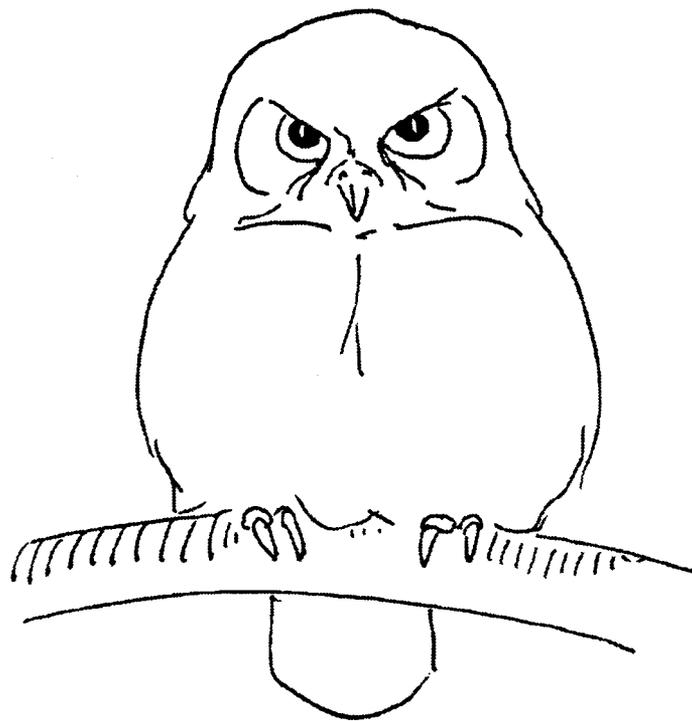


VERSLAGEN EN TECHNISCHE GEGEVENS

**Territorial behaviour and food composition
of two pairs of the little owl
Athene noctua Scopoli, 1769,
nesting at a distance of only 40 m apart**

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INTRODUCTION

The little owl *Athene noctua* (Scopoli, 1769) is a small, nocturnal predator, most active from dusk to dawn, with a two-hour break after midnight. There is little or no hunting during daytime, not even when the birds are raising young (Cramp, 1985). Contrary to these observations, the histology of the retina of the little owl was found to be quite similar to that of diurnal birds, and its colour vision has been reported to be as good as the song thrush's (*Turdus philomelos*; Voous, 1988), suggesting that the little owl may be more diurnal than usually expected.

The main food of the little owl comprises small mammals and birds, reptiles, amphibians, insects and earthworms (Cramp, 1985), although several authors have found different proportions in lists of prey. In the Moldavian SSR, the former DDR, France and Spain the number of invertebrate prey exceeded 50%, and in the last two cases was found to equal about 95% (Mikkola, 1983). Contrary to this, during two years of collecting pellets in Poland, Romanowski (1988) found 75% of vertebrate prey (mainly voles, *Microtus* sp.) and only 25% invertebrates. However, when comparing the number of prey in situations in which both vertebrates and invertebrates are taken, it is important to bear in mind that vertebrate and invertebrate prey deliver very different amounts of food in terms of biomass (e.g. vole versus beetle). Sometimes vertebrate prey, particularly voles and mice, forms a substantial part of the little owl's food (Voous, 1988), even if this is not well shown by the numbers of this prey. Despite this, one thing is clear - that the proportion of invertebrate prey increases gradually from central Europe to the Mediterranean countries (Mikkola, 1983).

The insects commonly eaten by the little owl include carabid, cetoniid, scarabaeid, and staphilinid beetles (Coleoptera); earwigs (Dermaptera); grasshoppers and mole crickets (Orthoptera); and even large numbers of ants (Formicidae). The little owl's diet contains at least 15 species of mammal. The most common are voles (*Microtus* sp., *Pitymys* sp.) and mice (*Mus musculus*, *Apodemus* sp.); in addition, shrews (*Sorex* sp., *Neomys* sp., *Suncus* sp., *Crocidura* sp.), moles (*Talpa* sp.), bats (*Rhinolophus* sp., *Myotis* sp., *Plecotus* sp., *Pipistrellus* sp., *Nyctalus* sp.), young rabbits (*Oryctolagus cuniculus*), hamsters (*Cricetus cricetus*, *Cricetulus migratorius*), rats (*Rattus* sp.), and hedgehogs (*Erinaceus europaeus*) are eaten. At least 60 species of birds are taken, up to the size of a thrush (*Turdus* sp.), the most frequent among these being starling (*Sturnus vulgaris*) and skylark (*Alauda arvensis*). Reptiles and amphibians most frequently taken are lizards (*Acanthodactylus* sp., *Psammodromus* sp., *Lacerta* sp.), slow-worms (*Anguis fragilis*), frogs and toads (*Discoglossus* sp., *Pelobates fuscus*, *Hyla* sp., *Rana* sp.). The little owl's diet infrequently also includes spiders (Araneae), scorpions (*Buthus* sp.), millipedes (*Julus* sp., *Polydesmus* sp., *Glomeris* sp.), slugs and snails (*Helix* sp., *Theba pisana*). Finally, the little owl is said to eat vegetable material such as berries and other fruits, corn, and green plants (Cramp, 1985; Voous, 1988).

The importance of earthworms (*Oligochaeta*) as food for the little owl is still underestimated. In some studies they do not appear in the list of prey at all - either not observed or not looked for (Jaksic and Marti, 1981; Romanowski, 1988; Obuch and Kürthy, 1995); in others, earthworms are prominent in the food of the little owl. In NW Switzerland, 54.6% of 207 items brought to the nest were earthworms (Glutz and Bauer, 1980), and Haverschmidt (1946) observed a pair of the little owl frequently hunting earthworms. During his observation, Haverschmidt (1946) also weighed the earthworms that were hunted and found that usually they were quite large: 15-20 cm long and weighing 7-9 g. The average common vole (*Microtus arvalis*) - a frequent prey of the little owl - weighs about 20 g (Romanowski, 1988). This subject should be analysed more extensively, as it may turn out that earthworms are a more important source of food for the little owl than was assumed.

The breeding season of the little owl in NW Europe usually lasts from the middle of March to the middle of August (Cramp, 1985); eggs are mainly laid from the middle of April to the middle of May (Glue and Scott, 1980). In most cases there is only one brood per year and lost clutches are only exceptionally replaced (Mikkola, 1993). Usually there are 4-5 eggs per clutch, incubated by the female only. The incubation period lasts 27-28 (23-35) days (Cramp, 1985) and starts when the first egg is laid. Unlike most other owls, however, incubation may also be delayed until the clutch is completed (Mikkola, 1983). Newly hatched young are fed mainly by the female. The male feeds them rarely, but he brings food to the female. She leaves the nest only for short resting periods, until the young are 14-16 days old. After approximately two weeks, both sexes share the feeding of the young. Young owls leave the nest after 30-35 days (Glue and Scott, 1980).

The little owl is a territorial resident bird. Usually the same territory is occupied during the entire year (Finck, 1990). Territorial advertisement (a call sounding like "hooi, hooi", Cramp, 1985) is uttered by the male, from an exposed perch. Rival-birds usually perch nearby; during peak activity of advertising it is possible to hear as many as six males competing with each other at the same time (Glue and Scott, 1980). The female does not utter the advertising call, but she is said to "participate" (Glutz and Bauer, 1980). Finally males pursue each other giving shrill keckering calls, but they do not fight (Cramp, 1985). In contrast to this, in captivity both male and female usually attack a rival vigorously after threatening it by ruffling both head and body feathers (Glutz and Bauer, 1980). In a natural environment, a rival can probably also be attacked by the owner of the territory if it does not flee, as experiments with a dummy bird, near which the advertising call was played, have shown (Finck, 1990). Advertisement activity does not occur throughout the year with the same intensity, but has its peak from late January to mid-April (Haverschmidt, 1946; Cramp, 1985).

The average territory size recorded at the beginning of February in southern England was 35 ha on water-meadows and 38 ha on mixed farmland (Glue and Scott, 1980). In

Germany during the period of November-February it was 19.8 ha (Finck, 1990). The size of the territory changes in the course of the year (Finck, 1990). The largest territories are defended in the period March-April (with an average of 28.1 ha). After this period, during the breeding and nesting season, the size of the territory decreases gradually to 1-4 ha (av. 1.6 ha) in July-August. In autumn, when the first-year birds disperse, the size of adult males' territories increases again (Finck, 1990; in that paper "territory" is defined as "defended area"). As the territories of the little owl at the beginning of breeding season comprise an average of over 25 ha, nests are usually located at a distance of at least a few hundred meters from each other. In Britain, the closest nests found were at a distance of 240 m to 320 m apart (Glue and Scott, 1980).

During my stay in the Netherlands, I had the unusual opportunity to observe two pairs of the little owl nesting at a distance of only 40 m apart. Until now just one comparable case (50 m distance between two nests) was recorded in Switzerland (Glutz and Bauer, 1980).

The aim of the present observations was to find out how these two pairs coexisted. There are several possibilities for sharing/separating the area with such a short distance between the nests :

I. Sharing/separating the area in space:

1. There could be two completely separated territories, with a strict border - with or without much antagonistic behaviour between these two pairs.
2. The area could be shared in some way between the two pairs.
3. One pair could be dominant over the other: one couple could use the whole area, the other having no permission to enter the surroundings of its neighbour's nest.

II. Sharing/separating area in time:

The area could be separated not only in space, but also a separate time of hunting and/or breeding.

In order to check these hypotheses, the breeding behaviour of these two couples was recorded and compared.

Additionally, the food of these two pairs of the little owl was studied. Special attention was paid to the importance of earthworms and other invertebrates as prey.

STUDY AREA

The study took place in central Holland, in the Betuwe region, which extends between the river Rhine and its branch, the Waal. In this area the population of the little owl is one of the densest recorded for in Netherlands (SOVON, 1987). Within the Betuwe region three main types of landscape can be distinguished: 1) the river forelands - strips

of land lying between the river-dike and the river (periodically inundated grasslands); 2) the river basins, and 3) the natural levees, both situated inside the dikes (Fuchs, 1985).

The basins are covered by very heavy clay, which causes high groundwater levels during winter. This is the main reason that these areas are uninhabited by people; they were traditionally used almost exclusively for hay-making. In contrast to this, the much lighter soil of the natural levees is intensively used for agriculture, especially for growing fruits. As a high proportion of the little owls in the Betuwe region nest in holes in apple trees (Fuchs, 1985), most of them occupy the natural levee areas.

During the last few decades, the little owl experienced problems finding suitable nesting places. More and more traditional "old type" orchards have been replaced by more productive low spindle-type trees, leaving the little owls deprived of their breeding places (Fuchs, 1985). Fortunately, at present, there are trends among citizens to move into the villages and to work in town. Most of these non-residents maintain their old-type orchards as a recreation place, thereby protecting quite a number of the little owls' nests. The little owls studied occupied such an orchard.

The orchard in which the little owls were observed is situated at Essebroek, Ingen, about 10 km from Rhenen. The orchard has a surface of 4675 m² and consists of 15 fruit-trees (mostly apple-trees), with a row of 12 pollard willows at the southern border (see map). The orchard is surrounded by three other orchards (of different type and age) and a house and road. To the north, the study area is bordered by an apple-orchard of approximately the same age as the one examined. Between these orchards, there is a grass strip (manege) about 20 m wide. The neighbouring orchard to the south is of recently planted low spindle-type, situated just next to the range of willows. The orchard to the east is a relatively young one of old-type trees, also directly bordering the study area. The west border of the orchard with the nesting trees is formed by a house, its carriage drive and a road.

Both nests are in holes in apple-trees. The first nesting-tree ("old nest") is situated on the north border of the orchard, the other ("new nest") in the middle. Between the nests there is a tree-less strip of about 40 m, more or less dividing the orchard into two parts. The "old nest-tree" is adjacent to only two other trees, the three of them growing in an isolated row near the fence. The fence next to the nest-tree is rather low, but every few meters there is a higher pole in it. The surroundings of the "new nest-tree" is different from the other one, because there are more trees in its vicinity. There is also a fence with poles near the "new nest", but a bit further away than in the case of the "old nest" (see map).

METHODS

The observations of the two pairs of little owl were carried out from the beginning of April to the middle of June 1996. The birds were observed from a tent, situated in such a

way that the entrances to both nests were visible. The observations were made 2 or 3 consecutive days per week, usually for 1.5 to 2 hours in the morning and in the evening at the beginning of the breeding season, and also during the day when the birds became active at different times of the day. The date and time of every observation was noted. Special attention was paid to the direction of birds' movements to determine the use of the area.

Besides behaviour observations, pellets of the little owl were collected in the surroundings of the nesting places. These were analysed using the microscope; remains were determined according to the keys of Husson (1962), Yalden (1977) and Pucek (1984). The number of vertebrates was calculated separately for each pellet on basis of predominant bone elements - mandibles and skulls for mammals, and mandibles, skulls and thigh-bones for birds. In the few cases of pellets containing only other types of bird bones, the species was identified using feathers. Insects were counted and identified on the basis of the remains of chitin exoskeletons. Presence of earthworm remains in the pellets was determined by searching for their chaetae (Yalden, 1977).

It was impossible to estimate the number of earthworms in a pellet, so the frequency of pellets containing earthworms was determined instead. Due to entirely different methods of analysing and investigating the importance of earthworms as the food of the little owl, the earthworms were described separately (they were not connected with the analysis of the different type food - vertebrates and other invertebrates).

Insect-traps were used to collect information about possible prey for the little owl in the surroundings of both nests. Collected insects were also useful for identification of invertebrate remains from pellets.

RESULTS

I. Breeding time

1. "Old nest"

The first time a bird was observed entering the "old nest"-hole was on 18 April; eggs were found the same day. Four eggs were laid and four young hatched between 7 and 15 May. As incubation usually takes 27-28 days (Cramp, 1985), eggs must have been laid between 9-17 April. One of the hatched young was smaller than the others. On 22 May the chicks were weighed:

1. 103g
2. 92g
3. 85g
4. 40g

From 10 June onward, loud calls of the chicks from the "old nest" could be heard, and on 20 June two of them were seen for the first time outside the nest, on the fence and poles near it, having some difficulties with flying. At the end of this observation at least one (probably both) of the chicks went back to the nest. On 21 June, one young was found in the nest and ringed. It seemed to be younger than the two observed the day before, so at this time it was clear there were at least three chicks in the "old nest".

2. "New nest"

On 17 April, a copulation near the "new nest" was observed, but the first time a bird was seen entering the nest was on 23 April (no observations were carried out between 18 and 23 April). In this case the eggs were also found on 18 April and the young hatched between 7 and 15 May. Five eggs were laid and five young hatched. On 22 May, the young were weighed:

1. 71g
2. 70.5g
3. 65g
4. 64g
5. 54g

Comparing the time of hatching, the eggs were probably laid at about the same time as in the "old nest", although the fact that these chicks were lighter than the ones from the other nest could also indicate that they were a few days younger (less than a week).

The "new nest" was closer to the tent from which the observations were made than the "old nest", so some notes on behaviour could be taken. After the young hatched, two types of behaviour could be recorded. One adult bird - probably the female - sat in the nest almost all the time, only taking short breeding pauses in tree number 1 (see map), while the other - probably the male - was observed hunting in the east orchard and delivering food to the nest.

On 27 May, four chicks were found dead and the last one was still alive but very weak. The dead young were not emaciated and two of them were decapitated. They died probably around the 26 May in the evening; they were still fresh when found. On 29 May the nest was checked again and this time it was empty; the last chick had also died.

It is hard to explain this unfortunate event. It seems unlikely that it was caused by disturbing the female by weighing her (22 May). Of course, as she might have left the nest for too long, the chicks could have died because of cold and/or hunger. This, however, is not very likely - 1) If the female left the nest on 22 May, the chicks would probably have died earlier; 2) on 26 and 27 May delivering food was still observed (an

earthworm, and a mouse or a vole); 3) during these days the female was also sitting in the nest, with pauses on tree number 1, and she must have divided prey for the chicks, because there was no prey found in the nest. A reason for chicks' death could have been some disease, a predator, or secondary toxicity from eating poisoned voles. An inhabitant of the area gave the information that in 1996 some farmers were using poison against voles and mice in order to protect young orchards.

II. Places of occurrence and directions of movements.

1. "Old nest"

At the beginning of the study (beginning of April), the birds were observed mainly in the close surroundings of the nest - near the nest hole, or in one of the closest trees. In addition, the birds also used to sit on some poles near the nest. During most of the time of the observations, only one bird of this couple was observed. The first time both birds were seen together was on 24 April.

At all times, the birds inhabiting the "old nest" approached the surroundings of their nest from the north orchard and returned in the same direction. No other directions of the birds' movements were observed. From 21 May onward, six days after chicks had been observed for the first time, the birds also started to use the area at the west side of the nest ("front trees") and a small area south of the nest, next to the house ("house-trees"; see map). They continued to fly to the north orchard. From this time on, the birds were observed much more often, especially near the nest. It was quite often possible to observe them perching just at the entrance of the nest or on the nearest pole. Also, the birds were hunting in the north orchard, and in the surroundings of the "front trees" and the "house-trees". For a schematic overview of all bird movements, see the map.

2. "New nest"

The birds of the "new nest" were seen mainly in tree number 1 (see map). This was the main place for long-term resting, breeding pauses, and both owls also rested there for a short while on their way from the east orchard to the nest. Mating behaviour was observed twice (once with copulation), in both cases in tree number 3. Other trees and also poles (poles less often than the other couple) were used only for short breaks.

The little owls of the "new nest" were almost always observed flying into the east or south orchard and returning to the surroundings of the nest from this area. While chicks were in the nest, it was possible to observe adult birds hunting in the east orchard. There was one case of a flushed bird (probably the female) flying away from the nest to the north orchard, because the observer approached the "new nest" from the south. During this flight the bird was left in peace by the other pair.

III. Time of activity.

At the beginning of the study, the birds of the "old nest" were seen less often than the ones from the "new nest". This was probably caused by the fact that birds from the "old nest" used to stay in the north orchard, where they were more difficult to observe from the vantage point. In April both pairs were flying around mainly in the evening from about 1 -1.5 hours before dusk (observations were stopped after dusk); later, at the beginning of May, from about 2 hours before dusk. During this period, the morning activity (shortly after dawn, when first observations were possible) was rarer - the birds were seen only a few times during one bout of observation and often used to sit in one place. The little owls were probably already active earlier. Once, while the observer was approaching the tent, two birds were flying away from the ground in the surroundings of the "new nest", where they had probably been hunting. The birds were not active during the day-time.

Six days after the chicks had been found, the entire pattern of activity changed. Both pairs also became active during the day-time, and were now observed with the same frequency. The birds were observed hunting from dawn until about 11.00 a.m., and occasionally longer. The frequency of the birds' appearance was higher than before, and less often was it possible to see a bird sitting in the same place for a longer time. After the chicks had died, the same pattern of activity as before hatching was resumed at the "new nest".

IV. Antagonistic behaviour

During the first day of observations, a tape with the advertising call was played near the orchard. The male from the "new nest" answered immediately to this. After five minutes, when the tape recorder was already turned off and the male from the "new nest" was still occasionally calling, the male from the "old nest" responded too. The uttering of both males, with intervals, lasted about 10 minutes. During consecutive observations, advertising calls were heard uncommonly and these were restricted mainly to April, before any young had hatched. Usually these calls did not last long and the other male did not answer. Once, after the male from the "new nest" had been calling for 2 minutes, the bird from the "old nest" answered. A strange fact was that the answer was not the advertising call, but 'the excitement call' "miau, kuwitt" (Cramp, 1985). Before the start of my observations, the birds were calling more frequently during the night (according to the inhabitants of the house).

From the middle of the incubation time and during the first weeks of raising the young (from the end of April to the end of May), no calls were heard. After the chicks from the "new nest" had been found dead (27 and 29 May), adults from this nest started to give 'excitement calls' in the east orchard. In the evening of 10 June, birds from the "old nest" were uttering this call in the area of the "house-trees" and around the "old nest", while

the chicks became very noisy. Excitement calls are said to be connected with heterosexual behaviour and also to fights between rivals (Cramp, 1985).

In summary, in the case of the "old nest", calls were uttered mainly from the north orchard and from the area of the "house-trees", whereas the other male called mainly from east orchard and the surroundings of its nest (see map).

During the whole period of the observations, no fighting or chasing was recorded between birds from different pairs. Even when the bird from the "new nest" was flushed and flew into the north orchard, usually occupied by the other couple, it was left alone by other pair.

V. Food

During the time of observations, 21 pellets were found around the "new nest" and 55 around the "old nest". A few times during the behaviour observations it was possible to recognize prey taken to the nest; these were small mammals or earthworms. The owls were also seen hunting for earthworms.

In the pellets of the "new nest", 205 remains of prey were identified - 10% of the items were vertebrates and 90% invertebrates. Earthworms (Oligochaeta) were found in 33% of the pellets. In the pellets of the "old nest", 1493 remains of prey were found - 3% consisted of vertebrates and 97% of invertebrates. Earthworms were found in 49% of the pellets. Combining the number of prey items found in the surroundings of both nests, a total of 1698 prey were identified - 96% of which were invertebrates and 4% were vertebrates; the frequency of earthworms was 47% (Table 1).

Among the invertebrate prey, the most abundant were beetles - especially larvae of Cantharidae - and earwigs (Dermaptera). Remains of four specimens of the snail *Balea biplicata* were found during the analyses of pellets from the surroundings of the "new nest" (Table 1).

Voles (*Microtus* sp.) were the main vertebrate prey for both nests. White-toothed shrews (*Crocidura* sp.) were the only other mammalian genus found in pellets in significant numbers. Other mammals and birds were not usual type of prey for both pairs observed (Table 1).

To determine whether the differences in food composition between the nests were significant, a Mann-Whitney U non-parametric test was performed. Both a full set and a set with indeterminate taxa removed were examined. Food composition of both pairs is not significantly different; $p=0.30$ for the full data set and even 0.36 for the corrected set.

Table 2 lists invertebrates caught in the insect-traps placed in the surroundings of both nests.

DISCUSSION

I. Territorial behaviour.

During all the observations, birds from the "old nest" were never seen flying to the east or south-east of the nest; no movement from the surroundings of this nest towards the east orchard, south orchard or surroundings of the "new nest" was observed. Birds from the "new nest" also did not fly in the direction of the area occupied by the other couple, with only one exceptional case of the bird that was flushed by man. Furthermore, antagonistic behaviour such as advertisement calls (Haverschmidt, 1946) was observed only occasionally, and birds from the two pairs were never seen fighting or chasing each other. All-in-all, this behaviour indicates that there are two separate territories with a stable border separating them. The tree-less strip between the two nests seems to be this border.

It is possible that most of the antagonistic behaviour took place before the start of this study and at the time of the observations the males were already habituated to each other. The ability to discriminate between songs of neighbouring males and non-neighbours was found in the ovenbird *Seiurus aurocapillus* (Weeden and Falls, 1959), the yellowthroat *Geothlypis trichas* (Wunderle, 1978), the great tit *Parus major* (Krebs, 1971), the field sparrow *Spizella pusilla* (Goldman, 1973), and the song sparrow *Melospiza melodia* (Kroodsmas, 1976; Harris and Lemon, 1976) by use of song playback. When a call was played near the neighbour's boundary, the males showed a higher response of aggression to the songs of strangers than to those of its neighbours (Wunderle, 1978). Such a tolerance to the songs of established neighbours might be an important survival value - the territorial male can save energy by reducing the numbers of "needless" boundary conflicts. Habituation seems to be an important mechanism for maintaining low levels of aggression between neighbouring males (Wunderle, 1978).

The flushed little owl which crossed the supposed territorial border was left alone; possibly it just was not noticed by the other birds, as it did not produce any sound.

The birds of the "old nest" did not use the area near the house before their chicks hatched. They also did not occur near their nest as often as afterwards (these were the places closest to the "new nest"; see map). This seems to indicate a strategy to omit contacts with the other pair as much as possible - the birds used to come close to the other territory only when they had to feed their young. Probably after the young are fledged, the adults will take them to the north orchard.

Nesting of two pairs of the little owl at a distance of only 40 m apart is exceptional. Until now just one comparable case of 50 m distance between two nests was recorded in Switzerland (Glutz and Bauer, 1980). This could be the result of the generally high density of the little owls in the surroundings of Essebroek. In the area of approximately 10 km² around the two pairs of the little owl observed, 14 other territories were recorded, adding up to approximately 1.6 pairs per km². The density of the little owl in

'optimal habitats' in central Europe is said to be 0.3-0.5 pairs/km² and rarely up to 1.5 pairs/km² (Cramp, 1985).

During the observations no differences in periods of activity between the two pairs were noted. The breeding time was also similar, so these two couples seem to be separated only by space. There was probably a difference in the type of starting incubation between the two nests. Analysing the chicks' weight, it seems that in the "old nest" the incubation started when the first egg was laid, while in the "new nest" this was probably delayed until the clutch was completed, as there were only minor differences among chick's weights.

It is surprising that, contrary to previous studies, during this study birds were often observed hunting during the day-time (almost till noon) in the period after the chicks hatched. Most authors describe the little owl as being most active from dusk to midnight and, after a two hour break, till dawn, with little or no hunting done during the day, even while raising young (references in Cramp, 1985); these observations seem to be incomplete.

The death of the chicks from the "new nest" should not be considered as an effect of the short distance between the two nests. Possibly this was accidental, because in 1995 chicks from both nests survived (P. Fuchs, pers. comm.) - two from the "old nest" and five from the "new nest".

II. Food

Some variance in the proportion of vertebrate and invertebrate prey and in the frequency of earthworms exists in the food composition of these two pairs. However, possibly due to a limited amount of collected data, a direct comparison of food composition revealed no significant difference.

The main food (by numbers) of both pairs studied consisted of invertebrates. This high proportion of invertebrates does not imply that vertebrates are not an important source of food though. There is a big difference between vertebrate and invertebrate prey biomass and the number of hunted specimens. Unfortunately, it was impossible to estimate the biomass of prey during this study, especially that of invertebrates, most of which could not be identified to species level because of insufficient characteristic remains. However, a study of the little owl's food in Spain showed that invertebrate prey comprising 94.7% of food in number of specimens, represented only 33.6% in biomass (Máñez, 1983).

It has been observed that the proportion of invertebrate prey increases gradually from central Europe to the Mediterranean countries (Mikkola, 1983), but the results of the present study (96% invertebrates on the basis of number of specimens, summarising data from both nests) are higher than the ones of Haverschmidt (1946) in Holland (84.7%; without earthworms) or Laursen (1981) in Denmark (86.8%) and comparable to

those of Thiollay (in Mikkola, 1983) in France (94.4%) and Herrera and Hiraldo (in Mikkola, 1983) in Spain (95.9%). Valentijn (1984) found an even higher proportion of invertebrates in Holland (98.5%), but he analysed pellets throughout the year, whereas the other studies (except for Laursen, 1981) considered the breeding season only.

Among invertebrate prey, an unusual high number of larvae of Cantharidae was found - 85% of all invertebrates. These larvae were also found in pellets of the little owl by Romanowski (1988), but not in such high numbers. Cantharidae larvae are an easy and valuable prey for the little owl in this area. In addition to Cantharidae larvae, the owls could also hunt a similar type of prey, Diptera larvae, which were caught in significant numbers in insect-traps in the surroundings of both nests. However, as these larvae - in contrast to those of Cantharidae - lack chitinized body parts, they leave no remains in pellets. Therefore their presence in the diet of the little owl could not directly be determined.

Snails are an unusual prey for the little owl. Up to now only two species, *Theba pisana* (Mienis, 1971) and *Helix* sp. (Cramp, 1985), were recorded in its pellets. It is interesting that during the present study the remains of four specimens of the snail *Balea biplicata* were found.

The observations of the little owl hunting earthworms or bringing them to the nest (Haverschmidt, 1946; Glutz and Bauer, 1980; pers. obs. in Holland and Poland) were confirmed by present pellets analyses. They showed that earthworms are an important source of food for the little owl. Past studies in which earthworms were not considered to be part of the diet (Jaksic and Marti, 1981; Valentijn, 1984; Romanowski, 1988; Obuch, 1992; Obuch and Kürthy, 1995) are incomplete. Investigating the chaetae of earthworms should be included in future pellet analyses of the little owl, and probably also other owls and birds of prey (e.g. kestrel, buzzard).

CONCLUSIONS

I. Territorial behaviour.

1. The two pairs of the little owl which were observed during this study seemed to occupy two separate territories with a strict border. There was only a small amount of antagonistic behaviour observed during this study. It is possible that there had been more of such behaviour in early spring.
2. No observation confirmed the hypothesis that pairs were separated in terms of time of hunting or breeding. This is therefore rejected.

II. Food

1. For both pairs of the little owl studied, invertebrates formed a proportionally significant food component (96% by numbers).

2. An unusual high number of Cantharidae larvae remains was determined in the pellets studied, 85% of all invertebrate prey.
3. The remains of four specimens of the snail *Balea biplicata* were found in pellets during the present study. This species has not previously been recorded in pellets of the little owl.
4. The pellet analyses confirmed the importance of earthworms as a source of food for the little owl.

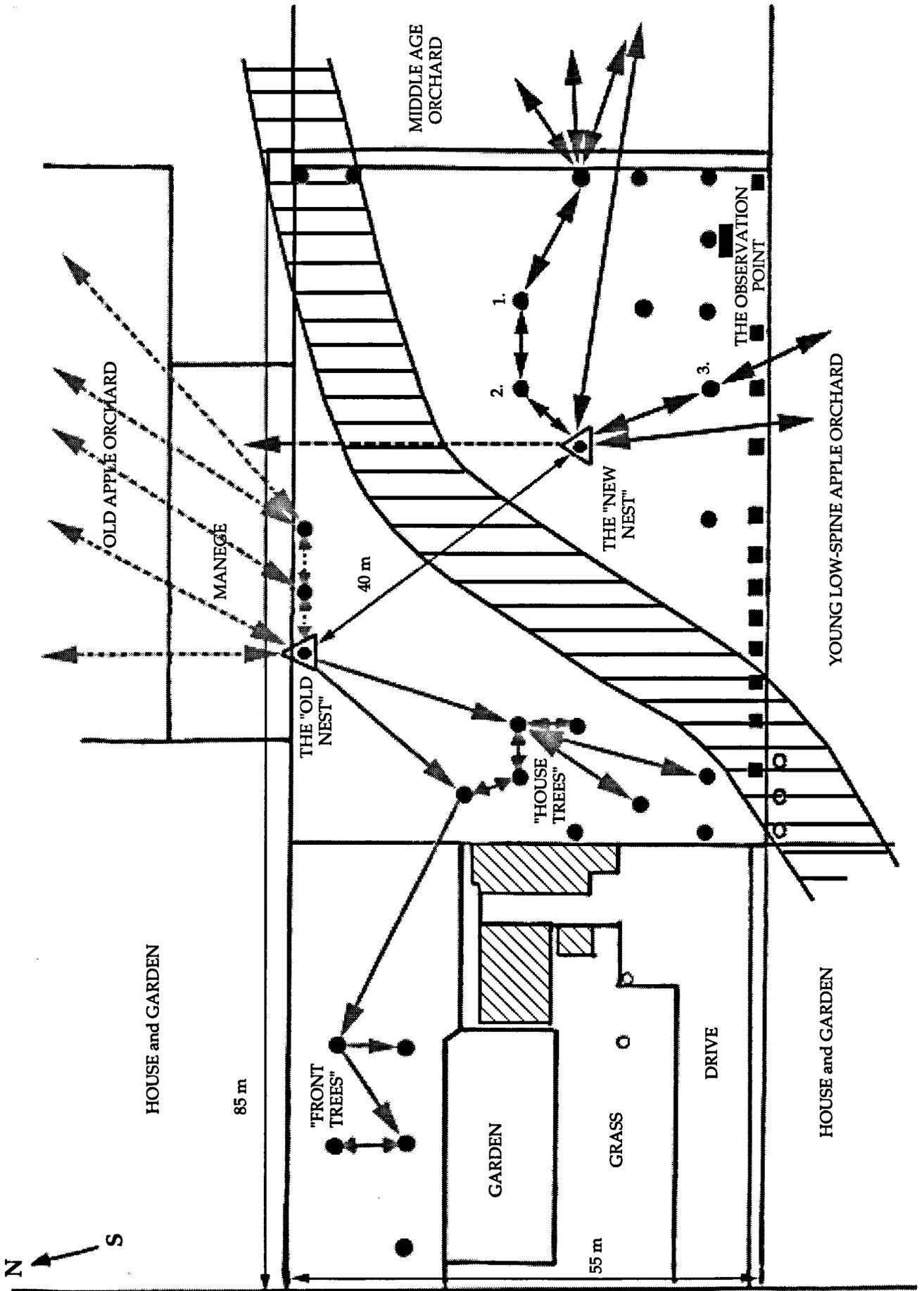
ACKNOWLEDGEMENTS

I wish to express my appreciation to drs. P. Fuchs for his help with selecting the study area and extending my knowledge of the little owl, and to dr. J. Wattel for his help with the organisation of my study and checking my report. I also would like to thank the following people for their help with identification of the little owl's prey remains: mr. Ben Brugger (insects), drs. Cees S. Roselaar (birds), dr. Peter van Bree (mammals), drs. Willemijn Prast (birds), and mr. Rob Moolenbeek (molluscs). Furthermore I would like to acknowledge two anonymous reviewers, Tineke Prins for her help with collecting literature, Xavier Pons for sending a Spanish article, Angela Hollis for checking the English, Lukasz Rejt for his drawing of the little owl on the front page, and Ruud Altenburg for the pictures and for his good advise regarding this report. I finally wish to express my special appreciation to Mardi Spitholt and Kok Hoekstra for taking care of me during my stay in the Betuwe.

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Legend of map

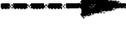
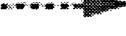
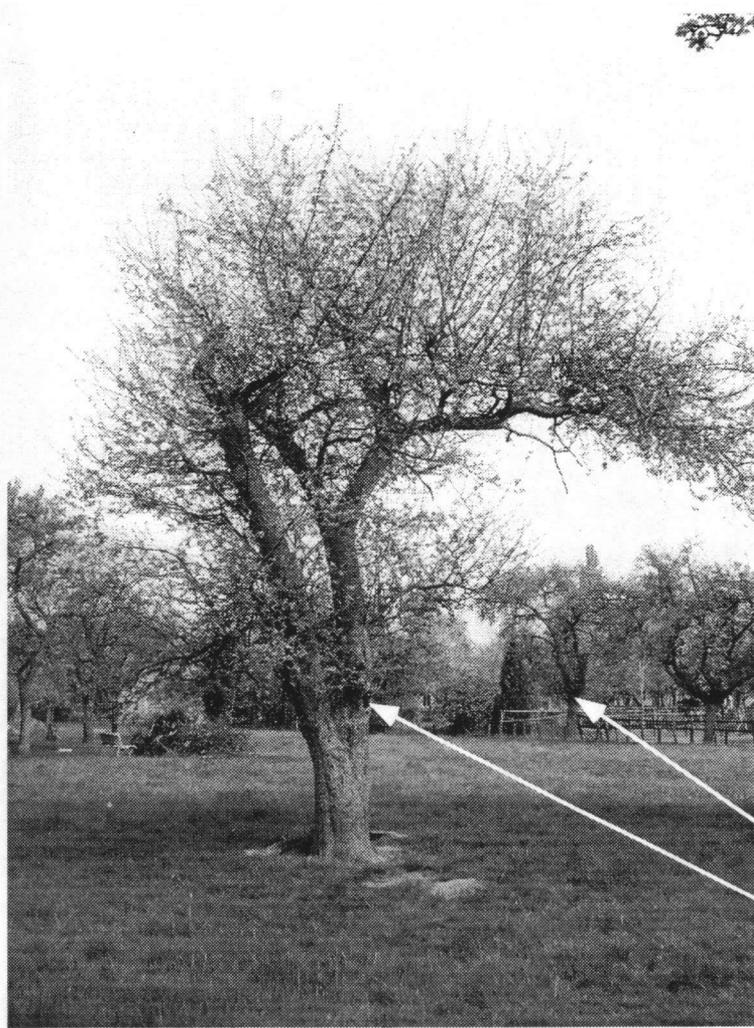
-  trees with nests
-  fruit trees
-  pollard willows
-  other trees
-  buildings
-  movements of birds from the "new nest"
-  single case of the movement of the bird flushed by approaching observer
-  movements of birds from the "old nest"
-  additional movements of birds from the "old nest" after hatching chicks
-  assumed border between the territories

Table 1. The food composition of both pairs of the little owl studied

| | | old nest | new nest | sum | |
|---------------------------------------|----------------------------|--------------------------|------------|------------|----|
| VERTEBRATES | | n | n | n | |
| Mammals | <i>Sorex araneus</i> | 1 | 0 | 1 | |
| | <i>Crocidura</i> sp. | 3 | 3 | 6 | |
| | <i>Crocidura russula</i> | 3 | 1 | 4 | |
| | <i>Microtus arvalis</i> | 14 | 6 | 20 | |
| | <i>Microtus agrestis</i> | 1 | 0 | 1 | |
| | <i>Microtus</i> sp. | 8 | 3 | 11 | |
| | Arvicolidae indet. | 6 | 1 | 7 | |
| | <i>Apodemus (Sylvemus)</i> | 2 | 1 | 3 | |
| | <i>Apodemus</i> sp. | 1 | 0 | 1 | |
| | Mammals indet. | 6 | 4 | 10 | |
| Birds | <i>Turdus pilaris</i> | 0 | 1 | 1 | |
| | <i>Turdus philomelos</i> | 0 | 1 | 1 | |
| total vertebrates | | 45 | 21 | 66 | |
| INVERTEBRATES | | | | | |
| Insects | | | | | |
| Dermaptera | | 59 | 14 | 73 | |
| Heteroptera | Corixidae | 1 | 0 | 1 | |
| Coleoptera larvae | Cantharidae | 1253 | 130 | 1383 | |
| | Hydrophilidae | 0 | 2 | 2 | |
| Coleoptera adults | Carabidae | <i>Pterostichus</i> sp. | 3 | 3 | 6 |
| | | <i>Nebria brevicolis</i> | 6 | 0 | 6 |
| | | <i>Amara</i> sp. | 0 | 1 | 1 |
| | | <i>Agonum</i> sp. | 3 | 0 | 3 |
| | | indeterminate | 53 | 9 | 62 |
| | Staphylinidae | 1 | 3 | 4 | |
| | Scarabaeidae | <i>Geotrupes</i> sp. | 0 | 1 | 1 |
| | | indeterminate | 4 | 1 | 5 |
| | Curculionidae | 36 | 5 | 41 | |
| | Hydrophilidae | <i>Helophorus</i> sp. | 5 | 0 | 5 |
| indeterminate | | 22 | 7 | 29 | |
| Elateridae | 2 | 3 | 5 | | |
| indeterminate | 0 | 1 | 1 | | |
| Molluscs | | | | | |
| | <i>Balea biplicata</i> | 0 | 4 | 4 | |
| total invertebrates | | 1448 | 184 | 1632 | |
| Frequency of earthworms (Oligochaeta) | | % 49.09 | % 33.33 | % 44.74 | |
| number of pellets | | n 55 | n 21 | n 76 | |

Table 2. Invertebrates caught in the insect-traps in the surroundings of both nests

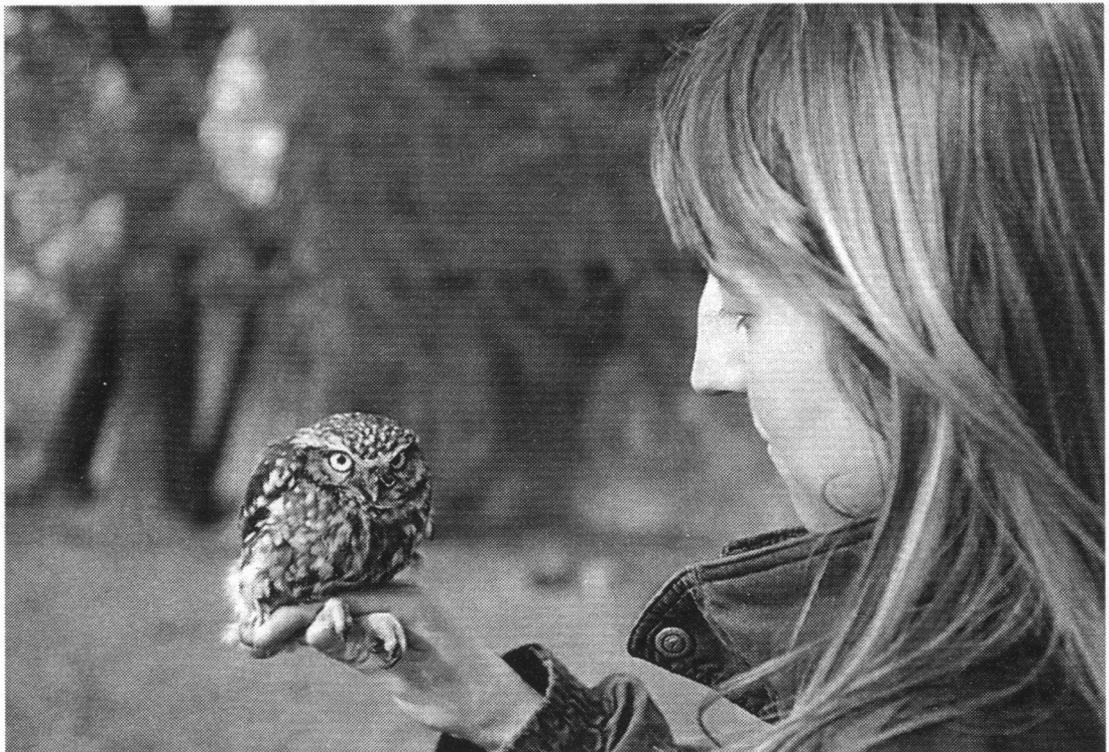
| INSECTS | | | n |
|----------------------------|----------------|--------------------------------|-----|
| Collembola | | | 8 |
| Coleoptera larvae | | | 3 |
| Coleoptera adults | Carabidae | <i>Pterostichus cupreus</i> | 1 |
| | | <i>Nebria brevicolis</i> | 6 |
| | | <i>Amara aenea</i> | 5 |
| | | <i>Harpalus tardus</i> | 1 |
| | | indeterminate | 1 |
| | | Staphylinidae | 11 |
| | Curculionidae | <i>Otiorhynchus singularis</i> | 1 |
| | | indeterminate (small) | 8 |
| | Elateridae | | 24 |
| | Chrysomelidae | | 2 |
| | Cryptophagidae | | 6 |
| Byrrhidae | | 1 | |
| Histeridae | | 1 | |
| Diptera larvae | Tipulidae | | 10 |
| | Stratioidae | <i>Beris</i> sp. | 1 |
| Diptera adults | Dolichopodidae | | 1 |
| Lepidoptera larvae | Geometridae | | 2 |
| Hymenoptera | Formicidae | | 108 |
| OTHER INVERTEBRATES | | | |
| Myriapoda | | | 4 |
| Arachnida | | | 99 |
| Acari | | | 3 |
| Crustacea | | | 50 |
| Earthworms (Oligochaeta) | | | 5 |
| total invertebrates | | | 362 |



The "old nest"

The "new nest"

1. Orchard with two nests studied



2. The author with a little owl



3. Two-week old chicks of the little owl from the "old nest".



4. Two-week old chicks of the little owl from the "old nest".

