OBSERVATIONS ON THE BARN OWL (TYTO ALBA GUTTATA) IN THE NETHERLANDS IN RELATION TO ITS ECOLOGY AND POPULATION FLUCTUATIONS

by

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CONTENTS

Introduction .................................................. 158
1. Biotope and habitat selection .......................... 159
   1a. Brief survey of the types of buildings used by the Barn Owl for nesting and roosting ........................................ 161
   (1) Farm buildings ......................................... 161
   (2) Churches ................................................ 162
   (3) Houses .................................................. 162
   (4) Castles and ruins ...................................... 162
   1b. Habitat selection in the Barn Owl .................. 163
2. Body weight, fat reserves and resistance to starvation in the Barn Owl .... 164
3. Breeding habits of the Barn Owl ........................ 168
4. Mortality bursts in European Barn Owl populations .......................... 170
   4a. The literature ......................................... 171
   4b. Taxidermist's records .................................. 174
   4c. A note on ringing data .................................. 176
5. Periodicity of mortality bursts in the Netherlands ......................... 177
7. Wanderjahre and the Barn Owl, and a solution to the problem of mass mortality bursts .............................................. 180
8. Disease and parasites as possible causes of population fluctuations in the Barn Owl, a digression .......................... 184
9. A note on the distribution and population of the Barn Owl in the Netherlands ..................................................... 187
Summary ......................................................... 192
Acknowledgements ............................................. 192
Literature ......................................................... 193

INTRODUCTION

The present work was carried out at the instigation of the State Institute for Nature Conservation Research (R.I.V.O.N.), Bilthoven, the Netherlands. The primary object of this study was an investigation into the possibility that an epidemic disease was responsible for observed large-scale fluctuations in the Barn Owl population in this country. At the same time, an investigation was made of the biology and ecology of this species. While in no way pretending to be complete, it is hoped that this study will throw some light on this interesting species and its
ecological significance. In the “Checklist” compiled by the Commission for the Netherlands Avifauna issued by the Netherlands Ornithological Union (1962), the Barn Owl (species 204) is described as being a “rather scarce” resident—which indicates numerically that its population is in the 250-2,500 breeding pairs class. The same publication restricts the forms found in this country to *T. alba guttata* BREHM. According to Voous (1960) the Barn Owl is, in the Netherlands, practically at the northern limit of its range—being primarily a bird of warmer regions with drier climates—and this fact should not be forgotten in a reading of the following. This point will be returned to later.

1. **BIOTOPES AND HABITAT SELECTION**

The Barn Owl is a true “Kulturbegleiter”—an associate species of the noösphere. Typical breeding sites are found in or near anthropogenic structures in the Netherlands, such as churches, farm buildings and ruins. These may be seen as extensions and replacements of the original habitat, which was almost certainly in rock-crevices. Trees are not often used for breeding but may be important in another connection (see below).

Popular nomenclature is often helpful in placing an animal in its surroundings. This is particularly so in the case of the Barn Owl where we find two types of names: topological (for example Barn Owl in English) or descriptive (such as Schleiereule in German). Most widespread among popular names is that of cat-owl, which is, however, applied more or less indiscriminately to several different species of owls. From the more northern provinces come the lugubrious designations of corpse-owl (lijkuil, lijkule) and churchyard owl (tsjerkhofsoele). More descriptive are the names from the southern provinces such as wreathed owl and golden owl. The official name, used throughout the country is the topological church owl (kerkuil).

The association of this bird with churches and graveyards—where in fact it is often to be seen—has lent an aura of ill-repute to it in some areas; attacks on it by farmers and farmworkers are often explainable on these grounds. That this is not new in the Netherlands can be seen from the painting by Hieronymous Bosch (?1450-1516) called the “Temptations of St. Anthony”, where the Barn Owl appears as a representative of the powers of darkness. In general it is still true to say that the Barn Owl is locally feared and the usual reaction is to drive it away or disturb the nest. It is not impossible that local gaps in the distribution can be attributed to this.
During our fieldwork, we were struck by the number of naturalists, farmers and ornithologists who were convinced of a decline in the numbers of this bird. To try and determine the validity of this impression, we made a study of the biotope and habitat selection of the Barn Owl.

**Figure 1.** Diagrammatic fieldsketches, showing Barn Owl habitats, associated with buildings. *Sketch 1* shows a fairly characteristic situation, to be found in many parts of the Netherlands. The important point here is the association of the Barn Owl with, firstly, human habitation and, secondly, with a territory showing irregularities e.g. differences of elevation—as here and in *Sketch 2*, where the same remarks apply. The nest-site is here, however, on a lower level than the hunting-territory (in Sketches 1 and 2, on the right of the drawing). *Sketch 3* gives an impression of the least common site for the Barn Owl (according to this survey); the alternations in territory here are provided by the canal banks, where many micro-rodents are to be found. *Sketch 4* illustrates another feature—the usage of open barns as roosting-posts along the hunting route. This farm was not used for nesting by the Barn Owl but the open barn (second building from the left) and the group of trees to the far right, were both used as resting-points on the hunting route. The hunting territory in this sketch is situated further to the right of the drawing.
in the Netherlands. The latter point must be emphasized since, as already pointed out, the bird is almost at its northern limit in this country and its biotope is unlikely to be typical for more than a small part of its total range.

Figure 1 shows sketches of typical farm buildings where the Barn Owl is at present known to roost and hunt over the surrounding countryside; it indicates the type of building where the owl is known to breed regularly as well (1). Of importance here are the factors of "openness" and a general lack of disturbance, for which the Barn Owl is particularly sensible in some areas. By "openness" we imply an easy access to the interior of the building by way of windows, holes, ventilation shafts, chimney stacks and suchlike. Roosting sites (Fig. 1 (4)) are frequently almost, or completely, open. In this sketch the roosting points are indicated with small circles; in practice these points are easily recognised by the characteristic dropping smears.

Modern farm buildings tend, on the average, to be more enclosed, partly for better product storage and partly for the exclusion of such "pests" as sparrows, starlings and especially pigeons. Similar measures can be seen in many churches where chicken-wire is used to close in belfry windows for example—to exclude similar "pests" and Jackdaws. The result is that the Barn Owl is denied access as well.

In Friesland, the presence of the Barn Owl and the Little Owl (Athene noctua) has long been encouraged by farmers as an anti-rodent measure. A typical feature of the large Frisean farmhouse is a decorative complex called the owl board (oeleboerd) on the front of the roof ridge. Centrally there is a large round opening called the owl hole (oelegat) giving access to the lofts of the building. Nowadays this may well be covered with glass, but there is usually sufficient room laterally for the owls to enter so that behind the oeleboerd the Barn Owl can and does nest and is not disturbed. For the sake of completeness, it should be added that this function of the oeleboerd, although endorsed by many Frisean farmers does not satisfy some historians, who prefer to see a religious allegorical significance. Be this as it may, both the Barn and Little Owl make a successful use of this structure.

1a. Brief survey of the types of buildings used by the Barn Owl for nesting and roosting

(1) Farm buildings

The most favoured sites are to be found in storage barns of some form or other. These usually have a ventilation system, roof windows or an
in Friesland, all giving access to the interior. Hay barns and ricks are not used for nesting, since these are disturbed at regular intervals. Nesting may take place in boxes intended for pigeons or doves, while a few farmers even provide special nesting boxes for the Barn Owl. Nesting may take place in barns on stacked straw, but more usually on the debris to be found on the floor between the rafters.

Open barns and impliment sheds (as shown in fig. 1 (4)) are used for roosting only.

(2) **Churches**

The usual Dutch name for the Barn Owl—church owl—indicates the association of the bird with church spires and belfries. While it is certainly true that it does occur in such places, it can be said that as many Barn Owls breed elsewhere as in churches in this country. In these buildings, however, a favourite site is the bell-loft, which is surprising in a bird with such sensitive hearing, but it does not appear to be unduly disturbed by bell-ringing. No correlation could be found between the height of the spire and the presence of owls: primary requisites are an easy access and a good hunting country in the surroundings. The nest itself can be found in a completely closed section of the loft, usually on the floor and in a corner.

(3) **Houses**

Although greatly attracted to anthropogenic structures, the Barn Owl avoids those where much disturbance occurs and for this reason, it is rare to find nests in inhabited houses. Once a house is left empty, however, the owl may appear very quickly. A typical case of this has been reported from Woerden (E. E. VAN DER VOO, pers. comm.), where, within a couple of months of it being left empty, a Barn Owl took up residence in the loft of a house. Deserted worker's barracks in the new polder of Oostelijk Flevoland were also quickly taken over by this bird, as will be detailed in a later publication.

(4) **Castles and ruins**

The majority of large castles, country houses and ruins in the Netherlands have been, or are, used by the Barn Owl as breeding and roosting sites. The more or less inaccessible roofs, gargoyles and gutters provide ample opportunity for nesting, while the parks surrounding such buildings usually provide ample hunting territory.

In ruins we see a return to the original habitat of this owl: crevice dwelling (which may in individual cases still take place in the Province
of Limburg), or under fallen walls. A good example of this is the ruined castle known as “Huys Ravenstein” (Prov. of Zuid Holland) and a good example of nesting in a ruined building with, however, a complete roof, is that of the Hamtoren not far from “Haarzuilen” Castle where this owl is also to be found.

In connection with the nesting of the Barn Owl in such buildings, we have often heard the remark that the bird nests high. Since the Barn Owl must enter a building where it can, it is usual that the roof and upper sections of a building are the first parts to be weathered, and thus provide access.

1b. Habitat selection in the Barn Owl

As already stated, the Barn Owl shows a preference for anthropogenic structures for its nesting and roosting sites, which it usually visits regularly year after year. The basic essentials for a good hunting territory in the surroundings of the building would appear to be the following:

1. The occurrence of relief—i.e. of difference in level.
2. Areas of rough ground—i.e. chiefly areas that are untended, or badly cared for.
3. An alternation of sparse and dense vegetation—e.g. coppices, grasslands and trees, bushes lining roads.

These features have been observed, in some form or other, in the neighbourhood of the large majority of nesting sites visited in this country. This type of country has also been established as being of importance for the occurrence of microrodent plagues (VAN WIJNGAARDEN 1957) and by ROOT (1957) for the occurrence of the White Stork (Ciconia c. ciconia) in the Netherlands. ROOTH (i.e.) stated: “As far as could be traced, there seems to be a special preference for habitats showing rather considerable differences of soil-types, altitude and ground water level at a relatively small distance”, and he added that the same applied in Spain and Schleswig-Holstein.

Although the habitat of the Barn Owl has not (as far as we are aware) been examined in detail in other European countries, the observations of ZABEL (1957) agree closely with our own in the Netherlands. ZABEL says (i.e.): “Sowohl Zechen- und Ziegeleigelände als auch Wald, Wiese, Bachtäler und Kulturlandschaft liegen in unmittelbarer Nähe der Scheune (where the nest was situated in his study). Diese Vielfältigkeit in der Landschaft trägt sicherlich zur Reichhaltigkeit des Speisezettels der
Eulen bei...” ZABEL’s designation of the Barn Owl biotope as “vielgestaltete” agrees with our own field observations.

Of the three points mentioned above, we can say that relief is doubly important, giving rise as it does, in the first place, to drier and wetter subterritories and hence to areas of vegetation which differ in their composition and density. Secondly, relief would appear to enhance the Barn Owl’s hunting, which, as is well known, is chiefly by sight. Rough untended areas allow prey populations to develop and the alternation of sparse and dense vegetation provides cover for several micro-rodent species as well as smaller species of birds which may be (locally) important as items of diet.

A detailed study of the diet of Dutch Barn Owls will be presented elsewhere, and it is sufficient here to refer to the exhaustive studies of UTTENDORFER (e.g. 1952) and to the publications of, e.g. KLAAS (1956), ZABEL (1957), BECKER (1958), while the classic paper by SOUTHERN (1954) on Strix aluco can be examined in comparison. It can be said here that, although certain species of micro-rodents are more common than others as prey, the variety of the latter indicates that for an “average” owl, a fairly diverse range of biotopes is hunted.

Of greater interest (especially in connection with a theory on the cause of the population fluctuations) is that our field observations indicate that, while hunting, the Barn Owl follows more or less fixed routes and that higher points in the hunting territory provide hunting or “look-out” posts where part of the territory can be surveyed. One of these posts may often serve as a “pellet post” also, where the owl expels undigestible food remains.

2. BODY WEIGHT, FAT RESERVES AND RESISTANCE TO STARVATION IN THE BARN OWL

Apart from a large number of publications which deal with the Barn Owl in an incidental fashion (e.g. ringing reports) there are also a number concerned with this bird directly and which are of interest and importance for the present study.

PIECHOCKI (1960) published a study on the weight-fat reserve balance of a number of owl species, including Tyto alba. SCHIFFERLI (1957) examined the mortality pattern of this species, comparing it with Strix aluco and derived further the mortality rates and life expectations for both species. The classic publication by SAUTER (1956) will be returned to later.

PIECHOCKI (loc.) published two tables of great interest reproduced here
as Tables 1 and 2, the latter examining the fat reserves of various species of owl, and from which it can be seen that the Barn Owl has the lowest percentages. While this is probably true of the Barn Owl throughout

TABLE 1

DIFFERENCE BETWEEN NORMAL (HEALTHY) WEIGHT AND STARVATION WEIGHT

<table>
<thead>
<tr>
<th>Species</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Net weight</td>
</tr>
<tr>
<td>Athene noctua</td>
<td>4</td>
<td>169</td>
</tr>
<tr>
<td>Asio otus</td>
<td>21</td>
<td>245</td>
</tr>
<tr>
<td>Tyto alba</td>
<td>25</td>
<td>291</td>
</tr>
<tr>
<td>Asio flammeus</td>
<td>5</td>
<td>347</td>
</tr>
<tr>
<td>Strix aluco</td>
<td>18</td>
<td>406</td>
</tr>
</tbody>
</table>

TABLE 2

FAT RESERVES AS PERCENTAGES OF TOTAL BODY WEIGHT

<table>
<thead>
<tr>
<th>Species</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Total weight</td>
</tr>
<tr>
<td>Athene noctua</td>
<td>4</td>
<td>196</td>
</tr>
<tr>
<td>Asio otus</td>
<td>2</td>
<td>277</td>
</tr>
<tr>
<td>Tyto alba</td>
<td>11</td>
<td>316</td>
</tr>
<tr>
<td>Asio flammeus</td>
<td>2</td>
<td>383</td>
</tr>
<tr>
<td>Strix aluco</td>
<td>2</td>
<td>487</td>
</tr>
</tbody>
</table>

its range (pers. comm. Professor Voous), this is of especial importance in the Netherlands, where, as already stated, the species approaches its northern limit. The reason for this will be shown later. Table 1 expresses the difference between the normal (i.e. healthy) weight of each of the owl species and their starvation weights. Once again, as might be expected, the difference for the Barn Owl is the lowest. Although Piechocki's samples are small, results by other workers, including the observations of the present writer, would seem to confirm their validity.

We may conclude from these two tables, as their original author did, that the low margin (normal-starvation) weight in the Barn Owl arises directly from its lower fat-reserves and it may well be that the fat-reserve
“safety factor” of 20% precludes long survival under certain unfavourable circumstances. If we plot the fat reserves against the difference in normal-starvation weight, as shown in Figure 2, the position of the Barn Owl becomes clearer: only _Athene noctua_ has a similar safety margin, but its fat reserves are much higher (an interspecies difference of 9.6%).

**Figure 2.** Graphical representation of data published by PIECHOCKI (1960), and showing the correlation between percentage fat reserves (F%) and percentage difference between normal-starvation weight (W%). The Barn Owl (_Tyto alba_) has a coordinate differing sharply from that of the other four owl species. Based on PIECHOCKI (1960).

_Asio flammeus, A. otus_ and _Strix aluco_ whose values are similar, have lower fat-reserves than _Athene noctua_, but the safety margin between normal and starvation weight is displaced along the positive axis of the graph. We may note here, in anticipation of later remarks that it is interesting to note that the most typical clinical finding during Barn Owl mortality bursts is a striking emaciation.

SCHIFFERLI (1957) presented observations which corroborate these findings. We have summarised his results in Table 3. Here we have observations for two species only (_Tyto alba_ and _Strix aluco_), but as we
Table 3
Annual mortality and life expectation in *Strix aluco* and *Tyto alba*
Based on Schifferli (1957)

<table>
<thead>
<tr>
<th></th>
<th><em>Strix aluco</em></th>
<th><em>Tyto alba</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mortality in 1st. year</td>
<td>47%</td>
<td>64%</td>
</tr>
<tr>
<td>Mortality in 2nd. year</td>
<td>45%</td>
<td>54%</td>
</tr>
<tr>
<td>Mortality from 3rd. year</td>
<td>24%</td>
<td>39%</td>
</tr>
</tbody>
</table>

Life expectations, in years

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>From 1st. year</td>
<td>2.2</td>
<td>1.3</td>
</tr>
<tr>
<td>From 2nd. year</td>
<td>2.7</td>
<td>1.7</td>
</tr>
<tr>
<td>From 3rd. year</td>
<td>3.7</td>
<td>2.1</td>
</tr>
</tbody>
</table>

have seen from Piechocki's results, *S. aluco* would appear to be typical of the group (*S. aluco, Asio flammeus* and *A. otus*) When we translate the life expectations into a graphical form (Fig. 3) the situation of the

Graph 1

Graph 2

\[ \Delta = \text{Tyto alba (Barn Owl)} \]
\[ \bullet = \text{Strix aluco (Tawny Owl)} \]
\[ \Phi = \text{difference between life expectation rates, per year} \]

**Figure 3.** Graph 1. Yearly mortality figures (based on data from Schifferli 1957). It will be seen that that of the Barn Owl (\( \Delta \)) is at a higher level than that of *Strix aluco*. Graph 2 shows in graphical form the life expectation rates for both species of owls. Here the opposite is true; the expectation for *S. aluco* is higher than that for the Barn Owl; in addition, the relative difference (\( \Phi \)) increases with time. **Key to abbreviations**: %M = mortality percentage (based on ringing results) in year (Y) 1, 2, or 3 of life. \( L_{ex} \) = life expectation in years, in year (Y) 1, 2, or 3. \( \Phi = \text{difference between life expectation rates (S. aluco—T. alba) per year.} \)
Barn Owl is clear, and further more the relative difference in life expectation increases with time.

Schifferli (1957) also made a study of the mortality pattern of these two owls (see Table 4) based on ringing results. Figure 4 is constructed from his results, while superimposed is a graph derived from the present author's studies on 810 Barn Owls from the Netherlands. The fit is excellent and agrees further more with one presented by Novrup's (1946) data. This mortality pattern is connected on the one hand with the foregoing considerations of the relationship between fat reserves and starvation on the one hand and the breeding habits on the other. All three are facets on the main problem: that of the origin of mass mortality outbursts in Barn Owl populations.

3. BREEDING HABITS OF THE BARN OWL

The picture of the breeding habits of the Barn Owl in Switzerland given by Schifferli appears in general to be valid for Netherlands conditions also, as far as our observations are concerned. Four to six eggs (Schifferli 1957: 201 eggs in 38 clutches, an average of 5.3 eggs) are produced in the months March and April, the female brooding as soon as one egg is laid. At the end of a period of about 30 days the young hatch, and may differ in age at hatching by several days. Remaining in the nest for about 8 weeks, the young are fully fledged after three months when they leave the parent territory and begin to hunt independently—i.e. around the beginning of August.

In a year with a high prey density, a second brood is produced, the eggs being laid in June to August. The second clutch does not appear
Figure 4. The monthly mortality pattern of the Barn Owl, according to three sources. (A) Original, based on the deaths of 810 owls in the Netherlands. (B) Based on data given by Novrup (1946) from a mortality “burst” in Denmark (see text). (C) Based on ringing returns in Switzerland, data from Schiffnerli (1957). The characteristic pattern is to be found in all three graphs, with February having the highest death-rate. Deaths sink to a minimum in summer, rising once more in early autumn. The graph derived from Schiffnerli’s figures is based on the returns of young birds only, see text. Graphs (B) and (C) give the number of dead owls found per month, while graph (A) expresses this as a percentage.

(under Netherlands conditions) to differ from the first in size, so that we may presume on the basis of the foregoing, an average nest of 5.3 eggs is once again present. Schiffnerli’s observations indicate that an average of 4.4 young are raised per breeding pair of Barn Owls, per clutch laid.

This implies that, in a “micro-rodent” year, an average of about 9 young will be produced by each breeding pair of owls, with which our observations in this country agree.

Young from the second brood will be hunting independently some time in November. Schiffnerli’s observations have shown, and once more our own from the Netherlands agree with this, that the mortality of young (i.e. first year owls) gradually increases from the beginning of the winter (October-November) reaching a peak in March (see Fig. 4).

Concluding this section, we can now offer the following preliminary
hypothesis for the winter mortality of the Barn Owl. *Tyto alba* has a low safety margin between its normal fat reserves and its starvation fat level. This, although true for the whole range of the species, is of little importance in many parts of its distribution, and also during the summer months (and is of no importance in young hatched in spring, these being fed by the adults at the nest). The low margin may also be of little importance during a mild winter, but in a normally cold winter the fat reserves may be very quickly exhausted (Piechocki (1960) suggested in 8 days). This exhaustion of the fat reserves may be due to the following factors, and particularly in recently fledged young, whose fat reserves will be lower than in adults:

1. Intense cold, when reserve fat is necessary for homostasis.
2. Lack of prey, when the reserves are used up during exceptionally long hunting periods; or a combination of 1 and 2.

Snow cover, sometimes suggested to be the sole factor responsible for the winter mortality, may well be of importance in camouflaging the prey, in increasing the length of the hunting periods and inducing, via some form of “snow blindness”, a type of stress condition, although the latter is not proven. Before going into further details, however, it is first necessary to consider the mortality bursts themselves in some detail.

4. MORTALITY BURSTS IN EUROPEAN BARN OWL POPULATIONS

As we have stated in the Introduction, the starting point of this investigation was the probable cause(s) of observed mass fluctuations in Dutch Barn Owl populations. That such bursts occurred has been known for some time, the earliest publication on this subject in the Netherlands dating from 1922. This was followed by a series of publications directly, or indirectly, concerned with the same problem. As can be seen from this chapter heading we shall not confine ourselves to the Netherlands, however, since it soon became apparent that the problem was of wider occurrence and significance.

There were three sources of information available about the population of Barn Owls both past and present. In the first place, the literature itself, which goes back to 1922 as already stated. Secondly, the summary of taxidermists record-books kept by the Ministry of Education, Arts and Sciences in The Hague and kindly put at my disposal through Messrs. C. J. S. Ruitter and H. J. A. de Reuver. These results were later compared with a third information source, which is however, less reliable than the preceding, namely the ringing records of the "Vogeltrekstation" in Leiden. Although these results are, for the most part, already published,
the author is grateful to Mr. J. Taapken for additional information on several points. In addition to these sources there were a number of observations arising from the authors work in the Netherlands itself.

4a. The literature

The publication mentioned above as dating from 1922 was issued by the Plantenziekttekundige Dienst (hereafter called the P.D.) in Wageningen. It concerned a mortality burst in the winter of 1921-22. Further information about this period was given in a second publication by the P.D. in 1932. Both these publications presented a map of the distribution of dead owls, reproduced here in Figure 5. The anonymous writer(s) of the 1922 publication came to the conclusion that the mortality (which involved at least 260 birds) was confined to clay soils and could not be correlated with the weather during that period. The mortality pattern is as shown in Figure 4 (a & b): February-March 50; March approx. 140; April and later 60 dead Barn Owls. An (unspecified) number of Owls were sent to the then State Serum Organisation in Rotterdam and to the Pathological Institute of the Veterinary Faculty at Utrecht. The post-mortem findings were, in both cases, that no disease and certainly no form of infectious disease, was responsible, rather the cause was seen as starvation as a result of the severe winter. The 1932 publication added little to this, but came to the conclusion, en passant, that the Barn Owl could very possibly be termed an "alluvial species".

In 1935 C. G. B. Ten Kate published an account of the following mortality burst which took place in the winter of 1934-35. In this case we have a detailed list of the places where dead owls were found and from this we have made a map (Fig. 6). It was estimated at the time that some 287 owls died in this period, but later this figure was shown to be higher. Ten Kate was responsible for the introduction of the coccidiosis hypothesis in the Netherlands, but withdrew this a year later (Ten Kate 1936).

Van IJzendoorn (1948) published an account of the mortality burst in the winter of 1947-48 which, in the Netherlands was particularly marked in the Wieringermeer area, although in fact the burst was certainly not confined to the Netherlands.

Between these two works another must be mentioned by the former author: Ten Kate (1946) described a mortality burst in the winter of 1944-45, which took place in a polder landscape (similar to that of the Wieringermeer). In this case some 50 owls were involved.

In 1952 Van IJzendoorn published a survey on Barn Owl disease
which summarised some of the literature on this subject. The author went into great detail about coccidia and the possibility of their being the cause of death which, however, he doubted. The interesting point

**Figure 5.** Map showing the distribution of dead owls in the winter of 1921-1922. Based on maps published by the Plantenziektenkundige Dienst (1922) and (1932).
FIGURE 6. Map showing the distribution of dead owls in the winter of 1934-1935. Constructed from data published by TEN KATE (1935). The figures "30" and "40" indicate that that number of owls was brought into a central point in that area. In a later note TEN KATE (1935) amended these figures.

in this publication is that VAN IJZENDOORN considered the disease to be a population regulation factor.

A number of works from other European countries deserve a short
mention here, since they shed some light on the problem of the occurrence and dynamics of the mortality bursts. Kühnau (1929) reported a burst from the Breslau area and was the first as far as we are aware to offer coccidiosis as a possible explanation for the phenomenon, although a specific organism was not found until 1932, and then in America! Emelis (1935) wrote about the same mortality burst as Ten Kate (1935), but in this case from Schleswig-Holstein, and both Niethammer (1938) and Stresemann (1935) considered the same burst as it occurred in Germany. The earliest documented account from Germany is much earlier, however, being that by Kleinschmidt (1912). Schüz (1948) examined the population density of the Barn Owl in the Württemburg area which was at a low level, as a result of the winter burst of 1947-48 (see Van IJzendoorn 1948). A later mortality burst in the winter of 1950-51, involved most of Europe and was considered by Krampitz (1954); his observations are confirmed by the author's study in the Netherlands.

From Denmark come two publications of interest: Novrup (1946) described the winter mortality of 1944-45 and Christiansen (1949) gave a general survey of avian disease in Denmark, mentioning the problem of the Barn Owl disease.

Although a census of the Barn Owl population in the British Isles was carried out in 1932 (Blaker 1932), there are no records known to us from that country of similar mortality bursts, unless an incidental remark by Witherby et al. (e.g. 1924) may be interpreted as the occurrence of a burst in the neighbourhood of Norwich in 1891.

4b. Taxidermists records

Table 5 shows the number of Barn Owls handled by taxidermists in the Netherlands from 1937 to 1957. These figures have been translated into a graphical form in Fig. 7. Before discussing this, the following reservations must be made:

(1) The figures presented for the war years are probably suspect in their accuracy.

(2) Not all Barn Owls dying in a mortality year will come into the hands of taxidermists.

(3) The peak shown for 1950-1952 cannot be further subdivided, since the original records have now been destroyed by the Ministry of Education Arts and Sciences.

(4) Since the war the demand for mounted birds has increased and, unfortunately enough, is still increasing. The rising tendency in the
The total number of owls handled by taxidermists may well be partly due to the dictates of fashion. The graph (Fig. 7) shows a number of peaks, indicating that "for some reason or other" more Barn Owls died in that period than otherwise. The first peak is in 1938-39, when 167 owls were handled and mounted (see Table 5). Ignoring the war years, the following peak is in 1947-48 when 488 owls were mounted (agreeing with the literature: VAN IJZENDOORN 1948). The following peak is misleading, as already stated,
### Table 5

The number of Barn Owls handled by taxidermists per year, over the period 1937-1957, throughout the Netherlands

<table>
<thead>
<tr>
<th>Period</th>
<th>Number of Barn Owls</th>
<th>Running total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1937-1938</td>
<td>82</td>
<td>82</td>
</tr>
<tr>
<td>1938-1939</td>
<td>167</td>
<td>249</td>
</tr>
<tr>
<td>1938-1939</td>
<td>167</td>
<td>249</td>
</tr>
<tr>
<td>1939-1940</td>
<td>72</td>
<td>321</td>
</tr>
<tr>
<td>1940-1941</td>
<td>39</td>
<td>360</td>
</tr>
<tr>
<td>1941-1942</td>
<td>36</td>
<td>396</td>
</tr>
<tr>
<td>1942-1943</td>
<td>49</td>
<td>445</td>
</tr>
<tr>
<td>1943-1944</td>
<td>133</td>
<td>578</td>
</tr>
<tr>
<td>1944-1945</td>
<td>135</td>
<td>713</td>
</tr>
<tr>
<td>1945-1946</td>
<td>230</td>
<td>943</td>
</tr>
<tr>
<td>1946-1947</td>
<td>292</td>
<td>1235</td>
</tr>
<tr>
<td>1947-1948</td>
<td>488</td>
<td>1723</td>
</tr>
<tr>
<td>1948-1949</td>
<td>248</td>
<td>1971</td>
</tr>
<tr>
<td>1949-1950</td>
<td>309</td>
<td>2280</td>
</tr>
<tr>
<td>1950-1951</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1951-1952</td>
<td>1130</td>
<td>3410</td>
</tr>
<tr>
<td>1952-1953</td>
<td>300</td>
<td>3710</td>
</tr>
<tr>
<td>1953-1954</td>
<td>488</td>
<td>4198</td>
</tr>
<tr>
<td>1954-1955</td>
<td>362</td>
<td>4560</td>
</tr>
<tr>
<td>1955-1956</td>
<td>160</td>
<td>4720</td>
</tr>
<tr>
<td>1956-1957</td>
<td>347</td>
<td>5067</td>
</tr>
</tbody>
</table>

representing as it does two years summed. Even when the average is taken (as has been done in the graph, Fig. 7) it is clear that a very large number of owls died in the period 1950-1952. Fortunately, we know from other sources that the bulk of the deaths were in 1950-51. The 1953 peak is not recorded in the literature (once more 488 owls were mounted), nor is that from 1957 (347 owls). These years will be returned to below.

4c. A note on ringing data

The *Rijksmuseum voor Natuurlijke Historie* in Leiden has carried out a ringing programme since 1911. The total number of birds ringed, per species, was published in 1940. Since that date detailed reports per species, per year have been issued.

We applied two treatments to this data: in the first place the total number of Barn Owls ringed in the period 1911-1940 was used to construct a hypothetical “working average” for the number ringed per year and this has been compared with the actual number ringed per year since 1940. In the second place the detailed results have been compared with the working average to construct a “discrepancy graph”, as shown in
Figure 8. The purpose of this is to indicate whether, on this basis, more or less owls have been ringed in a given year than on the average. A number of Dutch ornithologists have expressed grave doubts as to the validity of any conclusions drawn from this method, pointing out that the activities of one ringer who might prefer to ring owls to other birds, would distort the picture obtained, and that the number of birds ringed in any one year depends on the activity and number of ringers. While this may be true, it is interesting to note that once again a number of peaks are obtained indicating that more owls have been ringed on the average than in other years. The troughs in the discrepancy graph agree with the mortality bursts of 1947-48, 1950-51 and the unrecorded mortality in 1954-55 as shown in the taxidermist record graph. It should be remembered that troughs in the graph shown in Figure 8 are subject to a lag of one breeding season under normal conditions, i.e. Figures 7 and 8 are out of phase by one breeding season.

5. PERIODICITY OF MORTALITY BURSTS IN THE NETHERLANDS

To obtain any idea of the periodicity shown by the mortality bursts mentioned above, it is necessary to consider all sources of
information simultaneously. We make the following assumptions here:

1. That a marked increase in the number of Barn Owls handled by taxidermists in a particular year indicates an increased mortality in that year.
2. That the publications cited are reliable in their datings.
3. That troughs in the number of ringed owls are subject to a lag of one season if they are correlated with the foregoing sources of information.

Table 6 shows the years in which mortality bursts began, according to the three sources mentioned and the years in italics shown those years

<table>
<thead>
<tr>
<th>Taxidermist records</th>
<th>Ringing records</th>
<th>Literature records</th>
</tr>
</thead>
<tbody>
<tr>
<td>1938</td>
<td>1938</td>
<td>1921, 1934</td>
</tr>
<tr>
<td></td>
<td>1941</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1944</td>
<td>1944</td>
</tr>
<tr>
<td></td>
<td>1945</td>
<td></td>
</tr>
<tr>
<td>1947</td>
<td>1947</td>
<td>1947</td>
</tr>
<tr>
<td>1950</td>
<td>1950</td>
<td>1950</td>
</tr>
<tr>
<td>1953</td>
<td>1953</td>
<td></td>
</tr>
<tr>
<td>1956</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

where at least 2 sources agree. These years are: 1944, 1947, 1950, 1953— with perhaps an earlier period in 1938. We also know that a burst began in 1921 and 1934 from the literature and our observations have shown that another burst took place in 1958-59. Taking all these years into consideration, we see signs of a three-year cycle. At this stage, however, we do not wish to give much weight to this, since, as Slobodkin (1961) pointed out, the mean length of a population cycle may be expected to vary between 3 and 8 years, as a function of the census accuracy. Slobodkin (l.c.) has further shown that the most likely length for a population cycle is three years. It is therefore unreasonable to assume that a three-year cycle has been demonstrated for the Barn Owl. This periodicity must be seen, we believe, in the light of another factor—that of fluctuations in the micro-rodent populations of the Netherlands.
6. Micro-rodent cycles in the Netherlands and their relationship to fluctuations in the Barn Owl population

Data concerning the occurrence of micro-rodent cycles in the Netherlands has been collected by Van Wijngaarden (1957, 1957a) and in the first of these publications he gives a tabular summary of the occurrence of "plagues" through the period 1800 to 1956. For further details, the reader is referred to the paper in question; for the purposes of the present study the most important years have been extracted from Van Wijngaarden's table and are presented in a different form in Table 7, together with the locality where the micro-rodent plague took place. In addition we have added to this table such Barn Owl mortality bursts as may be reasonably considered to be associated with these plagues.

**Table 7**

<table>
<thead>
<tr>
<th>Owl mortality period</th>
<th>Micro-rodent plagues</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Years</strong></td>
<td><strong>Areas</strong></td>
</tr>
<tr>
<td>1921/22</td>
<td>Friesland, N.-Holland, N.-Brabant</td>
</tr>
<tr>
<td>1934/35</td>
<td>Friesland, Overijssel</td>
</tr>
<tr>
<td>1944/45</td>
<td>N.O.Polder</td>
</tr>
<tr>
<td>1947/48</td>
<td>Wieringermeer</td>
</tr>
</tbody>
</table>
| 1950/51              | Throughout Europe        | 1949/50 | Throughout most of the Netherlands.

We can in fact see a good fit between the two populations in their fluctuations. In particular we would emphasise here the micro-rodent peak in the Wieringermeer and the associated Barn Owl mortality burst since this micro-rodent cycle is, in fact (or was at the time), out of step with the rest of the neighbouring country. When we consider literature from outside the Netherlands we can see that such micro-rodent plague years occur with regular frequency throughout the European continent and are very frequently correlated from one country to another. In Scandinavia, for example, micro-rodents were plentiful in the following years: 1941-42; 1944-45; 1948-49-50 and 1952-53 (see Hagen 1956). Taking one year as an example, a high micro-rodent density was observed in the following countries: Denmark, Germany, Switzerland, Scandinavia
and the Netherlands. It seems possible, therefore, although not proven, that there is some large-scale synchronisation of micro-rodent plagues through Europe as a whole which would account for the simultaneous appearance of Barn Owl mortality bursts if these are correlated.

It is important here, however, to underline the significance of the remarks by HAGEN (l.c.) on the relative significance of micro-rodent densities. According to him the critical frequency would appear to be approximately 2 (using OLSTADS units; see WILDHAGEN 1952) for boreal and arctic owls. Conditions appertaining in years of micro-rodent abundance may exceed 10 units on the same scale and are in fact excessive for the needs of their predators. Furthermore a year not recognisable as a “peak” or “plague” year may in fact stimulate the owls as if it was, in other words, when the micro-rodent frequency exceeds a given threshold value (which may be different for each species of owl?).

We may conclude from this that relatively small changes in micro-rodent density may be sufficient to stimulate both a functional and a numerical response on the part of the owls, which effect would be greater in species which mature in their first year, such as the Barn Owl.

Although some correlation can be found between micro-rodent peaks and Barn Owl population peaks (as the result of both a functional and numerical response), this correlation may be shifted or masked by:

(1) The occurrence of a year which is in fact not a recognisable peak, but which functions as one as far as the Barn Owl is concerned and which can stimulate a second brood.

(2) Micro-rodent cycles may often have a duration other than three years and these irregularities would appear to depend largely on climatic conditions (HEROLD 1954; MAERCKS 1954; see also TEUNISSEN (1937) and VAN WIJNGAARDEN (1957) for examples of asynchronous cycles in the Netherlands).

Concluding we can say from the evidence that we have, it seems likely that there is some synchronisation of micro-rodent cycles in Europe and that these peaks precede the mortality bursts in the Barn Owl populations. A study of the occurrence of micro-rodent population dynamics throughout Europe would be of great interest in this connection and would serve to illuminate several problems centring around the population fluctuations of several species of owls and raptors.

7. “WANDERJAHRE” AND THE BARN OWL, AND A SOLUTION TO THE PROBLEM OF MASS MORTALITY BURSTS

The last remark in the preceding chapter brings us to the consideration
of another interesting phenomenon which was dealt with by Sauter (1956) in some detail in her study on the ecology of the Barn Owl based on ringing results. She found that certain years could be designated as *Wanderjahre*, i.e. years in which, for some reason or other, Barn Owls ringed in Germany spread out over the country and over the rest of the European continent as well. The *Wanderjahre* were 1928-29; 1934-35; 1937-38; 1947-48; 1950-51 and 1952-53. We shall now examine some facts known about these years from other sources.

1928-29: Kühnau reports a mortality burst in Germany. Dr. M. F. Mörzer Brujin (pers. comm.) observes large number of Barn Owls sitting on the ice of the frozen Zuider Zee. Stresemann (1930) reports on a mortality burst also.

1934-35: Ten Kate reports a mortality burst in the Netherlands; Eméis (1935) one in Schleswig-Holstein; and Niethammer (1938) and Stresemann (1935) one in Germany.

1937-38: No known observations on a mortality burst in this period, but the graph shown in Figure 7 shows a small peak here which may be a reflection of a mortality burst.

1947-48: There was a widespread mortality during this winter throughout most of Western Europe (see e.g. Van IJzendoorn 1952).

1950-51: Once more a high mortality over most of Europe (Krampitz 1953: see also Fig. 7).

1952-53: Little is known about this period (Sauter 1956). It is not clear from Figure 7 if the peak there can be ascribed to this burst.

Krampitz (1954) suspected that a *Wanderjahr* was, at the same time, a *Sterbejahr*, i.e. a year when a mortality burst, as we have called it, occurred. Sauter (*loc.*) had reservations about this, however, since she wished to define the latter term more carefully and divided a *Sterbejahr* into three types:

1. Mortality chiefly among young birds: e.g. 1938-39.
2. Mortality chiefly among older birds: e.g. 1943-44; 1947-48; 1950-51.
3. Mortality involving both classes: e.g. 1952-53; 1939-40 (?).

A *Wanderjahr*, according to Sauter, involves displacements of young birds chiefly, whereas older birds are not so frequently affected. Furthermore as Sauter suggests and Schifferli (1957) has shown, and as our observations confirm, the first winter is always more or less a *Sterbewinter* for the Barn Owl. Krampitz (1954) would appear to define the displacements of the Barn Owl population as "sinnlose Entfernung", due perhaps to some form of internal drive. This is, of course, reminiscent of stress syndrome but has, as far as we are aware, never been indicated in birds.
Sauter's conclusions (translated and shortened) were as follows:

(a) The dispersal during a Wanderjahr involves chiefly birds one year old, although older birds can also be involved.
(b) The dispersal is an autumn phenomenon, terminating around the middle of November.
(c) There is no direct correlation between dispersal and weather conditions.
(d) There is a connection with micro-rodent density.
(e) Years with a low micro-rodent density are not, however, necessarily dispersal years.
(f) Years with a high Barn Owl population are also not necessarily dispersal years.
(g) There must be a combination of two factors, a high density of Barn Owls and a falling density in the micro-rodent population.

We must examine this last point in more detail. Van Wijngaarden has shown that the majority of micro-rodent cycles in the Netherlands have a three year duration. The graph given by him is reproduced in Figure 9. This indicates that, in general, the third summer and autumn are "crash" periods in the cycle in which drastic reductions take place in micro-rodent density. In the spring and early summer, however, the density may be high enough to stimulate a second brood in the Barn.

![Figure 9](image-url)

**Figure 9.** Fluctuations in the density of Continental Vole populations during a three-year cycle, according to Van Wijngaarden (1957). $N_r$ = numbers of micro-rodents. The $L_c$ value is the critical value; above this level, voles will be noticed as a "plague".
Owl population. When this occurs, we must return to the considerations already mentioned in the chapter on the breeding of the Barn Owl (see page 169); in other words, we may expect an excess number of young (recently fledged) owls to be hunting in the months November and December. By this time, the density of micro-rodents will have fallen or will be falling (see Fig. 9; a detailed consideration of the situation in the Netherlands will be published elsewhere), and the young owls will be forced to hunt longer and further. It seems to us that we can see this dispersal as a density-dependent mechanism which operates as a result of the numerical response by the Barn Owl population to the increased density of the prey population. The high mortality which then follows the dispersal is explainable from the findings of Piechocki (1961) and has already been outlined above.

It seems not unreasonable to suggest the following mechanism whereby the fluctuations in Barn Owl populations operate. We postulate a feedback mechanism operating within the population and controlled by the prey density of the owl itself. The tendency would be towards a theoretical steady-state population, based on a steady-state prey population level. The feedback may be supposed to act on the hormonal regulators of the Barn Owl in such a way that, with increased prey density, a numerical response by the breeding Barn Owls occurs so that extra clutches or more eggs per clutch are produced. The operation of the feedback may be through the characteristic flight-pattern of the owl, on the number of prey caught per flight along the more or less fixed hunting route. This could also be expressed as the number of successful stops per route flight, which will be higher when the prey density is higher (This principle is identical with, for example, a census of earthworms in a lawn, or songbirds in a wood).

There is evidence to show that response in the Tawny Owl to prey density is similar (in principle) to that in the Barn Owl (Southern 1954) and the conclusions offered by Southern as to the dynamics of breeding in the Tawny Owl suggest a feedback mechanism very strongly. Generally speaking, we can suggest that the mechanism works in the following manner.

There are three conditions in which it operates in three different ways:
(a) A high prey density promotes (permits) breeding.
(b) A continued high density (or rapidly rising density) stimulates the reoccurrence of the breeding pattern (numerical response), or modifies it in some way.
(c) A low prey density checks (inhibits) breeding.
Since the feedback is coupled to a fluctuating prey population, it will itself fluctuate. At a certain point the owl oscillation will be high, while that of the prey falls or is at a minimum (as shown by practical observations and records), so that an out of step condition arises. In this way, the number of young Barn Owls hunting in a given winter reflects the micro-rodent density some 3-5 months earlier, i.e. when breeding began.

When the out of step condition occurs, there are two main alternatives:
(a) A change of diet, as in the Tawny Owl in the autumn and summer.
(b) An increase in hunting activity (an attempt, that is, to increase hunting efficiency)

b1. by means of more flights over the same hunting territory or,
b2. by means of an expansion of the hunting territory. In extremo, this signifies a Wanderjahr.

Since the Barn Owl is unable to make any radical changes in the constitution of its diet, the alternatives presented under b1 and b2 above are the logically expected reactions. The main solution or attempted solution to the problem is the attempted increase in the probability of kills by increased flight and increased flight radius. Here lies, in fact, the truth of van IJzendoom's remark that "owl invasions and owl mortality frequently go together", as suspected by Kramitz (1953).

When the prey density is low over very large areas, as seems possible, the increased flight activity leads to subsequent excessive demands on the already marginal fat reserves and, finally, to starvation and exhaustion. Cold spells will only serve to heighten this effect.

At this point, and in our opinion, at this point only, will disease become of importance as the actual cause of death. While parasites are always to be found in association with all types of birds, the healthy specimens will, as a rule, have little or no trouble with them, whereas weakened birds may well succumb to their parasites. It is hardly surprising that coccidia, bacteria and so forth have been found in Barn Owls offered for post-mortem examinations. These aspects will be considered in a separate chapter below.

8. DISEASE AND PARASITES AS POSSIBLE CAUSES OF POPULATION FLUCTUATIONS IN THE BARN OWL, A DIGRESSION

It should be made clear at this point that the author, as a parasitologist, was primarily interested in examining the occurrence of pathogens and assessing their role in causing fluctuations in Barn Owl populations. From the foregoing, it is clear that we cannot expect that any pathogens
will, in fact, at first hand greatly affect the density of the Barn Owl. It is necessary, however, to establish just how parasites and pathogens in general may be expected to function, particularly because there are a number of misconceptions of long standing.

Two main groups of pathogens can be considered as being involved in mass mortality phenomena in avian populations: bacteria and coccidia (under certain circumstances helminth parasites may also be involved, but not in the case of the Barn Owl).

**Bacteria**

Rooke (1946) observed an acid-fast disease in the Barn Owl resembling a form of tuberculosis. Harrison (1950, in discussion) regarded this as being of importance in the dynamics of avian populations in general. Two types of acid-fast organisms can be considered here, *Mycobacterium avium* and *M. muris*.

*Mycobacterium avium*, from the domestic fowl, can infect many species of birds if they come into contact with the carrier fowl as well as several species of mammals. The prerequisite for infection is in general crowding. However, this is not characteristic of the Barn Owl, although it is by no means impossible that a pair of owls on a farm may become infected in this way. The infection route may then pass via fowl or doves to the owls. It is certainly impossible, on the other hand, that a national population of Barn Owls should be affected in this manner and more or less simultaneously.

*Mycobacterium muris* is of more interest since it was first found in voles in Great Britain (Wells 1937). It was later shown (Wells 1946) to be distributed in three species of micro-rodents, *Apodemus sylvaticus*, *Microtus agrestis*, *Clethrionomys glareolus* and in the shrew *Sorex araneus*,—four important species of Barn Owl prey. Artificial infections have so far been limited to other rodents and the rabbit. There are, it would seem, no significant antigenic relationships with *M. avium* and although avian tuberculosis can occur in mammals, it has never been shown that *M. muris* can infect birds. Should this prove to be the case, then an interesting possibility may be considered: a mass infection of the Barn Owl would be understandable in years with a high micro-rodent population of one or more of the carrier species listed above. In America there have been a number of observations on tuberculosis and virus diseases of birds, but it must be admitted that their true significance is doubtful. Certainly, in the case of the Barn Owl, we must regard these pathogens as being excluded from the list of possible causes of mass mortality.
Coccidia

The theory that coccidia are involved in the Barn Owl disease is, on the other hand, obstinate and still persists in many places. Originating in Germany, the idea spread rapidly to many other countries. We hope to show, however, that this hypothesis is untenable and is based on an ignorance of the true nature and epidemiology of these organisms.

The coccidian in question is *Isospora buteonis* HENRY 1932, originally described from *Buteo swainsoni, B. borealis, Accipiter cooperi, Falco sparverius* and the owl *Asio flammeus*. EMEIS (1935), STRESEMANN (1935), NEISCHULZ (1935), CHRISTIANSEN (1949) and several other workers, including TEN KATE originally (but he later rejected the idea; 1935) have all attributed Barn Owl mass mortality to this pathogen. For example NIETHAMMER (1938) made the much quoted remark: “In manchen Jahre (zuletzt Winter 1934-1935) setzt Gegendweise ein Massasterben von Schleiereulen infolge von Coccidiose ein, die *Eimeria stediae* zugeschrieben und wahrscheinlich durch Mäuse übertragen wird”. Two things are of importance here: *E. stediae* is not a synonym for *Isospora buteonis* as some have supposed, and secondly (of more importance) *E. stediae* is a host-specific lagomorph parasite which cannot be transmitted to mice (which have *E. falciformis* as a specific form) and which certainly cannot be transmitted to any avian species.

KRAMPITZ (1953) doubted the *Isospora* hypothesis and SCHOLTYSECK and PRZYGODDA (e.g. 1956 and pers. comm.) share this view. The latter workers have found *I. buteonis* not only in *Tyto alba*, but in other owls as well (such as *Strix aluco, Athene noctua*) and also in various species of *Falconiformes*. Their conclusion was that the parasite was little, if at all, pathogenic; their specimens having been obtained from quite healthy Barn Owls. The crux of matter is, however, that so few Barn Owls have actually been examined post-mortem during a mortality burst. A few of those that were showed *I. buteonis* in the gut. We note here, for example, that SCHOLTYSECK and PRZYGODDA (1956) examined seven Barn Owls and found two (roughly 28%) infected. The figures are certainly small, but of the same order as the number of owls examined during a mortality burst! In 1934 in the Netherlands only three owls were submitted for examination, whereby one was found to be positive for *I. buteonis* (33% infection). In 1947-48, two birds were examined, both being positive (a 100% infection!).

It is, of course, impossible to conclude from these observations that coccidia were more plentiful than normal during the bursts, seeing the results of SCHOLTYSECK and PRZYGODDA.
Let us suppose, however, that coccidiosis in some form or other is in fact responsible for the occurrence of mortality bursts and see if this alters the characteristic picture in any way.

The pattern of infection will then be as follows: The nestlings will be infected from the parent droppings, via soiled prey and suchlike. Such an infection would not be massive, but certainly continuous. This is exactly the method employed in veterinary practice for the setting up of a resistance to coccidia in poultry, by way of coccidiostats. Let the infection in the Barn Owl be deadly, however, and see if the picture so obtained agrees in any way with the characteristic form once more. The prepatent period for Isospora is unknown, but will probably be of the order of 5 to 8 days. With a fairly normal level of mortality for avian coccidiosis we could expect that within about 10 days (perhaps more but in any case, before the young are fledged) between 50 and 70% of the young will have succumbed, or were dying. Only one nest would be infected in this way from one parent pair, however, unless a simultaneously massive infection occurs throughout the Barn Owl populations of several countries! Long-range infections would appear to be out of the question, although it is possible that small groups of owls roosting together (up to 20 perhaps—Dr. Kluijver, pers. comm.) may form small foci of the disease. However, this will certainly be exceptional, since this bird is notoriously ortstreu. This hypothetical picture does not agree at all with the observed picture of a mass mortality burst which lacks the entire disease pattern. In addition, one important clinical finding would surely not have escaped the notice of taxidermists so long: the bloody caecal cores and the hypertrophy of the caecae themselves are characteristic and striking signs of an acute coccidiosis. Other features of the Barn Owl disease syndrome are loss of weight, lethargy and various forms of necrosis.

Concluding this short digression on avian disease we can say that none of the hypotheses so far proposed is tenable for the Barn Owl; in particular that of coccidiosis may be once and for all discredited.

9. A NOTE ON THE DISTRIBUTION AND POPULATION OF THE BARN OWL IN THE NETHERLANDS

Some remarks have already been made on the habitat selection of Tyto alba; here we wish to make a few general remarks on its national distribution only. It would seem logical to expect that wherever what we have called typical Barn Owl country occurs, the bird will be found. There is, in some areas however, a lack of correlation between plague
zones (for micro-rodents) and the density of the Barn Owl population. This is especially so in the southern part of the Province of Limburg, where no plagues have been recorded, but where the Barn Owl is particularly common. In addition no mortality bursts have been recorded from this province and the records indicate in fact ten owls at most which might have been affected in this way, some of which may well have entered this province from neighbouring Germany.

We can conclude from this (once more echoing the words of HAGEN 1956), that what a "high density" of micro-rodents really is may be very different for an owl and a human observer in the same period. There is no doubt that micro-rodents occur in large numbers in South Limburg and the density would appear to be sufficient to support the Barn Owl population in a stable equilibrium.

Publications by the P. D. in Wageningen (1922 and 1932) suggest that this bird could be seen as an alluvial clay species (being confined in particular to areas of river clay). The correlation was thought to be via a prey species which occurred on such soils only. Figure 10 gives a rough impression of the distribution of soils of this type in the Netherlands; Figure 11 gives the distribution of the Barn Owl as established during the present study, i.e. up to and including April 1962. A comparison of this distribution with one given by the P.D. in 1932 as a result of a pellet census (Fig. 23 of that publication, page 57) shows a fair degree of agreement although several areas which were blank in the earlier map have now been filled in. When we examine the distribution of soil types in the Netherlands, that of the vole plague zones (VAN WIJNGAARDEN 1957, Map 1) and that of the Barn Owl, we may conclude to the following. Although the Barn Owl shows a preference for a particular type of habitat, it occurs there chiefly on alluvial and clay soils and usually not far from water. There would appear to be an upper limit for the surface area of water favoured, since in areas where broads, shallow lakes and suchlike occur, the Barn Owl is replaced by other owls.

Although the distribution of the Barn Owl in other European countries is not yet known in detail, it is probable that this will differ somewhat from the situation in the Netherlands, since this country is practically at the northern limit of the species range and is comparable in all probability with the situation in Denmark only. In addition, as we have pointed out elsewhere, the Netherlands occupies a very special position for several animal species, to which the Barn Owl might well be added.

In Figure 11 we have shown all municipalities where the Barn Owl
is known to breed or to have bred with success in the last decade. On the basis of these results it is possible to make a rough estimate of the total potential breeding population for this species in the Netherlands. We must, however, make the following reservations. In the first place, the results shown in Figure 11 are somewhat biassed, since we did, in
FIGURE 11. Map showing the present distribution of the Barn Owl (Tyto alba) in the Netherlands, according to the present survey. Municipalities where it is known that the species occurs and breeds (visited during survey or reliably documented) are stippled. No Barn Owls occur in the black areas.

fact, visit certain areas because it was known that the owl was breeding there; when studying a species in detail one naturally visits places where this can be carried out with the maximum of material. Secondly, some
of the municipalities are very much larger than others, so that is very much easier to get an idea of the total distribution in one than another. Lastly, unless so indicated on the map, the absence of a record of the Barn Owl does not necessarily imply that this bird has never occurred there. In some cases the local population was unaware of this bird until their attention was drawn to it and negative replies to the questionnaire which was circulated must be given a very different weight to the positive replies.

On the basis of our findings, however, that of about 600 breeding pairs for 20% of the country, we can conclude to a general population of around 3,000 breeding pairs for the whole country.

Although much has been said about a decline in the occurrence of the Barn Owl in several quarters, it is practically impossible to agree with this, or not, on the basis of the present work. It is true to say that locally the distribution pattern of the bird has been altered and that here and there it has disappeared altogether. The felling of trees serving as hunting posts is often involved in this, but we must surely see the felling of trees as a continuous process and one which will at most aggravate a particular local situation.

It is our opinion that the most important causes of recent changes and declines in local populations must be sought in the far-reaching changes in land management which have taken place in recent years and particularly since the Second World War. While these changes may have had little direct effect on the Barn Owl as species, they have certainly radically changed its hunting biotope. The reallocation programmes and agricultural improvement schemes generally operate according to the principle that the rough places shall be made smooth and the crooked straight, so that much of the variety originally present in the landscape is lost. That this variety (by way of alternations in elevation, vegetational types) is essential for the Barn Owl and other species is without doubt; the elimination of such variety leads to an irreversible disappearance of such species.

There are, however, many areas which cannot be changed by improvement schemes and it is to be expected that these areas will remain suitable for species like the Barn Owl for many years to come. It seems not unlikely that South Limburg, for example, will remain an important area for this species in the future.
A study has been made on the ecology and distribution of the Barn Owl (*Tyto alba*) in the Netherlands, in connection with the occurrence of mass mortality outbreaks. The following results have emerged:

1. Habitat selection: *Tyto alba* shows a preference for areas with alternations of elevation and of vegetational types, and for buildings offering easy access.

2. Body weight and starvation: On the basis of literature observations, correlated with field results, a comparative study has been made of the safety margin between normal and starvation weight, fat reserves, life expectation rates and also clutch sizes of this and other species of owls in relation to the phenomenon of mortality bursts in the Netherlands and other European countries.

3. Burst mortality: Recurrent mortality bursts are suggested to be coupled by way of a feedback breeding mechanism to fluctuations in micro-rodent population density, and that this is valid over much of the continent of Europe. *Wanderjahre* and *Sterbejahre* are to be seen as facets of the same phenomenon.

4. Disease and parasites: Mortality bursts cannot be caused by *coccidiosis* on the basis of the latter’s clinical picture and epidemiology. Parasites are important only when the owls have become weakened due to other causes.

5. Distribution: The Barn Owl is found in the Netherlands in areas where the following factors coincide: suitable hunting territories (as under 1 above), sufficient prey, which does not have to be at a “plague level” and the occurrence of anthropogenic structures. These areas are utilised chiefly on clay alluvial soils and in the neighbourhood of water.

6. Population and declines: On the basis of the present study, an estimated breeding population of 3,000 pairs occurs in the Netherlands. There would appear to be a number of local declines in the population, chiefly due to land improvement schemes. There is, however, no reason to expect the total disappearance of the Barn Owl in the Netherlands.

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Additional note

Since the preparation of this manuscript was closed (May 1962), Dr. KLUIJVER has drawn my attention to a recent publication by GRABER (1962) on "Food and Oxygen Consumption in three species of Owls (Strigidae)" in The Condor Vol. 64, pp. 473-488. Although we hope to deal with GRABER's results in a following publication in more detail, it is interesting to note that the latter's conclusions agree with those we have given above as the physiological balance of a number of owl species. In particular, Figure 2 of GRABER (p. 482) is of interest. I am indebted to Dr. KLUIJVER for drawing my attention to this paper and for his helpful comments on the manuscript as a whole after its completion.

LITERATURE


PLANTENZIEKTEKUNDIGE DIENST. 1922. Sterfte onder de Kerkuilen (Strix flammea) in 1922.


