number of recommendations can be made for the protection of the Barn Owl and its habitat. A number of other scarce species breeding in mixed farmland would also benefit from these. The maintenance of this diversity throughout the countryside is just as essential as site-protection of isolated areas of semi-natural habitats (Fuller 1982, O'Connor & Shrubb 1986, Batten *et al.* 1990). The following measures are desirable.

1. A campaign to increase public awareness of the importance of mixed farmland as regards wildlife, cultural history, scenery and recreation.
2. Habitat measures in farmland aimed at maintaining and increasing the area of standard

orchards, copses, marshes and pieces of marginal land. The management of such elements will be labour-intensive and will require volunteers.

3. The maintenance and planting of hedgerows and coppices (ideally with adjoining small (3-6 m wide) herbaceous strips) along water courses and parcel boundaries. These linear elements should average a minimum of 3-5 km per km^2 in areas with Barn Owl populations, and over 5 km per km^2 in core areas to create 'source' owl populations. An alternative could be the creation of scattered small woodlots fringed with broad (10-15 m) rough grassy strips which are extensively managed.
4. To better feeding conditions in winter, small mammals (voles and mice) can be attracted by placing heaps of unthreshed grain in marginal edges in Barn Owl haunts. Waste grain can also be put in uninhabited buildings where Barn Owls roost or hunt, in order to attract small mammals on which the owls can prey. In extreme winter conditions (prolonged deep snow cover), Barn Owls can be fed supplementary by interested farmers or volunteers.
5. Stimulation of ecological agriculture and promotion of traditional, extensive farming practices in the remaining areas with great landscape diversity (through notification of conservation areas and management agreements with individual farmers). Maintenance and setting up of extensive grassland areas (to be linked to areas where grassland waders breed and geese overwinter).
6. Discouragement of the extension of towns and villages and other large-scale developments (sand pits, recreation parks) in environmentally sensitive landscapes; roads should also not be built in these valuable areas.
7. Regular grass cutting to reduce vole populations along those stretches of metalled roads which are known to bring about high rates of traffic mortality among Barn Owls. This could also be achieved by planting trees and by creating high shrubs along these stretches.
8. Dirt roads should not be replaced any more by metalled roads in rural areas. These roads should as far as possible be kept for ramblers and cyclists, and through traffic should be limited.
9. Increase the accessibility of old buildings, farms and barns for the Barn Owl. Raise the number of nestboxes in mixed farmland areas where there is low traffic density.

The best strategy for nestbox programmes would be: (a) Firstly, safeguard all known traditional breeding sites in the region; (b) Secondly, build strongholds in the core areas by providing an ample supply of nestboxes in the prime habitats, in which an ultimate density of at least 10-20 boxes per 25 km^2 is desirable. (c) Finally, interconnect the strongholds by completing a network of nestboxes covering the whole region. However, areas with a typical sink structure should be avoided (uniform farmland, areas traversed by busy roads).

The combination of the measures abovementioned can be expected to lead both to higher reproduction and to lower mortality of the Barn Owl. What is more, such a broad land use strategy will favour not only the Barn Owl and other widely dispersed species in mixed farmland, but it will certainly also have a positive effect on other conservation interests including historic-cultural values and the scenery in the wider countryside (cf. Natuurmonumenten 1993).

Implementation can be realized by private initiatives of local farmers, landowners, gamekeepers and volunteer groups, and by governmental involvement. In the Netherlands, a detailed conservation plan for the Barn Owl has been made in which a number of the measures, such as the creation of rough grassland strips rich in small mammals, will be stimulated financially (Binsbergen 1994). In a number of selected areas (including Liemers and Achterhoek) experimental plots will be set up to test the impact of these measures on the local Barn Owl populations. Another instrument which is available is management agreements between the Dutch government and farmers (aiming at a total of

200.000 ha of rural areas) in which restrictions on farming for the benefit of landscape and wildlife are compensated for by grants (Harms *et al.* 1984, Kruk 1991). At European level, it is important to bring about changes in the Common Agricultural Policy which is still predominantly directed towards large-scale food production. In regions with traditional farming and a great landscape diversity, the rural planning policy should be aimed at a balance between agriculture and other land uses, such as forestry, tourism and nature conservation.

11.3 Further research required for more effective protection of the Barn Owl

To investigate and to increase the effectiveness of Barn Owl protection measures, the following research programm is desirable (see also van der Hut *et al.* 1992):

1. Annual monitoring of the Barn Owl population (number of breeding pairs and brood success) both regionally and nationally. Integral monitoring of sufficiently large census plots (at least 75-100 km^2) over a series of years (6-7 years at minimum) is required for an adequate survey of population trends.
2. National level analyses of ringing data to identify trends in dispersal and mortality and to determine to what extent these parameters are influenced by external factors (weather, food supply, pesticides use). This will allow better assessment of the impact of conservation measures. Setting up of long term ringing programmes of adult Barn Owls in a number of selected regions for further research into dispersal patterns and adult mortality.
3. National level research to compare the breeding success in nestboxes with that in other nest situations. Research into the relationship between nestbox density and the Barn Owl population in various landscape types.
4. Research into the ecology and population density of the vole and shrew species which form the staple food of the Barn Owl. Special attention needs be paid to their habitat selection in combination with research into the effect of different management regimes on their population level.
5. The starting up of habitat experiments for increase in food supply in a number of regions where there has been long running research already. In selected areas of these regions, herbaceous strips along hedgerows, lines of trees and wood edges will be created (particularly in areas where the habitat situation is critical, viz. where the average length of these woody landscape elements is around 2-3 km per km^2). Monitoring of the prey stock and the Barn Owl population and comparison of this with control areas where no measures are taken.
6. Continuing survey on the use of toxic pesticides and monitoring of their residue levels in Barn Owls.
7. Further research into the trend in Barn Owl road traffic deaths since 1960 and into the conditions under which owls are killed on roads.
8. Additional detailed research (using aerial photographs) to analyse changes in landscape elements and Barn Owl habitat features in the period 1955-1990 and its relation with trends in the owl's population performance.
9. Finally and generally: more scientific research into the specific ecosystems and the characteristic flora and fauna in farmland habitats, with special attention to conservation and management problems.

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13. SUMMARY

Over the last decades, the Barn Owl population has markedly decreased in range and breeding numbers in The Netherlands as in most western European countries. For effective conservation and population management, it is essential to know which factors are responsible for this decline. The present study deals with the Barn Owl population in the eastern part of The Netherlands. Population trends and demography (productivity, dispersal, mortality) were studied in two different districts (Liemers and Achterhoek) over two consecutive nine-year periods (1967-75 and 1976-84). Trends in population levels and demographic parameters are analysed in relation to external (environmental) factors in order to find explanatory factors behind the owl's population trends.

The outline of this article is as follows. The distribution, breeding densities and population trends of the Barn Owl in both study districts are reviewed in Chapter 4. Then the habitat selection and the feeding ecology are described (Chapter 5 and 6). The demography of the Barn Owl population is analysed in the Chapters 7-9, which deal respectively with the breeding performance, dispersal patterns and mortality (including causes of death) in Liemers and Achterhoek. In Chapter 10 these population parameters are brought together and discussed in relation to external factors, especially food supply, winter severity, deaths caused by human intervention (including road deaths and pesticides) and nest site availability. Furthermore, habitat changes in rural landscapes are taken into account as well as the effects of changes in farming practices on the Barn Owl population. In the final chapter, special attention is paid to bird species which are, like the Barn Owl, linked with farmland habitats. The over-all aim of this study is to contribute essential knowledge for conservation and management of important natural values in farmland, which forms the greater part of the countryside in western Europe.

Liemers consists predominantly of holocene polders and riverine areas; Achterhoek consists of pleistocene sandy landscape types (Figs. 1-2). Farming is the major form of land use in both districts. In Liemers the Barn Owl population has decreased markedly since 1960 (Table 1, Fig. 7). This applies particularly to the western and eastern parts of Liemers (Fig. 8), which have been subject to urbanisation and to large-scale land consolidation aimed at agricultural intensification. In contrast, in Achterhoek

the Barn Owl population increased in the period 1965-85. Landscape diversity is much better preserved in this district. More Barn Owls breed in small-scale mixed farmland than in large-scale uniform farmland (Table 2). Landscape diversity guarantees a well-buffered food supply, which is particularly important during the periodic troughs in the Common Vole population, the main prey of the Barn Owl (Tables 6-8, Figs. 13-17).

For both Liemers and Achterhoek, the main demographic parameters of the Barn Owl population are summarized in Table 21. In Liemers the breeding performance (mean number of fledglings per brood) was significantly higher than in Achterhoek. On the other hand, in Liemers the first-year mortality of Barn Owls was higher than in Achterhoek. In both districts no clear trends over time were noticed as regards breeding performance, dispersal patterns and mortality in adult Barn Owls. However, first-year mortality in Liemers in the second period (1976-84) proved to be higher than in the first period (1967-84) and in both periods in Achterhoek. In Liemers, productivity was too low to compensate for the high mortality in which road deaths took a heavy toll. This district proved to be a 'sink area', where the Barn Owl population persists only due to continuous net imports of owls. In contrast, Achterhoek is a 'source area' where productivity exceeds mortality; this district produces net exports of owls which can supply Barn Owl populations elsewhere. The relative importance of the various demographic parameters for the population balance is presented in a diagram (Fig. 25), which also gives a quantitative assessment of the sink (Liemers) and the source (Achterhoek). The existence of the sink and the source has been affirmed through analysing the dispersal patterns of Barn Owls in Liemers and Achterhoek, respectively (Figs. 20-21, Table 14).

The main factors which affect the Barn Owl population numbers negatively can be divided into five groups: 1. Deaths caused by human intervention (persecution, road mortality, pesticides); 2. Adverse weather conditions (severe frost, deep snow, persistent rain); 3. Reduced food supply (low vole densities, lessening diversity in prey species); 4. Urbanisation of rural areas and habitat changes on farmland (resulting in loss of prey-rich foraging habitats); 5. Reduced availability of suitable nesting sites. The impact of these environmental factors on the Barn Owl population in the study region proved to be time- and region-dependent.

It is assumed that toxic agrochemicals reduced the Barn Owl population in the 1960s ('pesticides era') to below the level that the landscape and food resources then could support. Deliberate persecution hardly occurs any more thanks to an intensive public awareness campaign. On the other hand, the proportion of Barn Owl road victims is very high (although less than the ringing recovery reports suggest: Table 19). An increase in road traffic deaths was found during the study period (Table 20). Very heavy losses due to road traffic were noticed in the urbanised parts of Liemers and nowadays these contribute substantially to the negative population balance in such sink areas. Only extremely harsh winters with prolonged snow cover (1962/63, 1978/79) have an effect on the number of breeding pairs through increased mortality (Fig. 26). Food shortage can cause serious mortality, particularly in winters with low vole densities (1968/1969, 1978/1979) and in uniform landscapes. Over the last decades, Common Vole populations have seriously decreased. This is especially so in Liemers, where nearly all 'vole plague areas' have been lost due to land consolidation and intensification of grassland management; so large areas of prey-rich foraging habitats for the Barn Owl have been disappeared (Fig. 27). In Liemers more drastic habitat changes have been occurred since 1960, including improvement and expansion of road networks, urbanisation, loss of many standard orchards and a great reduction in hedgerows (Fig. 28). In Achterhoek there have also been a number of unfavourable developments, but these were not so dramatic as those observed in Liemers (Fig. 29). There has been little increase in the size of villages, there are still many dirt roads and the total remaining length of hedgerows, wooded banks and tree lines is three times higher in Achterhoek than in Liemers (Table 22). This last is essential, because a significant relationship was found between the Barn Owl breeding density and the total length of hedgerows, tree lines and woodland edges (Fig. 32). The loss in nest site availability (which was great in the early years of the study period) has been offset by a major nestbox campaign, which proved to be very successful. About 1/3 of all the 200 nestboxes set up were used by breeding Barn Owls within 10 years after their placement (Fig. 12). The mean number of young raised in nestboxes was significantly higher than that of 'free' nest sites in buildings (Fig. 34). A steadily increasing percentage of Barn Owls is resorting to these nestboxes (Fig. 33). Today over 90%

of the Barn Owl pairs in Liemers and Achterhoek use these nestboxes for breeding. Recently (1990) very high Barn Owl densities (11-13 pairs per 100 km^2) have been noticed in small-scale landscapes with a large supply of nestboxes.

We can now evaluate the environmental factors which have determined the Barn Owl numbers during the last decades. In the beginning of the 1960s, a very strong decrease was found in the Barn Owl breeding population both in Liemers and in Achterhoek. This decline started with two successive poor vole years (1961 and 1962), the effect of which was strengthened by mass-mortality in the very extreme winter of 1962/63. Only a partial recovery was made by the end of the 1960s. Probably the key limiting factor was the effect of toxic pesticides which prevented the Barn Owl reaching the numbers which the contemporary landscape and the food-resource level could support. In the beginning of the 1970s the reduced impact of pesticides (partial ban) and the improved nest site availability (nestboxes) led to population growth in the better-preserved landscapes of Achterhoek. In Liemers, however, these improving external factors could not stop the population decline. The proximate factors causing this decline are the loss of foraging habitat (disappearance of vole-rich areas, large-scale reduction of hedgerows) and the sharply increased traffic density (causing high road mortality rates). Only the vicinity of source areas (such as Achterhoek) enabled the Liemers population to persist. In the 1980s, the decline continued in the most devastated landscapes of Liemers, accounted for by progressive agricultural intensification and also by urbanisation and the expansion of the main road network. In contrast, the Barn Owl population stabilized in the remaining small-scale landscapes of Liemers and increased in the mixed farmland of Achterhoek. Here the population grew in parallel with the increased supply of nestboxes, which supports evidence that nest site availability is the environmental limiting factor in well-preserved landscapes with a rich and buffered food supply. The relationships between the most important external (environmental) factors and the main internal (demographic) parameters, as found in this study for the 1980s, are presented in a diagram (Fig. 35).

A number of recommendations can be made for the protection of the Barn Owl and its habitat. Firstly, the conservation and provision of suitable nest sites is very important. On a regional scale, the following strategy is advisable. (1) Safeguard all known traditional breeding sites in the region, provide nestboxes if necessary. (2) Try to build Barn Owl strongholds (sources) by providing an ample supply of nestboxes (10-20 per 25 km^2) in the remaining regional core areas; the best opportunities are in small-scale mixed farmland (with a minimum of 3-5 km length of hedgerows, lines of trees and woodland edges per km^2) which are not intersected by busy roads. (3) Interconnect the strongholds by completing a network of nestboxes covering the whole region. However, areas with a typical sink structure should be avoided (uniform farmland, areas traversed by busy roads).

Long-term conservation of the Barn Owl is closely connected with agricultural developments and farming practices. Habitat measures in farmland are essential to improve the food supply (voles, mice, shrews). This means maintenance, expansion and management of landscape elements with low grassy and herbaceous vegetations (standard orchards, pieces of marginal land, rough edges along existing and newly planted hedgerows and woodlots). These habitat measures should be linked to a land use strategy which favours not only the Barn Owl and other scarce species associated with farmland, but also broader conservation interests including historic-cultural values and the scenery in the wider countryside.

Implementation can be realized by private initiatives (individual farmers, landowners, gamekeepers and volunteer groups) and by government involvement. The creation and management of such habitat components will be labour-intensive and will require volunteers as well as financial support. A policy instrument which is available is management agreements between the Dutch government and farmers (aiming at a total of 200.000 ha of rural land) in which restrictions on farming for the benefit of landscape and wildlife are compensated for by grants. Moreover the creation and management of low herbaceous margins (3-6 meter wide, left unmanured and unsprayed) along grasslands, fields, ditches, hedgerows and woodland edges, will be stimulated financially in a number of Barn Owl core areas in The Netherlands. At European level, it is important to bring about changes in the Common Agricultural Policy of the European Union, which is still predominantly directed towards large-scale food production. In regions with traditional farming and great landscape diversity, rural planning policy should be aimed at a balance between agriculture and other land uses, such as forestry, tourism and nature conservation.

Such a strategy will be profitable for other endangered bird species. For the purposes of this study, population trends of 50 scarce and characteristic breeding birds in Liemers and Achterhoek were monitored over the period 1965-80 (Appendix 6). Those species which show the most obvious changes in numbers were selected for further analysis (Table 23). In 22 species (44%) no apparent trends in breeding numbers were found. A total of 11 (22%) showed marked increases as against 17 species (34%) showing marked decreases. Birds from semi-natural habitats (open water, marshland, woodland) are relatively safe if they are non-migratory or winter in Europe. In contrast, many species breeding in mixed farmland are threatened, in which Africa-migrants run double risks. Dramatic examples in the study region are Garganey, Corncrake and Ortolan Bunting. Regarding this group of birds, habitat measures in the breeding range will be insufficient and intercontinental conservation measures need to be taken. There are better prospects for farmland birds with limited dispersals, such as the Barn Owl, the Grey Partridge, the Little Owl, and the Corn Bunting. Conservation measures regarding the local habitat (increasing the diversity in farmland environments including the supply of appropiate nest sites) certainly offer an opportunity for maintaining and increasing their breeding populations within a relatively short period of time (10-15 years).

To evaluate and to increase the effectiveness of protection measures, suggestions for a Barn Owl research programme are given (see section 11.3). Generally, more scientific research needs be done into characteristic ecosystems with associated flora and fauna in agricultural environments, with special attention to conservation and management problems.

14. REFERENCES

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15. SAMENVATTING

In de eerste helft van deze eeuw was de Kerkuil een algemeen voorkomende broedvogel op het platteland van Nederland en de meeste ons omringende landen. De afgelopen decennia is de soort echter in geheel West-Europa en in grote delen van Midden-Europa sterk achteruitgegaan. Het betreft hier kennelijk een lange termijn trend en geen schommelingen veroorzaakt door cyclische fluctuaties in de stand van de voornaamste prooisoort, de Veldmuis. De **sterke teruggang van de kerkuilstand** geldt ook voor Nederland. Er broedden tot 1960 in goede veldmuisjaren nog ruim 3000 paar Kerkuilen, verspreid over het gehele land. Tegen het eind van de zestiger jaren werd het aantal broedparen in Nederland op 500-800 paar geschat en in de zeventiger en eerste helft van de tachtiger jaren op slechts 300-500 paar (Braaksma & de Bruijn 1976, de Jong 1983). Intussen was de soort als broedvogel uit grote delen van Nederland verdwenen. Pas sinds 1988 tekent zich weer enig herstel af.

Inmiddels wordt de Kerkuil internationaal als bedreigde soort beschouwd en is de soort in vele landen op de 'rode lijst' van bedreigde en te beschermen soorten geplaatst (zie Osieck 1986). Onderzoekers noemen als **mogelijke oorzaken van de achteruitgang**: klimaatsfactoren (strenge winters), vervolging door mensen, vergiftiging door chemische middelen in gebruik in landbouw en industrie, verloren gaan van nestgelegenheid, bebouwing van het landelijk gebied en toename van het aantal verkeersslachtoffers. Vooral de laatste jaren wordt steeds meer als mogelijke oorzaak ook genoemd: veranderingen in het agrarische cultuurlandschap en in het grondgebruik, als gevolg van mechanisatie, intensivering en specialisatie in de landbouw.

Voor een effectieve bescherming is inzicht vereist, wat de hoofdoorzaken van de achteruitgang zijn en welke factoren slechts een bijrol spelen. Door goed inzicht in de **sleutelfactoren** die de aantallen beperken, kunnen de juiste beheersmaatregelen genomen worden. Voor een dergelijke analyse is het eerst van belang om na te gaan welke trends opgetreden zijn in de belangrijkste interne (demografische) parameters van de kerkuil-populatie, te weten het broedsucces, de dispersie en de sterfte. Daarna kan nagegaan worden welke externe factoren hierop aangrijpen. Vervolgens kunnen effectieve beschermingsmaatregelen opgesteld worden (Newton in Perrins *et al.* 1991).

Deze publikatie bespreekt de resultaten van een **langjarig populatie-onderzoek** uitgevoerd in een ca. 900 km^2 groot onderzoeksgebied in Oost-Nederland. De vraagstelling was gericht op: (a) Vaststelling van de aantalsontwikkeling van de Kerkuil over een lange reeks van jaren. (b) Regionale studie van belangrijke aspecten van de populatie-oecologie, met name biotoopkeus en voedselbiologie. (c) Analyse van de belangrijkste demografische aspecten (broedsucces, dispersie, sterfte). (d) Onderzoek naar verklarende externe factoren achter de geconstateerde aantalsontwikkeling, met name de invloed van strenge winters, veranderingen in het voedselaanbod, beschikbaarheid van nestgelegenheid, uitbreiding van het wegennet en veranderingen in het cultuurlandschap en het agrarisch grondgebruik. Teneinde trends in ruimte en tijd te ontdekken, zijn de ontwikkelingen in de kerkuilstand bestudeerd in twee verschillende streken (Liemers en Achterhoek) en in twee opeenvolgende negen-jarige onderzoeksperioden (1967-75 en 1976-84). De belangrijkste drijfveer achter dit onderzoek is de wens beter inzicht te krijgen in de oorzaken van de achteruitgang, teneinde de Kerkuil effectiever te kunnen beschermen.

Het **onderzoeksgebied** en de belangrijkste landschapstypen zijn weergegeven in Figuur 1 en 2. De Liemers wordt begrensd door de rivieren Rijn, IJssel en Oude IJssel. Het westelijk en oostelijk deel betreft uitgestrekt polder- en rivieren-landschappen. Centraal ligt een beboste stuwwal (Montferland), die geleidelijk overgaat in het kleinschalige landschap van de noordelijke Liemers (gevarieerd dekzand- en rivierenlandschap met veel heggen en bosjes). De Achterhoek is relatief dun bevolkt en landschappelijk zeer gevarieerd. Het westelijk deel is een kleinschalig dekzand-landschap met verspreide boerderijen, bouwlanden en graslanden afgewisseld met talloze houtwallen, boomrijen en bosjes. Het oostelijk deel betreft het hogergelegen plateau-landschap rond Winterswijk. Rond beekdalen liggen hier oude hoeven gegroepeerd met bouwlandcomplexen, graslanden en bossen. Flinke delen van de Achterhoek hebben een grootschaliger landschapsopbouw; dit betreft jonge heide-ontginningslandschappen met graslandcomplexen en naaldbos-plantages. Twee luchtfoto's geven een goede indruk van karakteristieke landschappen in Liemers en Achterhoek (Fig. 13-14).

Onderzoekmethodieken en materiaal. De kerkuilstand is jaarlijks nauwkeurig onderzocht in een vijftal proefgebieden ter grootte van 75-125 km^2, verspreid gelegen over het onderzoeksgebied (Fig. 3). Ieder jaar zijn in het voorjaar en de zomer alle potentiële broed- en verblijfplaatsen (kerken, boerderijen, oude gebouwen) door vrijwillige medewerkers onderzocht op het voorkomen van Kerkuilen. De aantallen broedparen in dit onderzoek zijn gebaseerd op werkelijk geconstateerde broedgevallen (legsel of jongen vastgesteld). In de periode 1967-84, zijn in totaal 346 broedparen geteld en nog eens 122 niet-broedende exemplaren. Hiernaast controleerden we jaarlijks systematisch het broedsucces, met name het aantal uitgevlogen jongen per broedsel. Vanaf het begin van het onderzoek zijn zoveel mogelijk jongen geringd (Fig. 4), om meer te weten te komen over het zwerfgedrag (dispersie) en over de sterfte (mortaliteit). In totaal werden 663 jonge Kerkuilen geringd, hetgeen uiteindelijk 133 terugmeldingen heeft opgeleverd die bruikbaar waren voor nadere analyse. Studie van de doodsoorzaken vond plaats (a) door analyse van ringterugmeldingen via het 'Vogeltrekstation Arnhem' te Heteren, en (b) door middel van gegevens bijeengebracht door leden van de 'Kerkuilwerkgroep Achterhoek-Liemers'. In totaal kon zo van 90 Kerkuilen de doodsoorzaak vastgesteld worden. Ter bestudering van de voedsel-oecologie zijn in de periode 1967-84 een groot aantal braakballen verzameld, verspreid in de tijd (verschillende seizoenen en jaren) en in de ruimte (verschillende landschapstypen). Dit leverde in totaal ca. 10.000 kerkuilprooien op (zie ook de Bruijn 1979). In 10 proefvlakken van 25 km^2 (verspreid over de verschillende landschappen over het gebied) zijn landschappelijke veranderingen in de periode 1955-1975 geanalyseerd, die van invloed kunnen zijn op de kwaliteit van het kerkuilbiotoop. Hiertoe zijn, met behulp van een digitale computer, diverse landschapsvariabelen van topografische kaarten opgemeten (bebouwd oppervlakte, dichtheid van het wegennet, lengte aan heggen en houtwallen, lengte aan bosranden etc.). Tenslotte verzamelden schrijver en vrijwillige medewerkers informatie over het broedvoorkomen van een vijftigtal schaarse en karakteristieke vogelsoorten in de streek, om trends in hun aantalsontwikkeling in de periode 1965-1980 te kunnen vaststellen. Dit om aanvullende oecologische informatie te verkrijgen ter verklaring van aantalsveranderingen, zoals die ook bij de Kerkuil optreden. Bovendien is het zo mogelijk om beschermingsmaatregelen voor de Kerkuil in een breder verband te plaatsen, waardoor meer kwetsbare soorten kunnen profiteren.

Aan de hand van de verzamelde inventarisatie-gegevens (zie Appendix 1) kan allereerst een beeld geschetst worden van de **globale aantalsontwikkelingen** in de vijf proefgebieden in de periode 1956-82. Zoals uit Tabel 1 blijkt, is de kerkuilstand in de Liemers in deze periode sterk teruggelopen; de teruggang is met name in de westelijke en oostelijke Liemers groot (afname met 75-85%). De populatie-ontwikkeling in de Achterhoek is daarentegen positief: na een teruggang in het begin van de zestiger jaren (o.a. veroorzaakt door de zeer strenge winter 1962/63) heeft de soort zich goed hersteld en is er zelfs sprake van een duidelijke toename, met name in de westelijke Achterhoek. Een tweetal kaartjes illustreren deze ontwikkeling (Fig. 5 en 6). Het voorkomen en de aantalsontwikkeling blijkt gerelateerd te kunnen worden aan bepaalde landschapstypen (Tabel 2). In min of meer natuurlijke landschappen (moerassen, venen en bosgebieden) broeden geen Kerkuilen. In het agrarisch cultuurlandschap komt de Kerkuil significant meer voor in gevarieerde landschapstypen (rivieren-, dekzand- en plateau-landschap) dan in de eenvormige landschappen (polders en heide-ontginningen). Zeer hoge dichtheden kwamen plaatselijk voor in het rivieren-landschap met meer dan 10 paar per 100 km^2 tot omstreeks 1960. In het dekzand-landschap en in het plateaulandschap broedden 5-10 paar per 100 km^2 in goede veldmuisjaren. Bij vergelijking van de periode 1956-62 met 1976-82, blijkt de Kerkuil significant afgenomen te zijn in het rivierenlandschap van de Liemers, waar in de zestiger en zeventiger jaren grootschalige ruilverkavelingen en dorpsuitbreidingen hebben plaatsgevonden. In de veel gaver bewaarde dekzand-landschappen en in het plateau-landschap van de Achterhoek is de kerkuilstand daarentegen op peil gebleven en lokaal zelfs toegenomen. In het veldmuis-topjaar 1990 werden in dit soort kleinschalige landschappen in het onderzoeksgebied in zes blokken van 100 km^2 dichtheden van 11–13 broedparen per blok vastgesteld!

De **precieze aantalsontwikkelingen** van de kerkuilstand zijn te analyseren door het proefvlak-onderzoek in de periode 1967-84, waarbij jaarlijks het aantal Kerkuilen (zowel broedparen als niet-broedende vogels) nauwkeurig is bijgehouden (Appendix 2). Statistische analyse wijst uit, dat er in deze periode sprake is van een teruggang in het totale aantal Kerkuilen in de Liemers en van een vooruitgang in de Achterhoek. Figuur 7 laat het jaarlijkse aantal broedparen zien in de proefvlakken in de Liemers (totaal 250 km^2) en in de proefvlakken in de Achterhoek (eveneens 250 km^2). In de Liemers varieerde het jaarlijkse aantal broedparen van 0–13 (gemiddeld 2.4) en in de Achterhoek van 3–22 (gemiddeld 5.3). De minimum waarde (0) werd gevonden in de Liemers in de veldmuisdaljaren 1969 en 1979, de hoogste dichtheid bereikte de Kerkuil in de westelijke Achterhoek in het veldmuis-topjaar 1984 (10.4 paar per 100 km^2). Dit laatste is een zeer hoge dichtheid, zoals ook blijkt uit vergelijking met buitenlandse onderzoeken in grote proefgebieden (Tabel 3). Een statistische analyse laat zien, dat in de periode 1967-84 de broedvogelstand in de beide proefvlakken in de Achterhoek vooruit is gegaan. In twee proefvlakken in de Liemers is de Kerkuil achteruitgegaan (westelijke en oostelijke Liemers); in de noordelijke Liemers kon geen trend in de stand worden aangetoond (Fig. 8).

In West- en Midden-Europa is de Kerkuil een uitgesproken vogel van het agrarische landschap. Het voorkeursbiotoop bestaat uit min of meer open cultuurlandschappen, met verspreide bosjes, heggen en houtwallen. De soort broedt gewoonlijk op zolders van oude gebouwen (boerderijen, kerken, landhuizen etc.). In Engeland broedt een groot deel van de populatie in holle bomen. Boombroedsels komen in Nederland tegenwoordig nauwelijks meer voor. In het onderzoeksgebied liggen de **nestplaatsen** van de Kerkuil voornamelijk in boerderijen, maar ook in kerken en kastelen (zie Tabel 4). Boerderijen met veel bijgebouwen en omringd door oud hout genieten de voorkeur (Fig. 9). Oorspronkelijk broedden de uilen in donkere hoeken op zolders, tussen balen hooi, onder het dakbeschot, in schoorstenen en -karakteristiek voor hier- in oude duivenhokken in de boerderijen (Fig. 10). Door het verdwijnen van oude gebouwen en restauraties van kerken gingen steeds meer broedplaatsen verloren of werden deze ontoegankelijk gemaakt voor uilen. Om deze negatieve ontwikkeling tegen te gaan, hebben wij vanaf het midden der zestiger jaren systematisch invliegopeningen van geschikte broedplaatsen weer open gemaakt. Tevens is een uitgebreide campagne gestart met het doel een groot aantal (speciaal voor de Kerkuil ontworpen) nestkasten te plaatsen in Liemers en Achterhoek (Fig. 11). In de loop van de periode 1967-84 zijn meer dan 200 nestkasten opgehangen in gebouwen, verspreid over het gehele gebied. Deze campagne bleek een groot succes: ongeveer 1/3 van alle kasten is binnen tien jaar na plaatsing door Kerkuilen als broedplaats gebruikt (zie Fig. 12). Het percentage bezette kasten was in Liemers en Achterhoek ongeveer even groot, maar de kasten in de Achterhoek werden gemiddeld langduriger bezet dan de kasten in de Liemers (Tabel 5).

Tabel 6 geeft een indruk van een aantal traditionele Kerkuil 'home ranges', d.w.z. de omgeving van de broedplaats met de jachtgebieden. **Voorkeursbiotopen** in het onderzoeksgebied zijn: (a) uitgestrekte graslandgebieden met veel heggen (rivieren-landschap, lokaal in polders en heide-ontginningen); (b) bouwland- en graslandcomplexen met oude boomgaarden en heggen (rivieren-landschap); (c) kleinschalige landschappen met een afwisseling van bouwlanden en graslanden met veel heggen, houtwallen en bosjes (dekzand- en plateau-landschap). Uiteindelijk blijkt de volgende combinatie van factoren het 'ideale' kerkuilbiotoop te karakteriseren: (1) De aanwezigheid van één of meer geschikte broedplaatsen: oude gebouwen, boerderijen met veel bijgebouwen (bij voorkeur met oud geboomte in de directe omgeving). (2) Min of meer open cultuurlandschap met veel verspreide heggen, houtwallen en bosjes. (3) De aanwezigheid van reliëf, hetgeen gepaard gaat verschillen in bodemgesteldheid en waterhuishouding. De hiermee samenhangende variatie in vegetatie en grondgebruik leidt tot een gevarieerde prooifauna. (4) De aanwezigheid van overhoekjes en cultuurland met een extensief grondgebruik, geschikt voor diverse 'muizen': ruige weitjes, hooiland, slootkanten en dijkhellingen, extensief beheerde brede wegbermen, braakliggend land, jonge bosaanplant, ruige stroken langs heggen en bosranden etc. De combinatie van deze factoren biedt aan Kerkuilen voldoende broed- en roest-gelegenheid, én een gegarandeerde rijke prooifauna in de verschillende seizoenen en jaren.

Kerkuilen jagen op twee manieren: vanaf zitplaatsen (zo ook binnen gebouwen) en in langzame jachtvluchten op 2-3 meter boven de grond. Hiermee zoeken ze naar kleine zoogdieren (woelmuizen, spitsmuizen en ware muizen), die met een snelle prooiduik geslagen worden. De **prooifauna** in de verschillende landschappen in het studiegebied is samengevat in een overzichts-schema (Tabel 7). Het meest talrijk zijn de Veldmuis *Microtus arvalis* en 'de' Bosspitsmuis *Sorex araneus/coronatus*; dit zijn ook de voornaamste prooisoorten van de Kerkuil. Veldmuizen komen voor in extensief beheerd grasland; onder de huidige agrarische cultuurdruk leven de meeste Veldmuizen langs slootkanten, in wegbermen en ook wel in en langs houtwallen. Veldmuis-populaties vertonen cyclische aantalsschommelingen, waarbij om de drie of vier jaar pieken voorkomen; deze worden steevast gevolgd door massale sterfte. Tot in de zestiger jaren kwamen in sommige delen van het Liemerse polder- en rivieren-land periodiek enorme veldmuisplagen voor. Dezelfde cyclische aantalsschommelingen treden ook buiten deze 'plaaggebieden' op, zij het op veel geringere schaal: hierdoor kan men spreken van goede veldmuisjaren en slechte veldmuisjaren. Een overzicht van de Veldmuis-cycli in de periode 1965-85 kan men vinden in Tabel 8. Bosspitsmuizen zijn eveneens zeer talrijk in het studiegebied en vormen na de Veldmuis de belangrijkste prooi voor de Kerkuil. Tegenwoordig onderscheidt men twee nauw verwante soorten: de Gewone Bosspitsmuis *Sorex araneus* en de Tweekleurige Bosspitsmuis *Sorex coronatus*. Beide soorten komen zowel in Achterhoek als Liemers voor, maar het is nog onbekend in welke verhouding; daarom zijn ze in deze studie, net als eerder (de Bruijn 1979), samengevat. Bosspitsmuizen komen algemeen voor in uiteenlopende biotopen: in ruige grazige begroeiingen, in en langs heggen en bosranden, in boomgaarden en in tuinen. Van de overige kleine zoogdieren kunnen nog een drietal soorten bijdragen aan het stapelvoedsel: Huisspitsmuis *Crocidura russula* (lokaal algemeen op erven, ook in heggen en houtwallen), Bosmuis *Apodemus sylvaticus* (algemeen in ruig grasland in houtwallen en bossen) en Huismuis *Mus musculus* (algemeen in en rond gebouwen en op erven). De overige potentiële prooisoorten (spitsmuizen, woelmuizen, ware muizen en ratten) zijn slechts plaatselijk en lokaal als kerkuilprooi van belang. De rijkste prooifauna (11-12 soorten) komt voor in de gevarieerde cultuurlandschappen (rivieren-, dekzand- en plateaulandschap); hierbinnen zijn 6-8 soorten wijdverspreid en algemeen. Daarentegen komen in de eenvormige polder- en heide-ontginningen slechts 7-10 prooisoorten voor, waarvan slechts 3-4 algemeen zijn. Een rijk én continu prooiaanbod is voor de Kerkuil dan ook het best gegarandeerd in gevarieerde cultuurlandschappen.

De **prooikeuze** van de Kerkuil in het studiegebied is uitgebreid bestudeerd (basisgegevens in Appendix 3). Het dieet in Liemers en Achterhoek is in een overzichtelijk schema gepresenteerd (Fig. 17), met een uitsplitsing naar seizoen (zomer-halfjaar tegenover winter-halfjaar) en naar het aanbod van de hoofd-prooisoort (veldmuisrijke jaren tegenover veldmuisarme jaren). In de Liemers speelt de Veldmuis een dominerende rol in het voedsel, in goede veldmuisjaren zelfs een alles-overheersende rol. In slechte veldmuisjaren is het van levensbelang voor de Kerkuil, dat er compensatie in de vorm van andere prooisoorten gevonden kan worden. Dit lukt wel in gevarieerde landschappen, waar Bosspitsmuizen, Huisspitsmuizen, Bosmuizen en Huismuizen in voldoende aantal leven (rivieren-, dekzand- en plateau-landschap). Daarentegen zijn bij veldmuisschaarste de overlevingskansen minimiem in eenvormige landschappen (polders en heide-ontginningen) en hetzelfde geldt voor het rivieren-landschap na grootschalige ruilverkavelingen. In de kleinschalige landschappen van de Achterhoek is er in het algemeen sprake van een rijkgeschakeerd prooiaanbod. De Veldmuis speelt een minder dominante rol, al werken ook hier de cyclische aantalsschommelingen merkbaar door in het dieet. Naast Veldmuis en Bosspitsmuis dragen ook Huisspitsmuis, Bosmuis en in Huismuis bij aan het stapelvoedsel. De grote landschappelijke variatie en de hiermee verbonden rijkgeschakeerde prooifauna in de Achterhoek staan garant voor een goed gebufferd prooiaanbod. Hierdoor hebben Kerkuilen bij veldmuisschaarste betere overlevingskansen en kunnen ze zelfs in veldmuisarme jaren gewoonlijk nog jongen groot brengen. Daarom leven de meeste Kerkuilen in gevarieerde cultuurlandschappen.

Kerkuil-populaties zijn niet alleen opgebouwd uit broedvogels, maar ook uit volgroeide vogels die niet tot broeden komen. Het aandeel broedvogels (**broedende segment**) was in de Achterhoek groter dan in Liemers en bedroeg gemiddeld 87% tegenover 81%. De meeste niet-broedende uilen betroffen solitaire vogels, maar ook niet-broedende paartjes en zelfs trio's werden vastgesteld (Tabel 9). In veldmuisrijke jaren nemen relatief meer uilen aan het broedproces deel dan in veldmuisarme jaren (Tabel 10). In de goede veldmuisjaren zijn er meer traditionele Kerkuil-territoria bezet door broedparen dan in veldmuisarme jaren (Tabel 11). Bij vergelijking van de twee opeenvolgende onderzoeksperioden (1967-75 en 1976-84) bleek in de Liemers een teruggang opgetreden te zijn in de bezettingsgraad van Kerkuil-territoria in veldmuisrijke jaren: in de eerste periode broedden gemiddeld in 51% van de traditionele territoria Kerkuilen, in de tweede periode nog slechts in gemiddeld 35%. Veel traditionele territoria in voormalige veldmuis-plaaggebieden in de Liemers worden tegenwoordig niet meer bezet, omdat door sterke intensivering van het agrarisch grondgebruik (verschuiving van hooiland naar weiland, sterk gestegen veebezetting) veldmuisplagen nauwelijks meer optreden. Dit was in de zestiger jaren nog in diverse gebieden het geval, hetgeen ook tot uiting kwam in zeer grote broedsels (Fig. 18). Er blijkt in het algemeen een sterk verband te bestaan tussen de veldmuizenstand en het **broedsucces**. Zowel in de Liemers als in de Achterhoek vliegen meer jongen per broedsel uit in goede dan in slechte veldmuisjaren. Berekend over het gehele gebied en de volledige onderzoeksperiode, bedroeg het gemiddelde aantal uitgevlogen jongen 3.4 in veldmuisrijke jaren en 2.9 jongen in veldmuisarme jaren (inclusief de mislukte broedsels). Broedsels met zes of meer uitgevlogen jongen zijn alleen in veldmuis-topjaren vastgesteld (Fig. 19). Tijdens het gehele onderzoek zijn in totaal vijf maal tweede broedsels vastgesteld (binnen een totale broedpopulatie van 19-29 broedparen): telkens één in de veldmuis-topjaren 1967, 1971, 1974, 1977 en 1984 (op het laatste na alle in de Liemers). Over de gehele onderzoeksperiode berekend, vlogen in de Liemers gemiddeld meer jongen per broedsel uit dan in de Achterhoek (resp. 3.7 en 3.1). In Tabel 12 is het broedsucces vergeleken voor de twee opeenvolgende perioden (1967-75 en 1976-84). In de Liemers blijkt het gemiddelde aantal jongen in veldmuisrijke jaren teruggelopen te zijn (van 4.3 naar 3.6), terwijl dit in veldmuisarme jaren op peil bleef (respectievelijk 2.8 en 3.0). Dit kan als volgt verklaard worden. In de eerste periode broedde in goede veldmuisjaren een groot deel van de populatie in de 'plaaggebieden', die vooral in de westelijke en oostelijke Liemers gelegen waren. Hier konden de uilen toen periodiek profiteren van een overdadig prooiaanbod en grote broedsels produceren. Deze situatie behoort thans tot het verleden (zie hierboven). De meeste Kerkuilen leven tegenwoordig in de kleinschalige landschappen van de noordelijke Liemers, waar ze goed blijken stand te houden en ook in veldmuisarme jaren meestal nog met succes broeden. In de Achterhoek zijn geen veranderingen in het broedsucces in de tijd opgetreden, noch in de veldmuisarme noch in de veldmuisrijke jaren. Beschouwen we het algehele broedsucces in beide opeenvolgende perioden, dan vlogen in de Liemers gemiddeld 4.0 en 3.5 jongen uit en in de

Achterhoek respectievelijk 3.3 en 3.0 jongen. Voor beide gebieden geldt dat het gevonden verschil statistisch niet significant is: al met al is er in het onderzoeksgebied dus geen duidelijke trend in het broedsucces in de tijd opgetreden.

Als resultaat van jarenlange systematisch ringonderzoek, kunnen we beschikken over 133 terugmeldingen (Liemers: 34, Achterhoek: 99). Dit maakt een analyse van het **zwerfgedrag (dispersie)** mogelijk. Figuur 20 laat zien, waar de uilen terecht zijn gekomen die als nestjong geringd zijn in Liemers en Achterhoek. Hierbij is onderscheid gemaakt tussen vogels die binnen één jaar na ringen zijn teruggemeld en de terugmeldingen van vogels op latere leeftijd. Voor beide categorieën geldt, dat 60-65% van de vogels binnen 50 km van de geboorteplaats zijn teruggemeld en nog eens 20-25% binnen 50-100 km. De uilen verspreiden zich in alle richtingen; volwassen uilen zijn relatief veel uit noordelijke richting teruggemeld. Er zijn enkele terugmeldingen boven de 250 km, de meeste van eerstejaars vogels die ver in zuidelijke richtingen zijn weggetrokken. De opbouw van Tabel 13 maakt analyse van trends in dispersie-patronen mogelijk. Uit een statistische analyse blijkt dan, dat er geen trend in afgelegde afstanden is: noch ruimtelijk (Liemerse uilen tegenover Achterhoekse uilen), noch in de loop der tijd (periode 1967-75 tegenover periode 1976-84).

Er treedt niet alleen emigratie uit het onderzoeksgebied op, er vestigen zich ook uilen die van elders afkomstig zijn. Figuur 21 laat de herkomst van immigranten zien. Van ongeveer 55% lag de geboorteplaats minder dan 50 km weg en ca. 25% was geboren op 50-100 km afstand. Bij verdere analyse kwam er een frappant verschil aan het licht in de herkomst van geringde vogels, die in Liemers respectievelijk Achterhoek doodgevonden zijn (Tabel 14). In de Achterhoek bleek 31% van de gevonden vogels tot de categorie 'immigranten' te behoren (vanuit de Liemers of van elders afkomstig); 69% was lokaal (in de Achterhoek zelf) geboren. Daarentegen was in de Liemers slechts 36% van de gevonden uilen lokaal geboren; de categorie 'immigranten' (vanuit de Achterhoek of van elders afkomstig) bedroeg in de Liemers liefst 64%! Dit verschil in verdeling naar herkomst is statistisch significant. De interessante conclusie luidt, dat de populatie-structuur in de Liemers kennelijk gedomineerd wordt door immigranten (vanuit de Achterhoek of van elders afkomstig). Deze streek functioneert als een '**sink**' (netto import gebied): een soort put of trog, waar lege territoria steeds voornamelijk door immigranten opgevuld worden. Daarentegen is de Achterhoek een '**source**' (netto exportgebied): een soort brongebied, waar een surplus aan uilen geproduceerd wordt die elders populaties kunnen aanvullen (vgl. Pulliam 1988).

De ringgegevens geven ook uitsluitsel over de **sterfte (mortaliteit)** van de uilen. Hierbij is onderscheid gemaakt tussen terugmeldingen binnen één jaar na ringen (als nestjong) en terugmeldingen van oudere vogels. Figuur 22 toont de verdeling van sterfte over de verschillende maanden van het jaar. De sterfte onder de eerstejaars vogels is relatief hoog gedurende de gehele herfst en winter (periode september t/m februari). Dit valt samen met het uitzwerven van de jongen in de herfst (met relatief veel verkeersslachtoffers), voorts is voedselgebrek in de winter een belangrijke factor. De sterfte van de volwassen uilen is geconcentreerd in de maanden december t/m februari; hier ontbreekt dus een herfstpiek.

Met behulp van jaarklassen-tabellen kan de leeftijdsgebonden sterfte berekend worden (Tabel 15). De sterfte onder eerstejaars vogels is significant hoger dan onder volwassen vogels (68% tegenover 49%). In Tabel 16 is de leeftijdsgebonden sterfte en levensverwachting vergeleken met enkele andere (buitenlandse) kerkuilpopulaties. Tabel 17 en 18 tonen de sterftecijfers van eerstejaars en volwassen Kerkuilen in Liemers en Achterhoek. Afhankelijk van de berekeningswijze, bedraagt de gemiddelde eerstejaars sterfte in de Liemers 75-79% en in de Achterhoek 62-65%; de gemiddelde jaarlijkse sterfte onder volwassen uilen bedraagt in de Liemers 47-50% en in de Achterhoek 41-49%. Voor zover het beschikbare materiaal het toelaat, is ook gekeken naar trends in de tijd. Er zijn geen aanwijzingen voor veranderingen in de sterfte onder volwassen vogels. Bij de eerstejaars vogels blijkt er in de Liemers in de tweede periode (1976-84) sprake te zijn van een extreem hoge sterfte (89%); de uilen werden gemiddeld slechts 183 dagen oud. Getoetst op exacte leeftijd bleek deze sterfte significant hoger te zijn dan in de eerste periode (1967-84) in de Liemers en in beide perioden in de Achterhoek (183 dagen tegenover een gemiddelde van 435 dagen). Deze toename in eerstejaars sterfte in de Liemers is de belangrijkste gevonden trend in de tijd in de demografie (voortplanting, dispersie, sterfte) van beide bestudeerde kerkuil-populaties.

Informatie over de **doodsoorzaken** kregen we via twee bronnen: via het 'Vogeltrekstation Arnhem' te Heteren (in totaal 48 ringterugmeldingen met bekende doodsoorzaak) en via gericht onderzoek uitgevoerd door leden van de 'Kerkuilwerkgroep Achterhoek-Liemers' (in totaal 42 gecontroleerde meldingen, berustend op eigen vondsten en betrouwbare mededelingen van boeren en buitenlui). Tabel 19 geeft een overzicht van de voornaamste doodsoorzaken, zoals vastgesteld bij deze twee typen van onderzoek (basisgegevens in Appendix 4). De ringterugmeldingen suggereren één alles-overheersende doodsoorzaak: verkeersslachtoffers (56%). Bij het 'eigen' onderzoek was het aandeel verkeersslachtoffers significant lager (24%). Nader onderzoek wees uit, dat er verschillende goede redenen te zijn om aan te nemen dat het aandeel van verkeersslachtoffers in het ringmateriaal systematisch oververtegenwoordigd is ten koste van andere doodsoorzaken (grotere vindkans van verkeersslachtoffers, bewuste foutieve opgave als zodanig om dubieuze andere doodsoorzaken te maskeren). Uitgaande van het totale materiaal (Tabel 20), waren de belangrijkste doodsoorzaken in het onderzoeksgebied in de jaren 1967-84:
1. Verkeersslachtoffers (gemiddeld 41%); 2. Sterfte door uitputting in strenge winters (17%); 3. Omgekomen door opsluiting in gebouwen (10%); 4. Doodgevlogen tegen allerlei obstakels, auto's uitgezonderd (9%); 5. Moedwillig gedood door mensen (7%); 6. Verdrinking (7%); 7. Vergiftiging (4%). Als belangrijkste directe oorzaak komt dus het verkeer naar voren. Er is hier sprake van een negatieve trend: gedurende dit onderzoek nam het aantal **verkeersslachtoffers** significant toe van 27% (in 1967-75) tot 53% (in 1976-84). Oorzaak is allereerst de uitbreiding en verbetering van het wegennet en de sterk toegenomen verkeersintensiteit. Kerkuilen worden aangelokt door de prooirijke bermen van (vooral rijks- en provinciale) wegen, waar dankzij 'natuurvriendelijk bermbeheer' sinds de zeventiger jaren grote aantallen veldmuizen leven. Het aandeel van de verkeersslachtoffers is in de Liemers significant hoger dan in de Achterhoek (resp. 51% en 33%). De verklaring hiervoor moet gezocht worden in het dichte netwerk van grote wegen in de Liemers én in het huidige geringe aanbod aan heggen, houtwallen en bosranden in deze streek; daarlangs kunnen de Kerkuilen namelijk veel veiliger jagen dan langs verkeerswegen, waar ze door hun langzame en lage jachtvluchten gemakkelijk sneuvelen in het moderne snelverkeer. Als tweede belangrijke doodsoorzaak geldt **verhongering door voedselschaarste**. Dit valt als doodsoorzaak lastiger vast te stellen dan in het geval van verkeersslachtoffers (zie discussie hierboven). De meeste duidelijke gevallen zijn bij dit onderzoek vastgesteld in de winters 1968/69 en 1978/79. Beide winters waren veldmuizenarm, bovendien lag er 2-3 weken aaneengesloten een flink pakket sneeuw. Het laatste gold ook in de winter 1981/82, maar deze was veldmuizenrijk. Er is toen vrijwel geen kerkuilsterfte in het studiegebied vastgesteld: voedselschaarste lijkt daarom primair de oorzaak van sterfte te zijn. Dit bleek ook uit het feit, dat in de Liemers en Achterhoek in de lange sneeuwrijke winter 1978/79 door ons bijgevoerde Kerkuilen in het algemeen goed overleefden. De voedselsituatie in de winter is in het algemeen sterk verslechterd door het verdwijnen van muizenrijke stoppelvelden en door de centrale opslag van geoogst graan in

goed afgesloten silo's (in plaats van ongedorst bij de boerderij). Tegenwoordig hebben Kerkuilen bij veldmuisschaarste nog de beste overlevingskansen in afwisselende landschappen met een gevarieerd en goed gebufferd prooiaanbod (zie Fig. 15 en 16).

Alle overige doodsoorzaken (steeds direct of indirect op menselijk handelen terug te voeren) zijn vermoedelijk slechts van secundair belang. Een uitzondering vormt **vergiftiging** veroorzaakt door persistente chemische middelen in gebruik in de landbouw (DDT, Dieldrin, Aldrin, methyl-kwik) en in de industrie (PCB's). Hoge concentraties van giftige residuen in dode Kerkuilen zijn vooral bekend uit de zestiger jaren en begin zeventiger jaren (vgl. Braaksma & de Bruijn 1976). Na een verbod op de meest giftige middelen omstreeks het begin zeventiger jaren, zijn hun residuen in Kerkuilen sterk teruggelopen (Fuchs & Thissen 1981). Recente vergiftigingsgevallen zijn schaars, zowel in het onderzoeksgebied als daarbuiten (onderzoek CDI/ Lelystad). Wel blijft het aannemelijk, dat persistente vergiffen het populatie-niveau van de Kerkuil in Nederland in de zestiger jaren en begin zeventiger jaren hebben gedrukt onder de draagkracht van het toenmalige landschap en voedselaanbod, zoals men dit ook voor bijvoorbeeld Oost-Engeland veronderstelt (Newton *et al.* 1991).

Aan het eind van de studie willen we trachten de gevonden aantals-ontwikkelingen van de Kerkuil in verband te brengen met trends in de belangrijkste demografische parameters, zowel in de ruimte (Liemers versus Achterhoek) als in de tijd (periode 1967-75 versus 1976-84). Daartoe zijn de gevonden waarden voor de diverse **interne (demografische) parameters** samengebracht in één overzichtstabel (Tabel 21). De belangrijkste conclusies zijn de volgende. In de Liemers neemt de kerkuilstand af, in de Achterhoek toe. In de Liemers nemen minder uilen aan het broedproces deel dan in de Achterhoek. Wel is het gemiddelde aantal uitgevlogen jongen per broedpaar in de Liemers groter dan in de Achterhoek. De sterfte onder eerstejaars vogels is in de Liemers hoger dan in de Achterhoek. Er kon tijdens deze studie geen trend in de tijd vastgesteld worden in het broedsucces en evenmin in de dispersie-patronen of in de mortaliteit onder volwassen uilen. Daarentegen is de eerstejaars sterfte in de Liemers in de tweede periode (1976-84) significant hoger dan in de eerste periode (1967-75) en in beide perioden in de Achterhoek. In Engeland heeft Percival (1990) een onderzoek uitgevoerd, welke demografische parameter relatief het sterkst doorwerkt op de populatiebalans. De sleutelfactor bleek de sterfte onder eerstejaars Kerkuilen te zijn: kleine wijzigingen in deze factor werken al sterk door op de gehele stand. De conclusie ligt dus voor de hand, dat toegenomen sterfte onder eerstejaars vogels in de Liemers (tot de extreem hoge waarde van 89%) de drijvende kracht is achter de geconstateerde teruggang in deze streek. De verklarende externe oorzaken moeten vooral in de westelijke en oostelijke Liemers gezocht worden, omdat hier de duidelijkste achteruitgang heeft plaatsgevonden. Voor de gehele onderzoeksperiode is uitgerekend, welke jongen-produktie bij de gevonden sterfte noodzakelijk is om de kerkuil-populaties van Liemers en Achterhoek in evenwicht te houden: de zogenaamde **kritische reproduktie**. Deze komt voor de Liemers neer op 4.9-5.5 jongen per broedsel en voor de Achterhoek op 2.5-3.2 jongen per broedsel. Deze waarde werd in de Liemers duidelijk niet gehaald (met gemiddeld 3.7 geproduceerde jongen) maar in de Achterhoek wel (met gemiddeld 3.1 jongen). In tegenstelling tot de situatie in de Achterhoek, kan in de Liemers de Kerkuil dus niet op termijn voortbestaan zonder aanvoer van buitenaf (netto import).

Het relatieve belang van de verschillende demografische parameters voor de jaarlijkse **populatie-balans** wordt zichtbaar in Figuur 25. Uitgegaan is van een (reële) populatie-grootte van 25 uilen zowel in Liemers als Achterhoek. Vervolgens zijn voor beide regio's de gevonden waarden ingevuld voor de grootte van het broedende segment (percentage uilen dat deelneemt aan het broedproces), het broedsucces (gemiddelde aantal uitgevlogen jongen per broedpaar), de overleving van jonge uilen (bepaald door de gemiddelde sterfte in het eerste jaar) en de overleving van volwassen uilen (bepaald door de gemiddelde jaarlijkse sterfte vanaf het tweede levensjaar). Op grond van de gevonden waarden zou na één jaar de Liemerse populatie afgenomen zijn tot 22 uilen (= -3) en de Achterhoekse populatie toegenomen tot 28 uilen (= +3). In werkelijkheid bedroeg op jaarbasis de afname -1 in de Liemers en de toename +1 in de Achterhoek (berekend uit gegevens in Appendix 2). De eindsom is kloppend te maken door middel van de nog ontbrekende factor, de dispersie (= balans tussen immigratie en emigratie). In de Liemers moet er dan jaarlijks een gemiddelde netto import van 2 uilen geweest zijn (sink area!) en in de Achterhoek een gemiddelde netto export van 2 uilen (source area!). Hiermee hebben we de populatie-balans voor beide regio's rond. Belangrijke conclusies zijn: (a) De hoge eerstejaars mortaliteit in de Liemers vormt de cruciale factor in de negatieve populatie-balans in deze regio; (b) Alleen dankzij de nabijheid van 'brongebieden' met een positieve populatie-balans (zoals de Achterhoek) is de Kerkuil in de Liemers nog niet als broedvogel uitgestorven.

Nu we de aantalsontwikkeling, de populatiebalans en het aandeel van de afzonderlijke interne (demografische) parameters geanalyseerd hebben, kunnen we zoeken naar de **verklarende externe (milieu) factoren**. De kernvraag uit een oogpunt van bescherming is: welke externe factoren beperken de aantalsontwikkeling? Er komen vijf factoren-complexen in aanmerking, die de kerkuilstand negatief kunnen beïnvloeden. (1) Directe doodsoorzaken door menselijk handelen (moedwillige vervolging, verkeer, pesticiden). (2) Ongunstige weerscondities (strenge vorst, langdurige sneeuw of regen). (3) Gereduceerd voedselaanbod (veldmuizenschaarste, geringe variatie aan prooisoorten). (4) Verlies aan biotoop door verandering in de landbouw en door dorpsuitbreiding. (5) Verloren gaan van nestgelegenheid.

Aan het eind van deze studie kunnen we de betekenis van deze factoren als volgt evalueren. (Ad 1) Moedwillige vervolging speelt geen rol meer van betekenis dankzij uitgebreide, geslaagde voorlichtingscampagnes. **Pesticiden** speelden waarschijnlijk een belangrijke beperkende rol in de zestiger jaren en begin zeventiger jaren, maar nadien niet meer dankzij een verbod op de meest persistente landbouwvergiffen. Ten aanzien van PCB's blijft echter waakzaamheid geboden. Het **verkeer** is als doodsoorzaak sterk toegenomen en veroorzaakt een substantiële sterfte (zie ook van den Tempel 1993). Het is aannemelijk, dat in gebieden met veel grote wegen met prooirijke bermen én met relatief weinig veilige alternatieve jachtgelegenheid (in de vorm van heggen of bosranden) -zoals thans in de westelijke en oostelijke Liemers- het verkeer wezenlijk bijdraagt aan de extreem hoge eerstejaars sterfte en daarmee in deze gebieden een reële beperkende factor vormt. (Ad 2) Alleen **extreem sneeuwrijke winters** (zoals 1962/63 en 1978/79) veroorzaken een dusdanig extra sterfte, dat hierdoor de stand negatief beïnvloed wordt. Gewoonlijk wordt hoge mortaliteit in de winter primair bepaald door voedselgebrek, waarbij in de periode 1960-84 in Nederland er 7 jaren in negatieve zin uitsprongen (Fig. 26). De invloed van andere weersfactoren (b.v. extreme regenval) dient nader onderzocht te worden aan de hand van het totale Nederlandse materiaal. (Ad 3) **Teruggelopen voedselaanbod**, vooral van de hoofdprooisoort (Veldmuis), werkt sterk door op de kerkuilstand. In de westelijke en oostelijke Liemers zijn duizenden hectares 'plaaggebied' voor de Kerkuil verloren gegaan door landbouwkundige intensivering van graslandgebieden (Fig. 27). Wanneer hier geen alternatieve jachtgebieden in de vorm van oude erven (Huisspitsmuis, Huismuis) en heggen en bosjes (Bosspitsmuis, Bosmuis) tegenover staan, is de bestaansbasis voor de Kerkuil weggevallen. Dit blijkt overduidelijk uit het feit, dat de soort zich alleen in kleinschalige landschappen met een gevarieerd prooiaanbod blijvend blijkt te handhaven (noordelijke Liemers en Achterhoek).

(Ad 4) In de loop van deze eeuw (en met name na 1950) zijn er grote **veranderingen in het cultuurlandschap** en in de agrarische bedrijfsvoering opgetreden, samen te vatten in de begrippen mechanisatie, schaalvergroting, intensivering en specialisatie. Tot 1960-1970 kwamen overal in Liemers en Achterhoek nog extensieve gemengde bedrijven voor, die in korte tijd verdwenen zijn of omgezet zijn in veel grootschaliger, gespecialiseerde bedrijven (intensieve melkveehouderijen). Parallel hiermee is het agrarische bouwplan vereenvoudigd en geïntensiveerd: op de weiden verscheen steeds meer vee, ouderwetse hooilanden werden snel zeldzaam en de teelt van vele soorten granen is vervangen door rassen snelgroeiende maïs. Om dit te kunnen realiseren is op grote schaal ingegrepen in de externe produktie-omstandigheden, onder meer door perceelsvergroting (vaak gepaard gaande met rooien van heggen en houtwallen) en sterke ontwatering (gevolgd door intensiever grondgebruik). Enorme schade aan natuur en landschap zijn aangericht bij grootschalige ruilverkavelingen, met name in de westelijke en oostelijke Liemers. Dit heeft tot grote achteruitgang (kwalitatief en kwantitatief) van het kerkuilbiotoop geleid. De toegenomen intensiteit in het grondgebruik komt in een serie foto's goed tot uiting (Fig. 30 en 31). In het kader van deze studie zijn in een tiental proefvlakken (elk 25 km^2) met een digitale computer vanaf topografische kaarten landschappelijke veranderingen opgemeten, die in de periode 1955-1975 zijn opgetreden. De meetresultaten staan in Appendix 5. De uitkomsten zijn vervolgens gegroepeerd in een tweetal data-sets (één voor de Liemers en één voor de Achterhoek), beide een oppervlakte van 100 km^2 betreffend (Tabel 22). Ter illustratie mogen de Figuren 28 en 29 gelden, die het proces van landschappelijke veranderingen in het proefvlak 2a (oostelijke Liemers) en het proefvlak 4a (westelijke Achterhoek) demonstreren. In de **Liemers** kwam een reeks ongunstige ontwikkelingen aan het licht: een groot verlies aan extensief beheerde (veldmuisrijke) graslandcomplexen en (hoogstam-)boomgaarden; de aanleg van een autosnelweg en veel verbetering en verharding van wegen; fikse dorpsuitbreidingen (sub-urbanisatie); een grote teruggang in heggen, boomrijen, ruige dijkhellingen en moerasjes waar Kerkuilen graag jagen. In de **Achterhoek** traden weliswaar vergelijkbare veranderingen op in de periode 1955-75, maar met minder dramatische gevolgen voor de Kerkuil: boomgaarden en veldmuisrijk grasland maakten hier vanouds minder onderdeel uit van het kerkuilbiotoop, waardoor het verlies in deze categorieën niet zo ingrijpend is; dorpsuitbreiding heeft in de Achterhoek slechts op beperkte schaal plaatsgevonden; er zijn ook hier veel wegen verhard, maar het aantal grote doorgaande wegen (gevaarlijk voor de Kerkuil!) is minder en er resteren nog vele zandwegen; er zijn relatief minder heggen en houtwallen verdwenen en het areaal aan resterende lijnvormige beplantingen en bosranden is in de Achterhoek driemaal groter dan in de Liemers. Dit heeft verstrekkende gevolgen voor de Kerkuil: een statistische analyse laat namelijk een zeer significant verband zien tussen de kerkuilstand (dichtheid aan broedparen) en de beschikbare lengte aan heggen, houtwallen, boomrijen en bosranden (Fig. 32). Verschillende verklaringen liggen voor de hand: (a) In zulke kleinschalige landschappen is het grondgebruik meestal extensiever dan in 'uitgeklede' grootschalige landschappen, hetgeen een gunstig effect heeft op het prooibestand van de Kerkuil. (b) Er leven relatief veel kleine zoogdieren in en langs heggen, houtwallen en bosranden, evenals in de smalle ruige stroken die deze elementen meestal vergezellen: dit zijn dan ook favoriete jachtgebieden voor de Kerkuil. (c) De aanwezigheid van veel van dit soort landschapselementen kan de Kerkuil weghouden van de voor hen veel gevaarlijker wegbermen. Voor een kerkuil-dichtheid van minstens 5 broedpaar per 100 km^2, is gemiddeld 3-5 km lengte aan heggen, houtwallen en bosranden per km^2 nodig; bij het huidige intensieve grondgebruik is voor het instandhouden en creëren van brongebieden voor de Kerkuil een minimale lengte van 5 km aan dergelijke lineaire landschapselementen per km^2 gewenst.

(5) **Teruglopende broedgelegenheid** vormt op veel plaatsen een reëel probleem: in 30 jaar tijds zijn ongeveer 25-40% van de oorspronkelijke broedplaatsen in het studiegebied voor Kerkuilen verloren gegaan door sloop en renovatie van oude gebouwen, het afsluiten van invliegopeningen van boerderijen en kerken etc. Aanvankelijk stond hier dikwijls geen vervangende broedgelegenheid tegenover. Om deze negatieve trend te keren, zijn vanaf 1967 geschikte broedplaatsen systematisch (weer) toegankelijk voor Kerkuilen gemaakt. Tevens hebben wij speciaal voor de Kerkuil een groot type nestkast ontworpen. Met behulp van een groeiend legertje medestanders (later verenigd in de Kerkuilwerkgroep Achterhoek-Liemers) zijn in de periode 1967-84 in totaal meer dan **200 nestkasten** geplaatst (Fig. 12). Het succes van deze langdurige campagne is groot: 1/3 van alle kasten werd binnen 10 jaar bezet en een steeds groter deel van de populatie broedt in de kasten (Fig. 33). In de periode 1976-84 broedde meer dan 75% in kasten en dit percentage was in 1990 al opgelopen tot boven de 90%! In de kerngebieden staan thans 15-25 kerkuilkasten per 100 km^2 en dit leidde recent (1990) in de noordelijke Liemers en in de Achterhoek tot ongekende dichtheden (11-13 broedpaar per 100 km^2): nagenoeg alle in kasten en met een hoog broedsucces (gemiddeld 3.9 jongen; n=70). Het succes wordt versterkt door de kasten te plaatsen in gebouwen bij 'kerkuil-vriendelijke' gastheren, in geschikt biotoop en bij voorkeur op flinke afstand van drukke doorgaande wegen. In de periode 1976-84 bleek het broedsucces van in kasten broedende Kerkuilen significant hoger te zijn dan 'vrij' in gebouwen broedende uilen: resp. 3.4 tegenover 2.5 jong per broedsel (Fig. 34). Voor de Achterhoek betekent dit het verschil tussen een negatieve en een positieve populatie-balans! Nestkasten zijn dan ook een belangrijk wapen gebleken in het strijd om het behoud van de Kerkuil in het cultuurland.

Uiteindelijk kunnen we de verschillende externe factoren, die de kerkuilstand in Liemers en Achterhoek de afgelopen decennia bepaald hebben, naast elkaar op een rij zetten. **De zestiger jaren** startten catastrofaal met twee opeenvolgende muizenarme winters (1961/62 en 1962/63), waarvan de laatste ook nog eens extreem lang en sneeuwrijk was. Na een sterke teruggang bleef in beide regio's herstel tot het vroegere peil uit. Er was toen al sprake van een geleidelijke landschappelijke verarming, afnemende broedgelegenheid en toenemende sterfte door het verkeer, maar vermoedelijk vormden giftige, persistente chemische middelen in de periode 1961-70 de beperkende factor waardoor de stand beneden de draagkracht van het toenmalige landschap en voedselaanbod bleef.

In **de zeventiger jaren** nam de kerkuilstand in de Liemers verder af, maar in de Achterhoek trad herstel op (Tabel 1). Inmiddels waren de meeste persistente vergiffen verboden en namen de residuen in Kerkuilen af. In deze periode vonden grootschalige veranderingen in de landbouw plaats, met intensivering van het grondgebruik, sloop van talloze hoogstamboomgaarden, heggen en houtwallen etc. De negatieve ontwikkelingen waren groter in de Liemers dan in de Achterhoek. Aan de positieve kant kwam de nestkast-campagne goed op gang. Toch had de afnemende werking van pesticiden en de verbeterde nestgelegenheid alleen een groei van de kerkuilstand tot gevolg in de relatief goed behouden kleinschalige landschappen in de Achterhoek. In de Liemers konden deze verbeterde externe factoren de achteruitgang niet keren: biotoopverlies door intensivering en schaalvergroting van de landbouw beperkte hier de uilenstand (teloorgang veldmuis-plaaggebieden, sterk verlies aan heggen, houtwallen en boomgaarden), en er was kennelijk onvoldoende aanvoer uit brongebieden (zoals de Achterhoek) om de hoge sterfte te compenseren.

In **de tachtiger jaren** zette de achteruitgang zich voort in de westelijke en oostelijke Liemers, nog eens versterkt door voortgezette sub-urbanisatie en verbetering van het snelwegennet. Deze factoren droegen bij aan de extreem hoge eerstejaars sterfte in de Liemers. In het kleinschalige landschap van de noordelijke Liemers stabiliseerde de stand zich en recent neemt de Kerkuil hier weer toe: het groeiend aantal nestkasten heeft hier wezenlijk aan bijgedragen. In de Achterhoek nam de Kerkuil eveneens parallel aan het groeiende nestkasten-aanbod toe; kennelijk was goede nestgelegenheid de beperkende factor in deze kleinschalige landschappen. Na succesvolle nestkast-campagnes, wordt de kerkuilstand in het agrarische cultuurlandschap thans bepaald door de aanwezige lengte aan heggen, boomrijen en bosranden.

De verbanden tussen de belangrijkste externe (milieu) factoren en de interne (demografische) processen, zoals deze in de tachtiger jaren in het studiegebied golden, zijn in een **relatie-schema** weergegeven (Fig. 35). Het landschap en het menselijk grondgebruik staan centraal: deze kunnen via het voedselaanbod zowel positief als negatief uitwerken op het broedsucces en de overleving. Er werken nog andere belangrijke factoren op het populatie-evenwicht. Goede broedgelegenheid (te optimaliseren door een ruim nestkasten-aanbod) werkt positief door op de jongenproduktie. Maar hoge sterfte door het verkeer (in sub-urbane gebieden met een dicht hoofdwegennet) kan de populatie-balans negatief doen doorslaan. In dergelijke 'sink areas' kunnen kerkuil-populaties op termijn alleen voortbestaan door aanvoer van vogels uit 'source areas', waar de jongenproduktie groter is dan de sterfte. Dergelijke onontbeerlijke **brongebieden** met een positieve populatie-balans hebben in het studiegebied als kenmerken: (a) het zijn kleinschalige agrarisch cultuurlandschappen, (b) met relatief weinig drukke doorgaande wegen en (c) met een groot aanbod aan optimale broedplaatsen voor de Kerkuil (gerealiseerd door een jarenlange nestkast-campagne).

In Achterhoek en Liemers leven nog meer bijzondere vogels behalve de Kerkuil. In de zestiger jaren broedden hier 135 van de 156 Nederlandse broedvogelsoorten! Vermaard om hun rijke avifauna zijn onder meer het moeraslandschap van de Oude Rijnstrangen bij Zevenaar, de beboste stuwwal van Montferland en het rijkgeschakeerde cultuurlandschap rond Winterswijk. In het kader van deze studie is de **aantalsontwikkeling van 50 schaarse en karakteristieke broedvogelsoorten** gevolgd. De geselecteerde soorten staan in Appendix 6. Bij vergelijking van het aantal broedparen in 1963-67 met het aantal in 1978-82, blijkt de stand van 22 soorten (44%) min of meer gelijk gebleven; 11 soorten (22%) zijn duidelijk vooruit gegaan en 17 soorten (34%) zijn duidelijk in aantal achteruit gegaan. De soorten uit beide laatste categorieën zijn nader geanalyseerd en ingedeeld op grond van twee criteria: (1) het voorkeursbiotoop in het studiegebied (broedvogels van gevarieerd cultuurland tegenover broedvogels van min of meer natuurlijke biotopen), en (2) het specifieke trekgedrag (standvogels en soorten die in Europa overwinteren tegenover de trekvogels die in Afrika overwinteren). De hieruit voortkomende 'oecologische soortsgroepen' vindt men in Tabel 23. De groep van soorten van min of meer natuurlijke biotopen (bos, moeras, open water) telt ongeveer evenveel soorten die toegenomen zijn (8) als soorten die afgenomen zijn (9). De scheidslijn tussen beide is duidelijk: afgenomen zijn de soorten, die naar Afrika trekken, toegenomen zijn de standvogels en soorten die in Europa overwinteren. Binnen de groep soorten die broeden in het gevarieerde cultuurlandschap zijn er veel meer soorten afgenomen (8) dan toegenomen (3). Hier is de scheidslijn veel minder strikt: weliswaar zijn ook hier alleen de in Europa overwinterende soorten toegenomen, maar de lijst van afgenomen soorten van het cultuurland telt niet alleen Afrika-trekkers maar ook soorten die rondzwerven of slechts over korte afstand trekken.

Vanuit de invalshoek **natuurbehoud** kan de conclusie getrokken worden, dat vogels van min of meer natuurlijke biotopen relatief veilig zijn voor zoverre ze niet naar Afrika trekken. Tot deze groep behoren soorten van open water en moeras, die geprofiteerd hebben van het graven van plassen en van de zuivering en verrijking van het watermilieu (Fuut, Kuifeend, Tafeleend) en tevens soorten van naaldbossen, die profiteren van grootschalige aanplanten en het verouderen van deze bossen (Kruisbek, Sperwer en Havik). Achteruitgegaan in deze groep zijn daarentegen de Afrika-trekkers; dit omvat broedvogels van uiteenlopende biotopen als moerassen en rietlanden (Woudaapje, Zwarte Stern, Rietzanger, Grote Karekiet), rivieroevers en gegraven plassen (Visdief, Oeverzwaluw) en heidevelden en halfopen bossen (Nachtzwaluw, Draaihals). Hier zijn beschermingsmaatregelen in de broedbiotopen vermoedelijk ontoereikend en moeten ook maatregelen in internationaal verband (bescherming tijdens de trek) en zelfs in intercontinentaal verband genomen worden (maatregelen in de overwinteringsgebieden).

Zorgelijk is de situatie voor de vogels die broeden en/of fourageren in het agrarische cultuurland. Slechts enkele soorten van deze groep zijn toegenomen: Buizerd, Roek en Kramsvogel, waarvan beide eerste geprofiteerd hebben van een betere bescherming en een verbod op persistente landbouwvergiffen. Groot is in deze groep echter het aantal bedreigde soorten (zie ter illustratie Fig. 36 en 37), waarvan de meeste inmiddels op de 'rode lijsten' van diverse landen staan. Structureel bedreigd zijn de vogels die in het studiegebied broeden in vochtige hooilanden (Zomertaling, Kwartelkoning, Tureluur, Paapje, Grauwe Gors) en in het kleinschalig cultuurland met heggen, houtwallen en bosjes (Roodborsttapuit, Boomleeuwerik, Ortolaan). Ronduit alarmerend is de situatie voor de soorten, die in beide bedreigde categorieën vallen (broedend in cultuurland én trekkend naar Afrika). Dramatische voorbeelden in Liemers en Achterhoek zijn de Zomertaling (in de periode 1965-80 teruggegaan van 90-125 naar 8-16 paar) en de Ortolaan (van 120-150 naar 18-23 paar). Meer hoop op korte termijn is er voor soorten in het cultuurland, die niet ver wegtrekken (Roodborsttapuit, Grauwe Gors). Voor deze vogels kunnen passende biotoopmaatregelen in het agrarische cultuurlandschap op relatief korte termijn (10-15 jaar) perspectief bieden. Bij een goede strategie en uitvoering kunnen vele andere diersoorten profiteren, met name soorten die buiten natuurreservaten verspreid in het boerenland leven of daar hun grootste dichtheid bereiken: zoals Steenmarter, Bunzing, Hamster, Boomkikker, Patrijs, Grutto én Kerkuil. Met een breed en afgewogen pakket van maatregelen zijn tevens belangrijke cultuurhistorische en landschappelijke waarden gediend: dit tot vreugde van vele mensen. Het behoud en herstel van natuur- en landschapswaarden in agrarische cultuurlandschappen is dan ook zeker zo belangrijk als het aankopen en beheren van 'klassieke natuurgebieden' en als het uitvoeren van natuurtechnische milieubouw ten behoeve van 'natuurontwikkeling' (vgl. Vera & Westhoff 1992, Natuurmonumenten 1993).

De volgende maatregelen zijn nodig voor de **bescherming van de Kerkuil en zijn leefgebied**. (1) Voorlichting in brede kring over de cultuurhistorische, landschappelijke, natuurwetenschappelijke en recreatieve waarden van gevarieerde agrarische cultuurlandschappen. (2) Handhaven danwel verbeteren van de kwaliteit van natuur en landschap in het gehele landelijke gebied. Het gaat daarbij ook om kleinere natuurgebieden en waardevolle landschapselementen buiten de zogenaamde 'Ecologische Hoofdstructuur'. (3) Bevorderen van een schone, duurzame (milieu-vriendelijke) landbouw. Ondersteunen van extensieve, stabiele vormen van landbouw en van landschapsonderhoud in kleinschalige gebieden door middel van beheersvergoedingen. Handhaven of aanwijzen van extensief beheerde graslandcomplexen, te koppelen aan weidevogelbeheer of ganzengebieden. (4) Behoud en waar mogelijk uitbreiding van de oppervlakte aan oude hoogstamboomgaarden, hakhoutbosjes, moerasjes en poelen. Het onderhoud hiervan is arbeidsintensief, inzet van organisaties en particulieren is hierbij onontbeerlijk. (5) Onderhoud van heggen, houtwallen en bosjes; aanleg van nieuwe lijnvormige elementen langs perceelsgrenzen en watergangen (niet langs wegen). Bij het huidige intensieve grondgebruik is voor de Kerkuil een gemiddelde randlengte aan houtwallen, heggen en bosranden van 3-5 km per km^2 noodzakelijk (in kerngebieden een lengte van meer dan 5 km per km^2). Vergroting van het prooibestand door aanleg en beheer van grazige, kruidenrijke stroken (3-6 meter breed) op de grens van landbouwpercelen en heggen, houtwallen, bosranden en watergangen. Een alternatief is de aanleg van bosjes of singels met 10-15 meter brede kruidenrijke stroken, die extensief beheerd worden. (6) Ter verbetering van de voedselsituatie in de winter kunnen (in overhoekjes in het cultuurland of aan de randen van natuurterreinen) graanmijten of hopen met oogstafval aangelegd worden om 'muizen' aan te trekken. Dergelijke muizenhaarden zijn ook te kweken in schuren, waar Kerkuilen roesten. Onder extreme wintercondities (bij een langdurig dik sneeuwpakket) kunnen vrijwilligers Kerkuilen bijvoeren met eendagskuikens of muizen. (7) Geen dorpsuitbreiding en andere grootschalige ingrepen (zoals afgravingen en recreatieparken) in rijkgeschakeerde landschappen. (8) Geen wegenaanleg langs waardevolle gradiënten. Geen verdere verharding van zandwegen in het buitengebied, deze medebestemmen voor fiets- en wandelrecreatie. Intensief bermbeheer (ter voorkoming van grote muizen-populaties) uitvoeren langs wegtrajecten waar veel verkeersslachtoffers onder Kerkuilen vallen; ook dichte en hoge wegbegeleidende beplanting kan hierbij helpen. (9) Oude gebouwen, boerderijen en schuren toegankelijk voor Kerkuilen maken, in combinatie met het plaatsen van nestkasten in geschikte gebouwen (met name in gevarieerde agrarische cultuurlandschappen die niet door doorgaande verkeerswegen doorsneden worden). In kerngebieden van de Kerkuil is een dichtheid van minimaal 10-20 nestkasten per 25 km^2 wenselijk. (10) De beste strategie voor regionale nestkast-campagnes is: (a) Stel eerst alle bekende traditionele broedplaatsen in de streek veilig; (b) Bouw vervolgens brongebieden ('sources') op door het plaatsen van een flink aantal nestkasten in bestaande kerngebieden met kerkuil-populaties; (c) Verbind tenslotte de kerngebieden met elkaar door een netwerk van nestkasten over de gehele streek. Wees echter terughoudend met het plaatsen van kasten in gebieden met een typische 'sink' structuur (grootschalige uniforme landschappen, gebieden doorsneden door drukke doorgaande wegen).

De combinatie van bovengenoemde maatregelen leidt tot een hogere reproduktie én een lagere mortaliteit van kerkuil-populaties. Uitvoering ervan zal tevens een scala van andere bedreigde soorten ten goede komen en belangrijke cultuurhistorische en landschappelijke waarden dienen. Omzetting van genoemde aanbevelingen in actieplannen kan geschieden door de diverse overheden, particuliere natuurbeschermings-organisaties, kerkuil-werkgroepen, wildbeheerseenheden en individuele boeren en vrijwilligers. In het kader van het '**soortbeschermingsplan Kerkuil**' (Binsbergen 1994) zullen een aantal van de genoemde maatregelen van overheidswege gestimuleerd en financieel ondersteund worden, waaronder het creëren van kruidenrijke stroken (onbemest en onbespoten) langs graslanden en akkers in een aantal geselecteerde gebieden (o.a. in Liemers en Achterhoek). Reeds beschikbaar instrumenten zijn de Regeling Onderhoudsovereenkomsten Landschapselementen (ROL) en de zogenaamde 'Relatienota', waarbij boeren op uiteindelijk 200.000 ha landbouwgrond in Nederland beheerscontracten met de overheid kunnen afsluiten voor aangepast beheer (met financiële compensatie) ten behoeve van natuur en landschap. In ruimer verband zijn aanpassingen nodig in de gemeenschappelijke landbouwpolitiek van de Europese Unie, die nu nog eenzijdig gericht is op grootschalige voedselproduktie. In regio's met een grote landschappelijke variatie moet in de toekomst het beleid gericht worden op een evenwicht tussen landbouw enerzijds en bosbouw, natuurbeheer en recreatie anderzijds.

Om de effectiviteit van diverse beschermingsmaatregelen te evalueren en te vergroten, is uitvoering van het volgende **onderzoekprogramma** gewenst (zie ook van der Hut *et al.* 1992). (1) Voortgezette monitoring van de aantalsontwikkeling en het broedsucces van de Kerkuil, zowel landelijk als regionaal (continuering van langlopende onderzoeken). (2) Analyseren van de ringgegevens in de landelijke databank ('Vogeltrekstation Arnhem' te Heteren) om regionale en jaarlijkse variatie in de dispersie en mortaliteit te onderzoeken. Nagaan in hoeverre gevonden trends in verband gebracht kunnen worden met externe variabelen (o.a. weer, voedselaanbod, nestgelegenheid). (3) Onderzoek naar de relatie tussen de dichtheid aan nestkasten en de kerkuilstand in verschillende regio's en landschapstypen. (4) Onderzoek naar de populatie-dichtheden van Veldmuis, 'Bosspitsmuis', Huisspitsmuis en Bosmuis in verschillende landschappen en de relatie met diverse beheersregimes. (5) Opstarten van biotoopproeven ter vergroting van het prooibestand (woelmuizen, spitsmuizen, ware muizen) door het creëren van grazige kruidenrijke stroken langs landbouwpercelen in gebieden met lopend kerkuil-onderzoek (o.a. Liemers-Achterhoek en Friesland). Monitoring van de 'muizen'- en de uilenstand (inclusief het broedsucces), ook ten opzichte van referentiegebieden waar geen biotoopmaatregelen genomen zijn. (6) Voortzetting van het onderzoek naar ongewenste nevenwerking van pesticiden op de fauna en controle op residuen in Kerkuilen. (7) Voortgezet onderzoek naar de omstandigheden waaronder Kerkuilen sneuvelen in het verkeer. (8) Detail-onderzoek naar veranderingen in het landschap en grondgebruik in relatie tot de kerkuilstand (periode 1955-1990) door analyse van luchtfoto's. (9) Meer prioriteit voor wetenschappelijk onderzoek van specifieke oecosystemen en levensgemeenschappen in agrarische cultuurlandschappen, met speciale aandacht voor toegepast onderzoek ten behoeve van het natuurbeheer.

Appendix 1. Number of regularly and irregularly occupied breeding territories in census plots in Liemers and Achterhoek during consecutive periods 1956-62, 1963-68, 1969-75 and 1976-82.

Census plot	Area (km^2)	Number of occupied territories			
		1956-62	1963-68	1969-75	1976-82
W Liemers (L1)	95	9 (5)	5 (4)	2 (5)	0 (2)
E Liemers (L2)	80	7 (3)	5 (3)	3 (2)	0 (4)
N Liemers (L3)	75	7 (3)	4 (3)	4 (3)	2 (6)
W Achterhoek (A1)	125	6 (6)	4 (6)	7 (6)	8 (7)
E Achterhoek (A2)	125	7 (4)	5 (4)	6 (8)	5 (8)
Liemers (L1+L2+L3)	250	23 (11)	14 (10)	9 (10)	2 (12)
Achterhoek (A1+A2)	250	13 (10)	9 (10)	13 (14)	13 (15)

NOTE. Regularly occupied territories were occupied by breeding Barn Owls in three or more years in the period concerned. Irregularly occupied territories (given in brackets) were occupied only once or twice in the period concerned.

Appendix 2. Annual numbers of breeding pairs and non-breeding individuals of the Barn Owl in five census plots in the period 1967-84. Breeding figures show number of pairs which actually bred (clutch laid).

Year	Number of breeding pairs					Number of non-breeding individuals				
	L1	L2	L3	A1	A2	L1	L2	L3	A1	A2
1967	4	4	3	6	4	4	2	1	3	2
1968	5	4	4	6	6	2	1	2	1	4
1969	0	0	0	2	1	2	0	1	2	3
1970	1	1	1	4	4	1	1	1	0	2
1971	3	2	3	6	5	1	1	2	1	2
1972	3	3	3	7	5	2	2	1	1	3
1973	1	2	3	7	4	2	1	1	2	1
1974	2	3	3	9	8	1	2	1	2	1
1975	2	3	4	10	9	2	1	1	2	2
1976	1	2	3	7	4	0	2	0	2	5
1977	2	2	3	9	5	0	1	0	1	5
1978	1	1	4	8	6	0	2	1	3	5
1979	0	0	0	6	3	0	0	2	2	0
1980	0	0	2	7	4	0	0	1	1	2
1981	1	1	3	11	6	0	0	1	0	0
1982	0	1	3	11	8	0	0	0	3	1
1983	0	1	3	9	9	0	1	0	3	1
1984	0	1	6	13	9	0	1	0	1	2

NOTE. Key to the census plots: L1 = W. Liemers (95 km^2), L2 = E. Liemers (80 km^2), L3 = N. Liemers (75 km^2), A1 = W. Achterhoek (125 km^2), A2 = E. Achterhoek (125 km^2).

Appendix 3. Diet of Barn Owls in Liemers and Achterhoek in relation to vole population level and to season, period 1967-84. Figures are percentages of prey numbers (items) taken by the owls.

Prey species	Liemers				Achterhoek			
	good vole years		poor vole years		good vole years		poor vole years	
	summer	winter	summer	winter	summer	winter	summer	winter
Microtus arvalis	69.5	56.9	42.7	23.8	40.4	28.0	26.5	15.5
Sorex araneus/coronatus	17.8	23.1	23.6	34.1	31.5	27.6	30.4	32.5
Crocidura russula	5.8	12.0	13.7	19.6	8.0	27.0	14.7	33.6
Apodemus sylvaticus	1.6	2.7	11.1	4.9	9.0	5.9	15.5	7.0
Mus musculus	1.4	1.5	1.2	4.7	3.1	3.5	3.5	3.0
Microtus agrestis	1.1	1.0	0.9	0.3	1.9	1.4	0.6	0.9
Clethrionomys glareolus	-	0.1	0.5	0.5	1.8	1.1	0.3	0.6
Sorex minutus	0.4	0.7	0.5	1.1	0.9	0.5	1.2	1.5
Micromys minutus	0.5	0.6	0.1	0.4	0.2	0.2	0.7	0.4
Neomys fodiens	-	-	-	0.1	0.3	0.2	-	0.2
Arvicola terrestris	0.2	0.1	0.2	0.1	0.9	0.7	1.9	0.8
Rattus norvegicus	0.1	0.4	0.6	0.7	0.4	0.4	0.3	0.1
Talpa europaea	-	0.1	0.2	0.1	0.1	0.1	0.3	-
Mustela nivalis	0.2	-	-	-	-	-	-	-
Aves sp.	0.6	0.7	2.9	9.5	0.9	3.3	4.0	3.7
Amphibia sp.	0.6	0.1	1.7	0.1	0.5	0.1	-	0.1
Arthropoda sp.	0.2	-	0.1	-	0.1	-	0.1	0.1
Total number of prey items	1015	1220	1026	1465	1291	1427	1096	1065
Number of pellet collections	9	8	8	9	10	9	10	9

NOTES. See Table 8 for a review of the good and the poor vole years. The food data from May-October were classified as 'summer', the data from November-April as 'winter'.

Appendix 4. Reports of recovery circumstances of Barn Owls in study area: ringing recoveries compared with other checked information. Figures show numbers of full-grown owls found dead in the period 1967-84 (percentages are given in brackets).

Reported cause of death	Liemers		Achterhoek		Total study area		
	Ringing recoveries	Other checked information	Ringing recoveries	Other checked information	Ringing recoveries	Other checked information	Total number of recoveries
Starved in hard winters	2	4	5	4	7 (14.6)	8 (19.0)	15 (16.7)
Road victim	14	6	13	4	27 (56.3)	10 (23.8)	37 (41.1)
Railway victim	1	1	1	1	2 (4.2)	2 (4.8)	4 (4.4)
Killed deliberately	1	2	-	3	1 (2.1)	5 (11.9)	6 (6.7)
Locked up unintentionally	3	2	1	3	4 (8.3)	5 (11.9)	9 (10.0)
Collided with obstacles	-	2	3	3	3 (6.2)	5 (11.9)	8 (8.9)
Drowned	-	-	3	3	3 (6.2)	3 (7.2)	6 (6.7)
Pesticides	-	1	-	3	- (-)	4 (9.5)	4 (4.4)
Taken by (avian) predator	-	-	1	-	1 (2.1)	- (-)	1 (1.1)
Totals	21	18	27	24	48 (100%)	42 (100%)	90 (100%)

NOTES. In addition to the above-mentioned recoveries, the following numbers of dead Barn Owls were reported without detailed data about the cause of death: Liemers - 21 (ringing recoveries: 12, other sources: 9), Achterhoek - 29 (ringing recoveries: 17, other sources: 12), total study area - 50 (ringing recoveries: 29, other sources: 21).

Appendix 5. Changes in habitat features on farmland plots in Liemers and Achterhoek: situation circa 1955 compared to the situation circa 1975. Figures concern sum total (area/length) of habitat variables per census plot (each sizing 25 km^2).

	Plot 1A		Plot 1B		Plot 2A		Plot 2B		Plot 3A		Plot 3B		Plot 4A		Plot 4B		Plot 5A		Plot 5B	
	1955	1975	1955	1975	1955	1975	1955	1975	1955	1975	1955	1975	1955	1975	1955	1975	1955	1975	1955	1975
Orchards (ha)	274	94	162	49	11	-	24	-	44	-	24	6	11	6	11	4	14	9	11	5
Small marshlands (ha)	9	3	81	57	2	-	4	-	12	11	11	7	-	-	-	-	-	-	-	-
Vole-rich grassland complexes (ha)	400	400	400	-	600	300	100	100	-	-	500	300	-	-	100	100	-	-	-	-
Villages (ha)	65	188	105	394	79	200	271	460	109	179	18	68	3	7	77	143	5	10	7	32
Woodlands (ha)	3	7	26	59	204	210	59	76	223	259	102	128	57	58	88	82	214	232	351	323
Dual highway (hm)	-	45	-	17	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-	-
Metalled roads (hm)	503	503	456	399	406	534	290	492	371	443	318	479	276	478	236	441	144	400	235	498
Unmetalled roads (hm)	356	189	327	245	424	191	648	203	385	109	691	336	1031	507	1200	963	972	603	1223	763
Hedgerows and wooded banks (hm)	165	78	142	54	424	133	421	152	231	48	562	254	709	279	854	538	154	88	152	86
Lines of trees without underlying hedges (hm)	-	18	5	29	5	66	8	75	21	44	15	95	31	28	84	87	433	315	248	295
Edges of woodland (hm)	10	30	78	155	155	166	129	192	225	280	161	241	185	188	260	237	520	531	750	744
Edges of marshland (hm)	24	8	119	61	3	-	17	-	29	26	43	23	-	-	-	-	-	-	-	-
Rough field slopes (hm)	17	13	85	46	48	28	83	42	129	81	126	76	381	206	426	315	607	384	466	329
Banks of dikes (hm)	31	22	155	141	-	-	-	-	151	143	-	75	-	-	-	-	-	-	-	-

NOTE. Figures are based on exact measurements taken from topographical maps on scale 1:25.000 with exception of the area of extensive (vole-rich) grassland-complexes which was estimated on basis of various sources (see text). The location of the census plots is shown in Figure 3.

Appendix 6. Changes in status of 50 scarce and characteristic breeding species in study area (Liemers and Achterhoek; total area size 900 km^2). Figures indicate estimated numbers of breeding pairs in the periods 1963-67 and 1978-82. The upper part of the table refers to species which have increased (*n*=11), the middle part to species which have decreased (*n*=17); the latest part of the table presents species which showed no marked changes in status during the census period (*n*=22). The breeding status in both periods is categorized in frequency classes: 0 = no breeding, 1 = 1-3 pairs, 2 = 4-10 pairs, 3 = 11-25 pairs, 4 = 26-50 pairs, 5 = 51-100 pairs, 6 = 101-250 pairs, 7 = 251-500 pairs, 8 = 501-1000 pairs.

Species which have increased	Number of breeding pairs		Change in status (frequency class)
	1963-67	1978-82	
Great Crested Grebe *Podiceps cristatus*	40-50	110-120	4 → 6
Grey Heron *Ardea cinerea*	15-20	70-95	3 → 5
Gadwall *Anas strepera*	0	3-5	0 → 2
Pochard *Aythya ferina*	5-10	25-30	2 → 4
Tufted Duck *Aythya fuligula*	2-3	20-25	1 → 3
Goshawk *Accipiter gentilis*	7-10	35-45	2 → 4
Sparrowhawk *Accipiter nisus*	15-20	50-65	3 → 5
Buzzard *Buteo buteo*	45-55	140-170	4 → 6
Fieldfare *Turdus pilaris*	0	5-10	0 → 2
Crossbill *Loxia curvirostra*	0-1	2-7	0 → 2
Rook *Corvus frugilegus*	200-250	850-1050	6 → 8

Species which have decreased	Number of breeding pairs		Change in status (frequency class)
	1963-67	1978-82	
Little Bittern *Ixobrychus minutus*	10-13	0-2	3 → 1
Garganey *Anas querquedula*	90-125	8-16	6 → 3
Corncrake *Crex crex*	4-16	1-4	3 → 1
Redshank *Tringa totanus*	55-75	15-25	5 → 3
Common Tern *Sterna hirundo*	15-25	0-3	3 → 1
Black Tern *Chlidonias niger*	65-110	15-30	5 → 3
Wryneck *Jynx torquilla*	3-7	0-1	2 → 0
Nightjar *Caprimulgus europaeus*	11-14	1-2	3 → 1
Woodlark *Lullula arborea*	8-12	0	2 → 0
Sand Martin *Riparia riparia*	600-750	175-225	8 → 6
Bluethroat *Luscinia svevica*	12-17	1-3	3 → 1
Whinchat *Saxicola rubetra*	20-35	5-10	4 → 2
Stonechat *Saxicola torquata*	90-125	15-25	6 → 3
Sedge Warbler *Acrocephalus schoenobaenus*	165-210	9-18	6 → 3
Great Reed Warbler *Acrocephalus arundinaceus*	50-65	13-19	5 → 3
Ortolan Bunting *Emberiza hortulana*	120-150	18-23	6 → 3
Corn Bunting *Miliaria calandra*	8-14	1-4	3 → 1

Appendix 6. (continued) Surveyed species which show no marked change in breeding occurrence (remaining stable or changing ± one step in frequency class). Figures in brackets show breeding status in the two periods (1963-67 and 1978-82, respectively). Key: see head of the table.

Bittern *Botaurus stellaris* (3/3)	Little Ringed Plover *Charadrius dubius* (3/4)
Mute Swan *Cygnus olor* (3/4)	Snipe *Gallinago gallinago* (5/4)
Shelduck *Tadorna tadorna* (2/3)	Kingfisher *Alcedo atthis* (2/2)
Shoveler *Anas clypeata* (6/5)	Middle Spotted Woodpecker *Dendrocopus medius* (1/0)
Pintail *Anas acuta* (1/0)	Black Woodpecker *Dryocopus martius* (5/5)
Honeybuzzard *Pernis apivorus* (3/3)	Bearded Tit *Panurus biarmicus* (2/1)
Marsh Harrier *Circus aeruginosus* (1/1)	Grey Wagtail *Motacilla cinerea* (2/3)
Hobby *Falco subbuteo* (4/4)	Savi's Warbler *Locustella luscinoides* (2/1)
Spotted Crake *Porzana porzana* (2/1)	Red-backed Shrike *Lanius collurio* (3/2)
Curlew *Numenius arquata* (4/4)	Goldfinch *Carduelis carduelis* (2/2)
Ruff *Philomachus pugnax* (1/0)	Serin *Serinus serinus* (1/2)