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Contribution to the population biology of the pond bat, Myotis dasycneme, (Boie, 1825)

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With 14 tables, 12 figures in the text and 1 plate

Abstract

A quantitative study of the population biology of pond bats *(Myotis dasycneme)* is based on 1139 specimens banded in summer roosts, and 3000 bandings in winter quarters. This revealed estimations of population parameters, like sex rate rate of adults-subadults-juveniles, survival rate, and rate of capture. Results were obtained on summer and winter biotopes, migration, and synanthropy. They explain almost completely the recent geographical distribution of the pond bat in N. W. Europe. Tentative suggestions are made on this distribution in prehistorical times.

Kurzfassung

Die quantitative Untersuchung zur Populationsbiologie der Teichfledermaus *(Myotis dasycneme)* stützt sich auf Beringungsresultate von 1139 Tieren aus Sommerquartieren und etwa 3000 aus Winter-quartieren. Es ergab sich eine Bestimmung von Populationsparametern, wie des Geschlechterver-hältnisses, des Verhältnisses der Anzahl adulter, subadulter und juveniler Tiere, der Überlebens-rate, der Wahrscheinlichkeit, daß ein bestimmtes Tier vom Untersucher eingefangen wird. Die gewonnenen Resultate über die Sommer- und Winterbiologie, über Migration und Synanthropie erklären fast restlos die heutige geographische Verbreitung der Teichfledermaus in Nordwest-Europa. Eine Hypothese über die vorgeschichtliche Verbreitung dieser Art wird vorgelegt.

CONTENTS

1. Introduction

Bats are living almost everywhere in big numbers and under rather different ecological circumstances. This provides many opportunities for chiropterological research all over the world resulting in an extensive international literature on the subject.

Some geographical regions have special advantages as to variety in biotopes and species. The middle european range, with its temperate climate, is rather poor in bat species, but sufficiently rich in geophysical variations and in climatological differences between the seasons of the year.

As regards pond bats, dutch investigators are in a privileged position. Their country does not only possess relatively richly populated winter quarters of the species (which may be found in nearby Belgium and Denmark too), but also a number

of large nursing colonies. The only other places where summer habitats of pond bats of any importance have been found are located in Russia. These circumstances enable the authors to strive at an extension of the current morpho-taxonomical definition of the species by a study on its population biology. In the present paper, this study is mainly based on quantitative observations of banded and unbanded specimens in winter quarters as well as in nursing roosts.

Here again, it is a great advantage to be able to lean on results of an extensive bat banding investigation which was started many years ago in the limburgian marl cave area by BELS (1952).

2. Quantitative population data

In a previous paper our quantitative data on populations of pond bats, hibernating in the caves of S. Limburg, have been recorded and analysed (BEZEM, SLUITER & v. HEERDT 1960).

We are able to add a number of population data of this species, gathered from nursing colonies this time. They are recorded in this chapter, and results concerning composition and statistics of the populations of winter- and summer quarters will be compared.

During the period from 1954 till 1969, ten nursing roosts have been found in the northern parts of the Netherlands: one in the province of N. Holland (Oostzaan), and nine in the province of Friesland. A description of these sites will be given in the next chapter (3.2.2).

Samples from nursing colonies have been taken once yearly, either at the end of July or the beginning of August, and all specimens caught have been banded. Their numbers are recorded on table 1 for each roost separately. They are pooled for periods of different length, each period beginning in the year when a place was found to be a bat roost and ending in the year when the roost was no longer searched for some reason. In most cases we did not want to disturb the colony too much by sampling; in others the bats had been scared away by restoration of the church roof, where they lived under.

Table 1. Numbers of pond bats, banded or recaptured with a ring in nursing roosts. In Wartena circa 50 non-juvenile females have been caught, but not banded. In Tjerkwerd a colony of circa 300 specimens has been observed.

Place	Period	Juveniles		Non-juveniles		Totals
		males	females	males	females	
Kollum	1954/63	152	143	4	280	579
Oostzaan	1957/59	8	10	0	12	30
Wommels	1959/64	38	60	2	101	201
Berlikum	1961/63	33	38	3	73	147
Oosterend	1965/67	25	16	2	60	103
Sloten	1965/67	31	38	1	96	166
Goutum	1966/67	16	9	2	22	49
Beetgum	1967	6	8	1	24	39
Wartena	1968	—	—	—	—	—
Tjerkwerd	1969	—	—	—	—	—
Totals	1954/69	309	322	15	668	1314

2.1. Composition of samples

The composition of pond bat samples as to sex and age of the individuals has been studied by scoring numbers of males and females, and, if possible, those of juveniles, subadults and adults.

The latter three categories may be defined as follows:

J u v e n i l e s belong to the first year-class. Consequently, they are 6 to 8 weeks old at the moment of our summer campaign (end of July) and about 7 months when captured during our winter campaign (beginning of January).

S u b a d u l t f e m a l e s are non-juvenile, but non-parous females. Accordingly, they do not lactate in July, and by this characteristic they may be distinguished from adult females externally.

Like in other species of the genus *Myotis* (SLUITER et al. 1951, 1954 and 1961), it may be supposed that female pond bats do not reach sexual maturity before August of their second year. Accordingly, subadults are 1.1 years old at the end of July and almost 1.6 year in January.

A d u l t f e m a l e s are supposed to be two or more years old. They form the breeding part of a nursing colony, and the external characteristics of lactation are still visible in July.

2.1.1. Sex ratio

As usual in myotids, non-juvenile males are rarely found in nursing colonies of pond bats. According to table 1, the fraction of males in the non-juvenile part of the sample can be calculated as 0.02 in July. Regarding the juvenile part, however, the male fraction is found to be 0.49 (table 1), which indicates that males and females are born in equal numbers.

During a previous investigation of the sex ratio in a winter population of pond bats, hibernating in the caves of S. Limburg, juveniles and non-juveniles have not been scored separately. Overall, a male fraction of 0,52 resulted (BEZEM et al. 1960, p. 528). Apparently, the sex ratio in the species is almost fifty-fifty at any time of the year.

The adult males and females roost almost completely segregated during the breeding time, but almost unsegregated during hibernation.

2.1.2. Adults, subadults and juveniles

Subadult females have been scored separately in the nursing colony at Kollum, except in 1961. In table 2, the annual numbers of bats caught there during the period from 1955 till 1963 are recorded. The scores in the years 1954 and 1963 are omitted, as the sampling has been incomplete during these years.

2.1.2.1. Adults-juveniles

The occurrence of more than one young in a litter is known to be very rare in bats of the genus *Myotis* generally. On the assumption that each adult female pond bat produces one young annually, the number of juveniles ought to be at most equal to the number of adult females in the population of a nursing colony.

In our samples, however, we find more juveniles as a rule. According to table 2, in Kollum 241 juveniles were caught in total against 179 adults. This means that at

Table 2. Scores of pond bats in the nursing colony at Kollum.

| Year | Juveniles | | Subadult | Adult | Totals |
	males	females	females	females	
1955	25	34	7	48	114
1956	14	8	3	14	39
1957	21	19	7	31	78
1958	23	12	1	31	67
1959	13	13	7	14	47
1960	14	15	1	11	41
1962	16	14	6	30	66
Totals	126	115	32	179	452
Means	18.0	16.4	4.5	25.5	64.5

least 25% of the adults should be missing in the samples, if our assumption on birth rate is right. This contradiction may be explained by a sampling effect, as the chances to be caught are evidently different for adults and juveniles. During daytime, the population of the nursing colony living on the church loft at Kollum is found in one big cluster between the ridge-pole and the apex of the roof. As soon as the investigator puts his hand into this cluster in order to collect bats, many of them start to escape. The adults and subadults are always the first to fly away and to reach a ridge where they can hide undisturbed. The juveniles, being newly fledged, hesitate some time before they start flying, and many of them first try to escape by running along the ridge-pole. Consequently, juveniles are more easily caught than adults.

We have got the impression that generally not more than one third of the total number of bats present on the loft might actually be caught in this way. There is some evidence supporting this impression which originates from observations we have made in the nursing colony on a church loft at Berlikum. We have sampled this colony during three years successively (1961/63), and we have got a mean annual sample size of almost 50 specimens (cf. table 1). From 1964 on, this colony has been disturbed no longer by sampling, in order to be able to study the habits of the bats when flying out in the evening. Annual observations of the number of specimens leaving at night in the end of July during four subsequent years have yielded a rather constant population size fluctuating around a mean of about 150 specimens, being three times the mean sample size mentioned above.

Considerable fluctuations in the annual samples as shown in table 2 may be explained mainly from differences in the ambient temperature on the loft at the times of collecting. High temperatures cause high alertness of the animals, even in daytime, corresponding with an increase of their chance to escape the collector. This does not exclude the possibility of annual fluctuations in population size. The question, whether such fluctuations of appreciable size do occur or not, cannot be answered by regarding our sample sizes. Large annual fluctuations in birth rate are not likely to occur in a pond bat population, as each female produces only one young per annum at most. So, increase in litter size cannot compensate here a serious loss by extreme mortality and/or emigration. Accordingly, appreciable annual fluctuations in population size would depend on an unbalance between mortality and emigration on one side, and immigration on the other. No evidence has been found for such an unbalance in our case (cf. 2.2.4.2.).

2.1.2.2. Subadult females

Only females can be regarded here, as subadult males are rarely found in nursing colonies. During the act of catching, subadults are supposed to behave in the same way as adults and quite differently from juveniles (cf. 2.1.2.1.). Therefore, the fraction of subadults in the non-juvenile part of the population may be estimated by the fraction found in the non-juvenile sampling totals.

According to table 2, 32 subadults have been caught against 179 adults yielding a fraction of subadults in the sample of 0.15. As we will show below from the survival rate (cf. 2.2.2.), this fraction can be estimated as 0.30 in the Kollum population, indicating that 50 % of the subadult females belonging to this population and being alive at the moment of sampling, are not present on the loft at this moment. As an explanation for this absence, it may be remembered that subadults are less bound to live in a nursing colony than juveniles and adult females. According to our definitions given above (cf. 2.1.), subadults are no longer dependent on adult females on the one hand, and they do not yet breed, on the other. It is, therefore, quite acceptable that many of them should spend the summer in other roosts than where they have been born, like all males do. We are however inclined to think that these strayers will return the following spring — when they have become adults — to the colony to which they originally belonged, in order to give birth to their first young at the same roost as they themselves have been born. Doing so, they help to regulate the population size of their colony. This point will be further discussed below (cf. 2.2.4.2.).

2.2. Population statistics

2.2.1. Mark-recapture data

As is shown in table 1, a total of 1314 pond bats have been banded or recaptured with a ring in the dutch nursing colonies. Of those, 579 specimens, including juvenile, subadult and adult males and females, have been found at Kollum during a series of 10 subsequent years (1954/63). These numbers make the mark-recapture data of Kollum more suitable for an attempt to estimate population parameters than those of the other summer roosts of pond bats. To increase the accuracy of the estimates, the following data had to be omitted for reasons mentioned below:

a. The scores of bats caught in 1963, as sampling was biased then by restoration of the church roof at Kollum.

b. The scores of all males, as males are hardly represented in the recaptures (cf. 2.1.1.).

c. The scores of the females which have been banded as juveniles and never recaptured. Their omission is needed, as their rate of capture after one year (when they are subadults) appeared to be rather lower than normal (cf. 2.1.2.2.).

If a juvenile has been recaptured one or more times, the year of first recapture has been taken as the year of banding of a non-juvenile specimen.

So, mark-recapture data of a rather small number of individuals remain for statistical treatment. Many of them have been banded and never seen again; others have been recaptured once or several times at Kollum, as is shown in table 3.

Numbers of recaptures depend on three factors:

The rate of survival, the rate of capture, and the number of years during which the annual sampling has been continued after the year of banding.

Table 3. Numbers of non-juvenile female pond bats marked and recaptured at Kollum.

Year	Individ. banded	Individ. recapt.	Recaptured				
			1 time	2 times	3 times	4 times	total times
1954	24	7	4	1	1	1	13
1955	51	13	6	5	2	0	22
1956	12	2	1	0	1	0	4
1957	26	9	4	4	1	0	15
1958	19	7	5	1	0	1	11
1959	13	0	0	0	0	0	0
1960	3	0	0	0	0	0	0
1961	27	3	3	0	0	0	3
Totals	175	41	23	11	5	2	68

Table 4. Initial numbers and numbers of recaptures.

After	Kollum, summers of 1955/62		S. Limburg, winters of 1940/57	
	Init. number	Recaptured	Init. number	Recaptured
1 year	241	41	970	125
2 years	200	27	880	53
3 years	188	15	808	39
4 years	166	10	852	33
5 years			754	16

If we arrange these mark-recapture data in the same way as described before in connection with our statistical study on winter populations of bats (SLUITER et al. 1956, p. 66—69), initial numbers and numbers of recaptures result as recorded in table 4.

If we plot the logarithm of the fraction of recapture against time according to the method of BEZEM (SLUITER et al. 1956, p. 74—75), we are able again to estimate rates of survival and capture of pond bats, and to compare summer with winter results of the species.

The graphs in fig. 1 show that a straight regression fits the points satisfactorily in accordance with the assumption that the probability of survival is independent of age and remains unchanged throughout the period of investigation (cf. BEZEM in SLUITER et al. 1956, p. 76 and 77).

The slope of these lines and their intersection with the vertical axis, yield estimates of the survival rate and the rate of capture, respectively.

2.2.2. Rate of survival

2.2.2.1. Females

From the regression lines recorded in fig. 1 annual survival rates of 0.70 and 0.67 result for pond bats in summer and winter populations, respectively. These estimates are almost equal, as they ought to be.
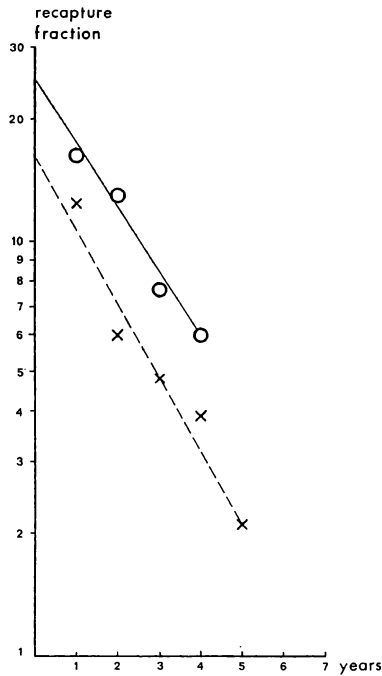
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Figure 1. Fraction of recapture (× 100) plotted logarithmically against years since ringing of non-juvenile pond bat females (cf. table 4) in a summer roost (○), and of males and females combined in winter roosts (×). The latter data are cited from BEZEM, SLUITER & VAN HEERDT (1960).

As an illustration of the consequences of a value of the survival rate as 0.70, we have calculated according to the method of BEZEM (cf. SLUITER et al. 1956, p. 74, formula 25) values for life span as 13 years, expectation of life as 2.8 years.

Age distribution in fractions for each year-class found in the non-juvenile female part of the Kollum population in July, and based on a survival rate of 0.70 is recorded in table 5.

It must be remembered that the individuals aged 1.1 year represent the subadults. Hence, we find a fraction of 0.300 for subadults in this population. We used this value above already for our considerations on the subadult fraction in a sample (cf. 2.1.2.2.), argueing that 50 % of them is absent on the church loft at Kollum during summer.

According to table 5, out of 1000 bats 12 are expected to be still alive after 10 years. Actually, we have, between 1950 and 1964, recaptured 7 pond bats 10

Table 5. Age distribution in the Kollum population in july.

Age in years	Fraction	Age in years	Fraction
1.1	0.300	6.1	0.050
2.1	0.210	7.1	0.035
3.1	0.147	8.1	0.025
4.1	0.103	9.1	0.017
5.1	0.072	10.1	0.012

years after banding out of an initial number of almost 1000 (unpubl. data from S. Limburg). The oldest pond bat ever recaptured had the age of 15.5 years at least (VAN HEERDT & SLUITER 1961).

2.2.2.2. Males

As has been shown earlier (BEZEM et al. 1960, p. 522), according to results obtained from the winter population of this species in S. Limburg, male and female pond bats are likely to have the same probability of survival.

Although no appreciable numbers of recaptured males in Kollum are scored, we are still able to add some evidence for this conclusion. As we have mentioned before, birth rates of the sexes are equal, and the sex ratio of adults is likely to be almost fifty-fifty at any time of the year (cf. 2.1.1.). So, the male survival rate is likely to be equal to the female one, meaning that life tables as recorded above for females (cf. 2.2.2.1.) should be applicable to males too.

2.2.3. Rate of capture

The rate of capture depends on two chances: first, the chance that an individual is present at the sampling place at the moment of collecting; secondly, if it is, the chance that it is actually caught by the collector.

On the former chance we will speculate below (2.2.4.2.). The latter evidently depends on place and time of collecting, for instance: whether one tries to find bats individually hiding somewhere in a large cave during the hibernation period, or to catch them when they are clustering on the ridge-pole of a church loft during the nursing period, when they are often very alert and able to fly off immediately. In a cave the difficulty is to find them, on a loft it is to catch them.

In the caves of S. Limburg a value of the rate of capture of 0.17 resulted (BEZEM et al. 1960, p. 524), but on the loft at Kollum this value is 0.25. In the former case, this value applies to both sexes if aged 0.6 year and older; in the latter, to females from the age of 2.1. years on.

For subadults the rate of capture on a loft should be one half of the adult capture rate, according to our considerations in 2.1.2.2. For weanlings and sucklings no capture rate can be derived from regression lines like those in fig. 1.

2.2.4. Population size

Population sizes could not be scored directly in the Kollum colony. Therefore, population dynamics can only be studied by regarding sample sizes. As we pointed out before (cf. 2.1.2.1.) considerable annual fluctuations of samples are not likely to reflect corresponding fluctuations in population size. In this paragraph we will deal with constancy on the long run, immigration-emigration, and estimation of population size.

2.2.4.1. Constancy

If we use constancy of sample sizes in the sense of Kendall's rank correlation test as an indication for absence of trend in population size, it follows from table 6 that these sizes show no trend to increase nor to decrease as the years go by during the period of investigation.

Table 6.   Sample sizes in Kollum 1955/63.

Year	Sample
1955	114
1956	39
1957	78
1958	67
1959	47
1960	41
1961	81
1962	66

P/ Kendall   0.72

2.2.4.2. Immigration — emigration

Generally, losses by emigration and mortality will be balanced by gains by immigration and birth in a constant population. Our Kollum samples might be composed of "natives" and „immigrants". A number of recaptured animals could be identified as natives being banded as juveniles at the same place. Of the greater part of the individuals in a sample the place of birth is not known. Thus, the question whether there are any immigrants among them or not cannot be answered directly.

Nevertheless, there is some evidence which enables us to speculate on emigration. As mentioned before, we have got the impression that generally not more than one third of the total number of bats present on the loft may be actually caught as a consequence of our way of sampling (cf. 2.1.2.1.). The greater part of the sample consists of juveniles, which can be more easily caught than non-juveniles. We will try to estimate the chance to be caught for adults and juveniles separately in the following way. According to table 2, 241 juveniles + 179 adults = 420 specimens in total have been caught during the period of investigation. This probably corresponds with a total number of circa 3 × 420 = 1260 specimens having been present on the loft during our sampling visits all together. To our opinion, numbers of adults and juveniles in this total must have been almost equal at the dates of sampling (cf. 2.1.2.1.). So, 1260 : 2 = 630 adults are assumed to have been there really. Actually 179 adults were caught, meaning that their chance to be caught is in fact 179 : 630 = 0.29, against a chance of 241 : 630 = 0.38 for juveniles.

Comparing the chance to be caught for adults of 0.29 with the rate of capture for adults in the population as a whole which we estimated before as 0.25 (cf. 2.2.3.), it may be concluded that the majority of the adult females belonging to the Kollum population has been actually present at this loft at the moment of sampling.

On the other hand, emigration might affect our estimate of the survival rate if it is permanent, meaning that it is not followed by reimmigration of the same individual at some time during the period of investigation (cf. SLUITER et al. 1956, p. 66). Considering the fact that the estimate of the survival rate found in the hibernating quarters based on a large number of banded specimens and the estimate of the same rate found in a summer quarter based on a much smaller number (cf. table 4) are in very close agreement (cf. 2.2.2.1.), one is inclined to think that permanent emigration out of a pond bat population is rather rare. Accordingly, the same holds for immigration.

2.2.4.3. Estimation of population size

An estimate of the mean number of adult females belonging to the Kollum colony at the moment of sampling can be made by multiplying the mean sample size over 7 years (cf. table 2) with $1/q$, if q is the rate of capture. For $q = 0.25$, this number is 102 specimens.

If we assume the chance to be caught 0.29 (cf. 2.2.4.2.) for the subadult females which are present on this loft, their mean number would be 16 specimens.

The rate of capture of juveniles cannot be estimated, but their number might be almost equal to the number of adult females (cf. 2.1.2.1.).

Overall, a colony size of $102 + 16 + 102 = 220$ specimens results. It must be remembered that a nursing colony reaches its maximum at the moment when all young are born, which is probably realised in mid-June for pond bats in Friesland. So, the mean size we estimated above at the end of July should be rather near the peak size of the colony.

2.2.5. Ring damage

It is generally known that a ring may cause an inflammation of the wing membrane. In such a case, we either change the ring over to the other wing or, if it has become inreadable, a new ring is put on that wing. Numbers of this occurrence have been scored over periods of 13 years in the frisian nursing colonies, as well as in the limburgian hibernating caves. They are recorded in the tables 7 and 8 respectively. According to these tables, there does not seem to be a trend in the percentages damaged.

Overall, however, there is a clear difference between the percentages of damage found in nurseries (28,5 %) and in hibernating quarters (10,4 %). An explanation of this difference might be found in the following consideration. A bat which has been banded in January will bite its ring, fly about for some hours, and go back soon to the hibernation torpidity again. After awakening in spring, it should have got accustomed to wearing a ring gradually. But, after it is banded in July it has to fly

Table 7. Instances of ring damage in pond bats banded in Friesland during the summers of 1954/66.

Recaptured after:	1 year	2 years	3 years	4 years	Totals
Damaged:	15	8	6	3	32
Undamaged:	48	17	10	11	86
Totals	63	25	16	14	118
Percentage damaged:	23.8	32.0	37.5	21.4	28.5

Table 8. Instances of ring damage in pond bats banded in S. Limburg during the winters of 1950/62.

Recaptured after:	1 year	2 years	3 years	4 years	Totals
Damaged:	7	3	1	1	12
Undamaged:	60	19	16	8	103
Totals	67	22	17	9	115
Percentage damaged:	10.4	13.6	5.9	11.1	10.4

for food each night, so it will be bothered more by the ring. Consequently, this ring is likely to be bitten more often than in the former case which increases the risk of inflammation of the wing membrane.

Our data ring damage do not allow conclusions on ring mortality. Occasionally, the inflammation is found to be sufficiently serious indeed to lame the wing, and so to cause the death of the animal, if the ring is not taken off.

According to the sample sizes recorded in table 6, the number of these casualties is not likely to have affected the population size of the Kollum colony during the period of 7 subsequent years of our banding activity. In addition, notwithstanding the fact that the damage caused by banding in nursing colonies is larger than in hibernation quarters, the estimates of the survival rate have been shown to be practically equal (cf. 2.2.2.). All this suggests that ring damage has not appreciable decreased the survival rate in our investigations concerned here.

Nevertheless, we feel obliged to warn against the „banding sport", which is done by some naturalists on any species, at any place, in any season, and for any purpose. To our opinion, bat banding ought to be restricted as much as possible. If there is a good reason to band, winter is the best season to do it. Some precautions are to be excercised even then. The bats must not be disturbed more than once a winter, and not more than about one fourth of a population ought to be caught and banded. Banding in nurseries can be better omitted at all; it ought never to be done before all young bats have become fledged.

In accordance with the above considerations, our banding of pond bats has been stopped since 1957 in the winter quarters, and since 1968 in the summer quarters.

3. Biogeography

3.1. Geographical distribution

Considerations in this paragraph on the recent distribution of the pond bat in Europe are partly based on a literature study of HANAK & GAISLER (1965). From the map in their fig. 1, showing the localities of occurrence, one gets the impression that the species is widely, though discontinuously, distributed in the broad zone between the 45 [th] and the 60 [th] degree of northern latitude all over Europe. Looking more closely at this figure, one agrees with these authors that some care ought to be exercised when interpreting these data. First, out of a total of 82 localities indicated on the map 73 refer to the finding of either a single specimen or a very small colony. Secondly, summer and winter distribution may be essentially different in this species.

For a proper interpretation it seems preferable to regard mainly nine localities indicated by HANAK & GAISLER (1965, p. 120) which yield considerable numbers of pond bats. Therefore, we have drawn only these localities again on the map of our fig. 2, showing the sites of four rich hibernating areas and five rich summer areas. Their distribution suggests the occurrence of different population centres scattered over a large part of Europe. Each centre should include at least one summer area and one winter area. Their mutual connections ought to be demonstrated by adequate recoveries of banded specimens.

In trying to combine the black and white symbols on fig. 2 to population centres, those in Russia cannot be regarded here, as no banding data from these localities are known to us.
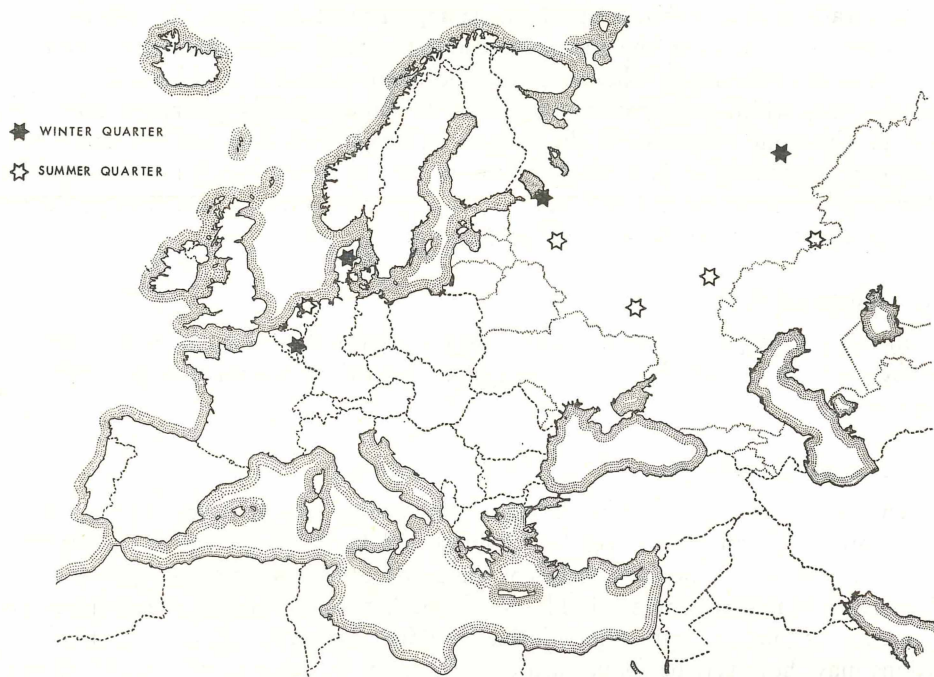
Figure 2. Localities of the main summer and winter quarters of the pond bat known in Europe. After HANAK & GAISLER (1965, fig. 1).

According to KUZJAKIN (1950, cited from personal communication of Dr. HANAK), at least two population centres are known in Russia which are represented by large nursing colonies roosting on small wooden church lofts, one at Valdaj (Seliger Lake) and the other at Volsk (Lower Volga). The corresponding hibernating quarters are not known.

As to the other symbols in Europe (fig. 2), we know the dutch-belgian hibernating area to belong to summer haunts in the Netherlands. This will be proved below (cf. 3.3.). Although almost 4000 pond bats have been banded in this population centre, it could not be shown to include the hibernating caves of this species known in Denmark. So, we are inclined to think that the pond bats living in Denmark represent a seperate centre, of which the corresponding summer haunts are not known as yet.

From the above, we conclude that in Europe, apart from Russia, only two population centres of the pond bat at most are known, both located in a small part of the continent near the coast of the North Sea. In the present paper, we will deal mainly with one of these centres ranging through the Benelux states and the adjoining parts of W. Germany. All sites where pond bats have been found in this range are drawn in our figs. 5 and 6. As far as the Netherlands are concerned, these indications originate from the paper of BELS (1952) and from our own additional investigations. The belgian data are cited from FAIRON (1967, p. 17), and those of W. Germany have been kindly communicated to us by Dr. R. FELDMANN (Bösperde) in 1969 in addition to his paper on this subject (1963).

Generally spoken, habitats in this range appear to be distributed as follows. Summer haunts, characterised by the occurrence of nursing roosts, are concentrated in the northern Netherlands, whereas winter roosts are located in a rather narrow semicircular zone which corresponds with the N. W. borders of the german central hilly region. This zone continues in the belgian Ardennes including also the dutch cave area near Maastricht in S. Limburg. Here, as well as in the belgian region between Namur and Dinant, pond bat caves are so much concentrated that they could not be drawn separately on the maps of fig. 5 and 6.

3.2. Ecological data

In this paragraph we will try to explain the distribution of the pond bat habitats in the range described above by means of ecological data from literature and own experience.

3.2.1. The winter biotope

The pond bat is found hibernating almost exclusively in caves. These may be either artificial limestone caves (S. Limburg and Belgium), or natural caves (Belgium and Germany), or even mine-corridors and other subterranean quarries. The circumstances making caves suitable as hibernating roosts for bats are obvious: low temperatures (but no frost), high relative humidity, darkness, quietness. Similar conditions may, however, be found also elsewhere, for instance in cellars of buildings and in subterranean fortresses. Bats of many species will hibernate there too, but pond bats never do as far as we know. For some unknown reason they seem to be bound to hibernate in caves, though this forces them to shift from their low-land summer haunts to hilly regions each time as winter comes near. They will, however, penetrate not further into the hills than circa 50 km. and visit no caves occurring more than 300 m above sea level, as a rule (oral communication of Dr. R. FELDMANN 1969). This is, therefore, one of the main factors determining the winter distribution of the species in the range concerned here.

In the subterranean rooms and corridors concerned, pond bats are found hibernating either singly or in small groups (from 2 to 10 individuals). They may hang or lie almost everywhere from the ceiling to the floor, either in a completely exposed position, or more or less protected in holes and crevices (cf. BEZEM et al. 1964). As climatological conditions change in a cave during winter, they shift to other positions within this cave (cf. DAAN & WICHERS 1968).

The number of pond bats found in one cave depends rather on its size. Small caves generally contain from 1 to 10 individuals, large ones up to circa 50. In one instance, STRELKOV (1958) counted as much as 680 pond bats in one Russian winter quarter.

3.2.2 The summer biotope

All authors on the pond bat agree that it lives in low-land plains near stagnant fresh water during summer. Apart from their preference for a temperate climate (cf. 3.2.2.3.), this must be the main factor determining their summer distribution in the range concerned here. Summer roosts are almost exclusively found in buildings. Roost localities are chosen so that they may be warmed up by the sun as much as possible, for instance, on church lofts, but also in smaller hiding places situated

either under roofs or in double brick-walls. KUZJAKIN (1950, cited from personal communications of Dr. HANAK) has found some male and a few non-breeding female pond bats in hollow trees. They were, either or not, living amongst a colony of another bat species.
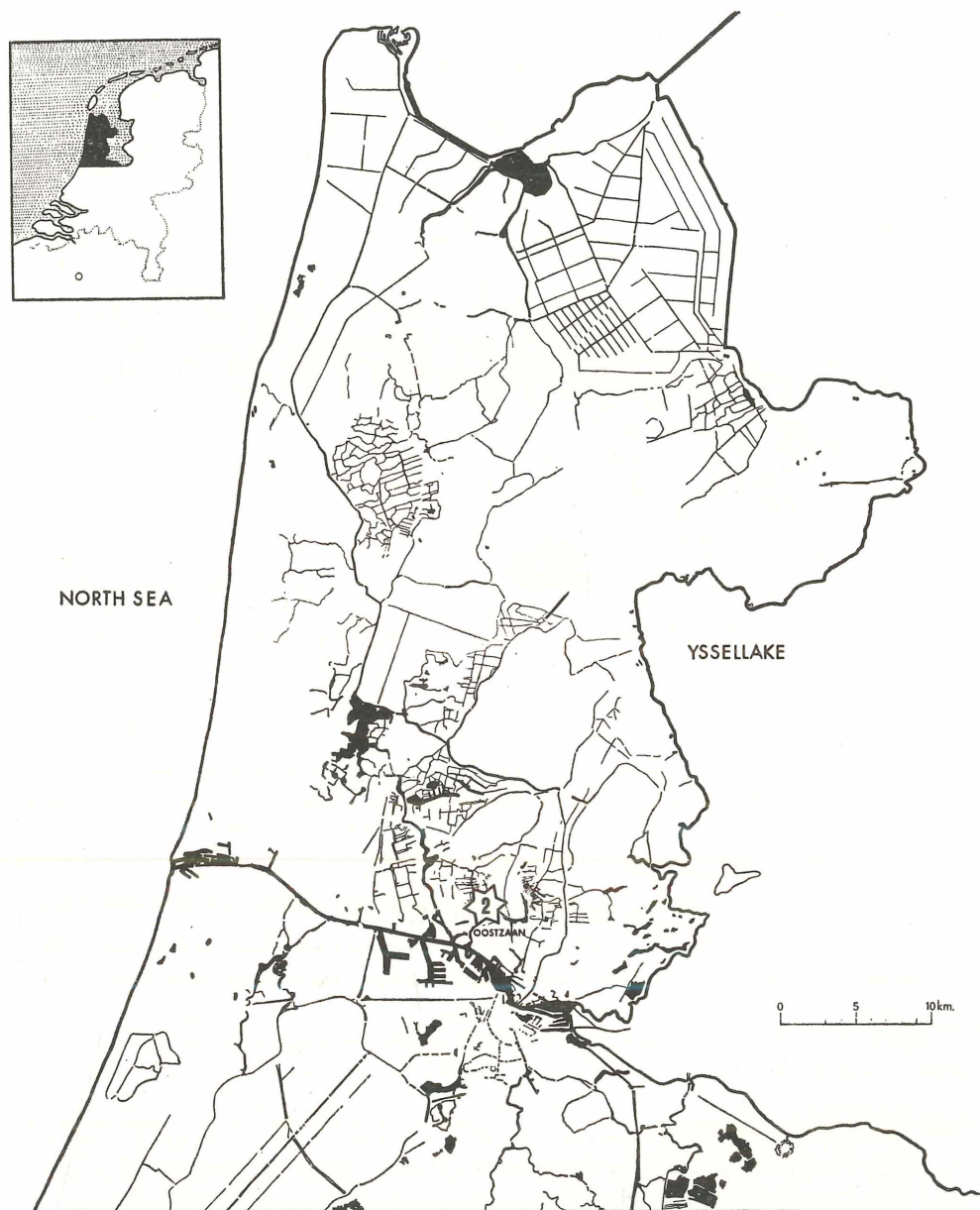

Figure 3. Lakes and canals in the dutch province of N. Holland.
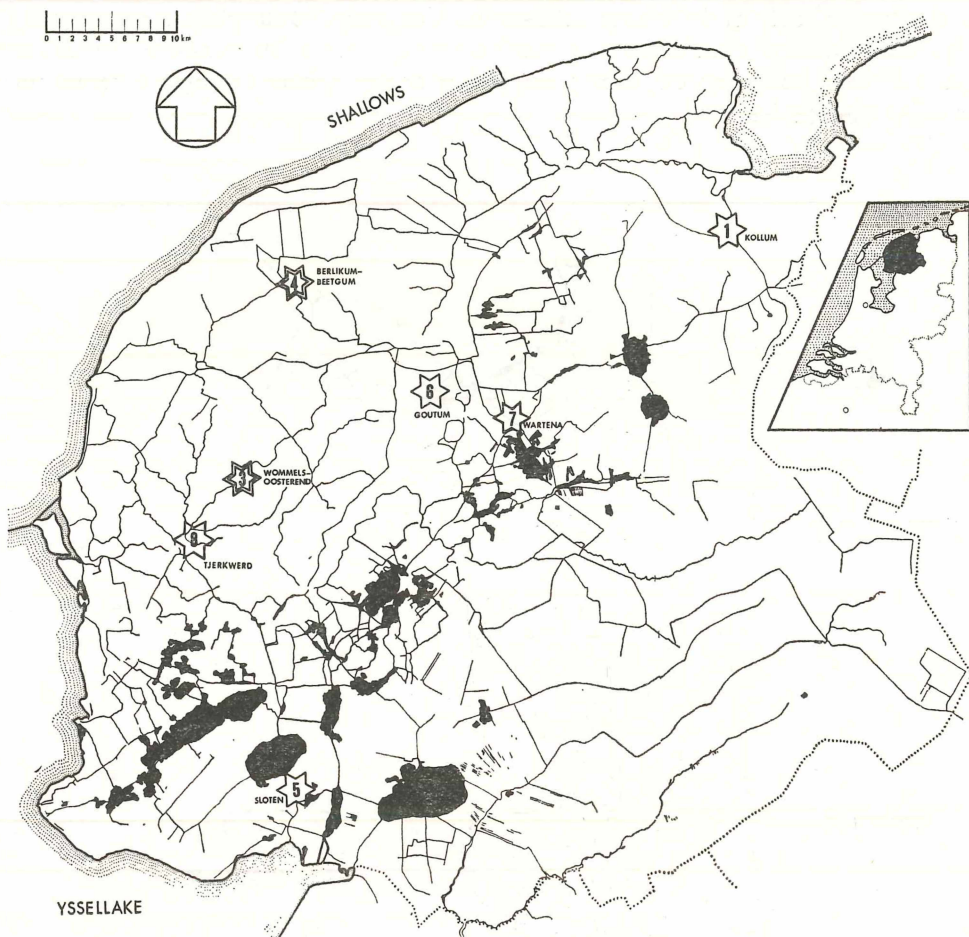The star indicates the roost of the nursing colony nr. 2.

Figure 4.   Lakes and canals in the dutch province of Friesland.
The stars indicate the roosts of the nursing colonies nrs. 1, 3—8. A double star means
that a colony is known to use two lofts as a roosting place.

3.2.2.1. Dutch nursing roosts

In 1954 the first nursing roost of the pond bat in N. W. Europe has been found
on a church loft at Kollum, a village in the dutch province of Friesland. Since then,
up to ten of these roosts in total have been spotted, all located in a rather small
area which is confined to the northern Netherlands: nine in Friesland, and one in the
province of N. Holland. Their topography is shown on a small scale map in fig. 6,
and on a much larger scale in the figs. 3 and 4.

According to recoveries of banded specimens, it may be concluded that only in
two instances one couple of roosts, situated circa 2 km apart, belongs to the same
nursing colony. In our opinion, the roosts mentioned below do represent eight sepa-
rate nursing colonies (cf. 2.2.4.2.):

1. The Kollum population.
2. The Oostzaan population.

3. The Wommels-Oosterend population.
4. The Berlikum-Beetgum population.
5. The Sloten population.
6. The Goutum population.
7. The Wartena population.
8. The Tjerkwerd population.

Periods of investigation and sample sizes have been recorded in table 1.

In two instances (nrs 2 and 7) the colony was roosting in the draft course in a double brick-wall of a house. The bats used as exits some very small ventilation slits at heights from five (Wartena) to eight (Oostzaan) meters above ground-level. Incidental countings have yielded from 50 to 100 specimens flying out of these slits in the evening. Catching for sampling has been done by fixing a wire-cage on the exits.

The remaining eight other roosts have been found on church lofts. In case of the colonies 1, 3 (both roosts), 4 (Beetgum), 5, 6 and 8, the lofts are rather equal in volume, height, and roofing material. They all have a wooden, △-shaped roof covered with slates. Mostly, the bats can be found clustering between the ridge-pole and the apex of the roof in the darkest part of the loft (cf. plate I). The height of the apex above loft floor level varies from 2,5 to 5 meters.

In Berlikum (nr. 4) the church loft is dome-shaped with a wooden roof, covered with zinc. Here the bats also prefer to cluster in a rather exposed position at places at the inner side of the roof, circa 2,5 m above loft floor level. On each loft they may also use much more protected roosting places, situated between and behind heavy rafters, in order to hide away, for instance, when they are scared. In all instances there is plenty of room to fly about on the loft. The exits used by the bats are nearly always located near the loft floor on the level of the eaves-gutter.

3.2.2.2. The feeding grounds

N. Holland and Friesland consist for the main part of the typical dutch, low, flat, and open polder-land. It is poor in trees and very rich in stagnant fresh water, both in reed-bordered canals and in ditches. In addition many small and some large lakes occur (cf. figs 3 and 4). Large numbers of small villages lie rather continuously spread over the country, each with its own little church, providing roosts that seem suitable for pond bats almost everywhere.

In many languages, the name of these bats suggests that they depend on ponds and lakes as feeding places. According to the localities of their nursing roosts concerned here (cf. figs. 3 and 4), however, this seems not to be quite true, as only two out of ten are situated on the margin of a lake (Sloten and Wartena). The other eight are surrounded by a landscape formed mainly by meadows and for a smaller part by arable land with various low-growing crops.

An extensive study of the way of life of pond bats in this kind of biotope, occurring in and around Berlikum, will be published elsewhere.

3.2.2.3. The climate

Large numbers of pond bats reassemble in the dutch summer haunts described above, after hibernation. They are supposed to feed there from April till October on flying insects only, which causes them to depend largely on local weather conditions.

Table 9.   Climatological data from the northern Netherlands in 1967.

	Weather	Day temperature (°C)			Mean precipitation (mm)	Sunshine (hrs)	Wind			
							speed (m/sec)		dom. direction	
Month		mean	mean min.	mean max.			mean	max.	dir.	%
April		8.0	4.0	10.5	48	190	7.6	15	N. E.	21
May		13.5	8.5	16.5	80	220	5.9	16	S.	21
June		15.5	11.0	17.5	37	39	6.5	17	N. W.	22
July		19.0	14.0	22.0	51	245	5.8	13	S. W.	21
August		17.5	13.5	20.5	70	182	5.8	15	S. W.	27
September		15.5	12.0	18.0	103	114	6.2	16	S. W.	25

To give an impression of the climate in N. Holland and Friesland, we have summarized in table 9 the adequate data from the Royal Netherlands Meteorological Institute (de Bilt) on temperature, precipitation, sunshine, and wind during the year 1967, which has been a relatively dry year.

Regarding the data of this table one is not surprised to observe the pond bats feeding during many cool, rainy and windy nights on grounds which provide little shelter generally. Their behaviour under different weather conditions will be dealt with in a future paper. Kuzjakin (1950, cited from pers. comm. of Dr. Hanak) observed them in Russia to fly out for feeding at an ambient temperature as low as 5° C, and he saw them do so at rainy nights as well.

Conclusion

The particular combination of ecological conditions described above (3. 2.) is supposed to be optimal for pond bats, since it is obviously preferred by them. Hence, these conditions explain to a large extent the rather peculiar concentration of their non-russian european population in a relatively small range near the North Sea coast (cf. 3.1.).

3.3. Migration

It is generally known that bats, like birds, are able to cover long distances, as a consequence of their capacity to fly. Many instances are found of bats migrating over hundreds of kilometers.

Unlike migratory birds, bats are not bound to avoid the hardships of winter by retreating to regions with a mild climate. Their capacity to hibernate allows them virtually to spend the winter in the cellar of the same house as where they have got their summer roost on the loft.

As regards bird migration, it is taken for granted that a genuine migration, i. e. a regular seasonal shifting between given summer and winter haunts, is meant. In the case of bats, this is not always a matter of course, as the habit of genuine migration is for them not an obligatory condition to survive.

Nevertheless, some bat species have developed a preference for special winter and summer biotopes which, if they are situated some distance apart, might introduce a similar tendency to genuine migration as is common in migratory birds.

According to the distribution of its winter and summer areas (cf. 3.1. and 3.2.), the pond bat is likely to be such a species. It is the aim of this chapter to prove that

they are real „migratory bats", to describe their migrating habits, and to guess how they came to develop them.

3.3.1. Material and method

As with birds, banding and waiting for recoveries of bats is the common way to investigate their migration. It must be remembered here that this method is a rather laborious one, as only from 1 to 2 % of the banded bats is recovered as a so-called foreign return, which means that it is found outside the banding area; furthermore, that foreign returns of bats mostly refer to recoveries of either a sick individual or a specimen that has been dead for an unknown time and by an unknown cause. We are inclined to think that the ring itself may have caused in some instances the lethal loss of condition (cf. 2.2.5.).

Even if a bat is recovered alive on its migration route, the date of its recovery may lead to false conclusions. Bats which have become incapable to fly, and cannot get any food for this reason. may succeed in living on for a rather long time by going into hibernating torpidity at the place where they happened to break down on their way to regular winter or summer quarters. For instance, seven pond bats recovered in December have not been found in regular hibernation quarters. So, they have broken down most probably during autumn migration already. In the same way, some returns recorded in May might refer to specimens which have broken down during spring migration.

Finally, it must be realized that a genuine migration cannot, in fact, be demonstrated by banding bats at one place and recovering them at another (cf. RYBERG 1947, p. 66). To prove a migration v i c e v e r s a between two given places, they ought to be banded and recovered at both places.

In the present paper we are dealing with banding of pond bats, which has been performed in winter as well as in summer quarters. In addition to the dutch scores in the caves of S. Limburg, we were able to profit by a considerable number of bandings of pond bats in Belgium by our colleagues of the Royal Institute of Natural Sciences of Belgium (cf. FAIRON 1967), and by a much smaller number of german bandings (personal communications from Dr. FELDMANN 1969). Total numbers of bandings in winter quarters which are relevant to the present investigation are scored in table 10.

In the dutch nursing roosts we have banded 1139 pond bats, and we have got 19 foreign returns of them during the period from 1954 till 1969.

3.3.2. Results of banding in winter areas

It has been shown by BELS (1952, p. 51) that pond bats which hibernate in the caves of S. Limburg migrate northward in spring and that they fly back to these caves in the autumn.

Table 10.   Numbers of pond bats banded in winter quarters.

Country	Period	Banded	Foreign returns
The Netherlands	1940/57	1957	34
Belgium	1940/66	924	7
Germany	1953/68	79	0
	Totals	2960	41

Table 11.   New foreign returns of pond bats banded in the caves of S. Limburg. B = Belgium.

Band nr.	Sex	Date banded	Place banded	Date retaken	Place retaken	Dist. in km	Direction
8590	♂	27. 12. 45	Maastricht	5. 12. 51	St. Oedenrode	83	N. N. W.
9064	♂	28. 12. 46	Maastricht	5. 12. 52	Oostzaan	190	N. N. W.
7978	♀	28. 2. 51	Ravensbos	8. 3. 53	Tilff (B)	38	S. S. W.
19261	♂	6. 1. 53	Maastricht	29. 3. 54	Den Bosch	100	N. W.
20763	♀	5. 1. 55	Maastricht	10. 11. 55	Ooltgensplaat	135	N. W.
20656	♀	4. 1. 55	Valkenburg	11. 3. 56	Rochefort (B)	90	S. W.
21061	♂	7. 1. 56	Gronsveld	8. 5. 56	Den Bosch	102	N. W.
21206	♀	10. 1. 56	Bemelen	15. 4. 57	Vught	95	N. W.
21287	♀	3. 1. 57	Meerssen	20. 6. 57	Oostzaan	180	N. N. W.
20689	♂	4. 1. 55	Sibbe	20. 1. 58	Vught	95	N. W.
21416	♀	6. 1. 57	Maastricht	.. 7. 58	Zaandam	187	N. N. W.

BELS banded 1454 specimens out of which 23 foreign returns have been recorded till 1952. During the next 5 years we added 503 bandings in the same caves and got 11 new foreign returns out of the total. They are recorded in table 11.

Place and time of these recoveries quite agree with the conclusions of Bels mentioned above.

In fig. 5, all dutch and belgian results, and one recovery of a female banded in 1966 in a cave at Monschau in the Eiffel (personal letter from Dr. ROER of the Museum Alexander Koenig at Bonn) are drawn together. The sexes are indicated by different symbols. According to the time of the recovery, different symbols are used to indicate whether the bat may be supposed to have been either o n i t s w a y t o respectively i n its summer area, — or to (in) its winter area.

Since 1952, the occurrence of nursing roosts of the pond bat situated in the northern parts of the Netherlands came to our knowledge (cf. 3.2.2.). This provides new evidence in favour of BELS' conclusion.

Summarizing the results of banding in hibernating quarters, we might extend the conclusion of BELS in the following way: pond bats of both sexes which hibernate in the dutch-belgian cave area migrate to summer haunts which are known now to exist in N. Holland and Friesland, and return to this cave area in the autumn.

3.3.3. Results of banding in a summer area

As we pointed out above (3.3.1.), the investigation of a genuine migration is not complete as long as banding has been done in hibernating quarters only. For this reason, we have started our banding practice in pond bat nurseries as soon as they were discovered (cf. 3.2.2.1.). The foreign returns we have got out of 1139 specimens banded are recorded in table 12.

The sites of these recoveries are indicated on the map of fig. 6.

The results are twofold:

a. In three instances a bat, banded in a frisian nursery, has been recovered alive while hibernating in a cave in the dutch-belgian cave area, amply 300 km S. of the place of banding. Two of them refer to the same individual which has been recovered in two subsequent winters, in the same cave near Denée.

b. Another sixteen recoveries have been made E. of the place of banding at varying distances. Three specimens have been found alive while hibernating in caves
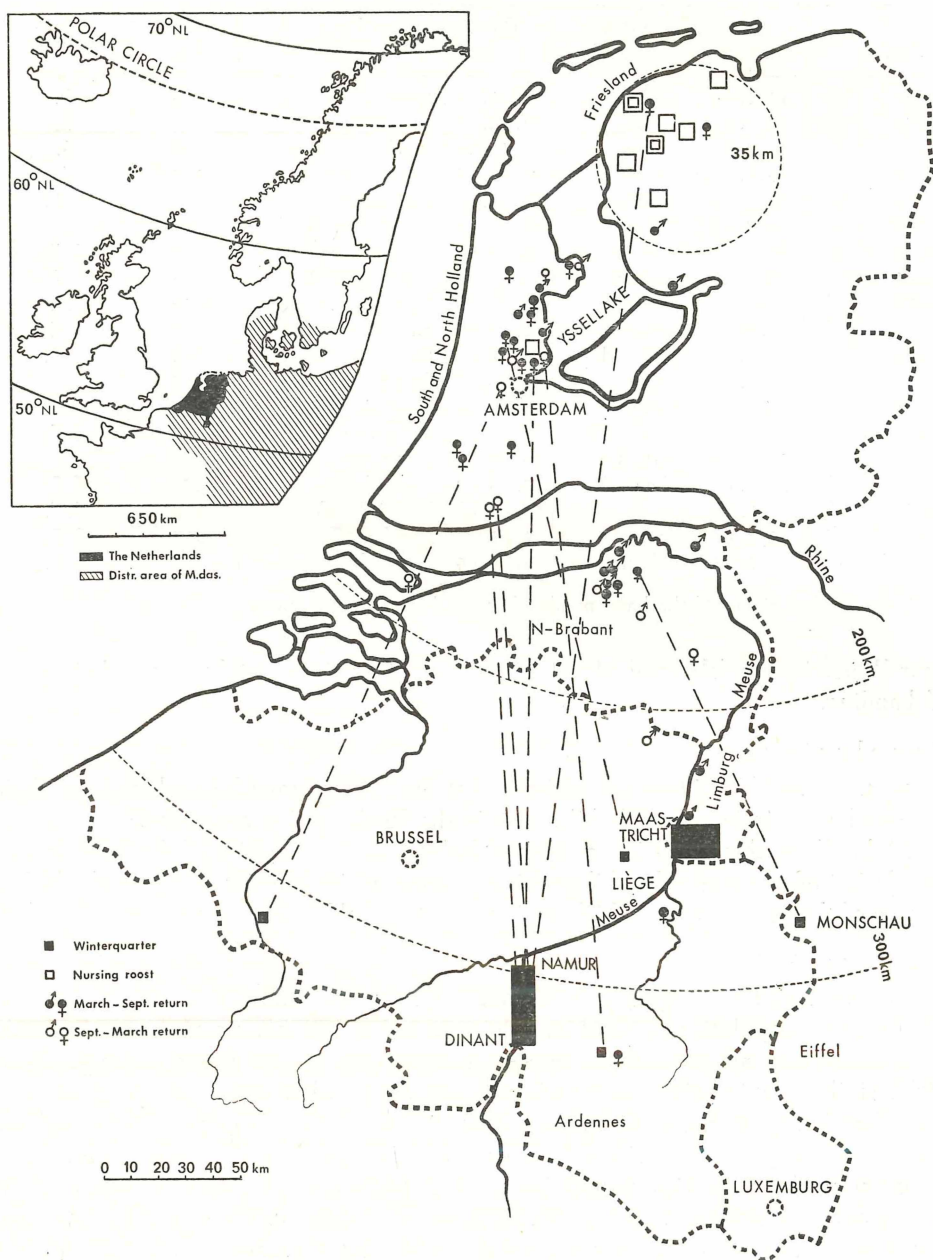
Figure 5. All foreign returns of 2960 pond bats banded in winter quarters (black squares) during the years 1940—1968. The dotted lines connect places of banding in Belgium and Germany with the places of recovery ($\male$ or $\female$). If no dotted line is drawn, the place of banding is situated near Maastricht (cf table 11, and BELS 1952, table 29).

Table 12.   Foreign returns of pond bats banded in nursing roosts in N. Holland and Friesland.
B = Belgium; G = Germany.

Band nr.	Sex	Date banded	Place banded	Date retaken	Place retaken	Dist. km	Direction
19609	♀	10. 6. 54	Kollum	1. 5. 55	Pieterzijl	8	E.
19755	♂	28. 7. 56	Kollum	22. 12. 56	Groningen	28	E.
19728	♀	30. 7. 55	Kollum	26. 12. 56	Denée (B)	330	S.
19728	♀	30. 7. 55	Kollum	29. 12. 57	Denée (B)	330	S.
19754	♀	28. 7. 56	Kollum	28. 12. 56	Fiestel (G)	195	S. E.
19758	♂	28. 7. 56	Kollum	22. 3. 58	Remouchamps (B)	317	S.
19681	♀	30. 7. 55	Kollum	28. 4. 58	Coevorden	80	S. E.
19641	♂	30. 7. 55	Kollum	16. 6. 58	Bramsche (G)	155	S. E.
19859	♀	23. 7. 58	Kollum	11. 12. 58	Haulerwijk	26	S. E.
19879	♂	23. 7. 58	Kollum	12. 8. 59	Bad Oeynhausen (G)	212	S. E.
5890	♀	27. 7. 59	Wommels	2. 9. 60	Horn (G)	261	S. E.
21930	♀	25. 7. 61	Kollum	24. 10. 61	Bremen (G)	175	E.
21955	♀	25. 7. 61	Kollum	5. 1. 62	Warstein (G)	245	S. E.
2457	♂	28. 7. 66	Oosterend	18. 11. 66	Münster (G)	190	S. E.
2040	♀	25. 7. 62	Berlikum	26. 4. 67	Ehrentrup (G)	250	S. E.
2167	♂	24. 7. 63	Wommels	17. 3. 68	Antfeld (G)	280	S. E.
2416	♂	26. 7. 66	Goutum	11. 4. 68	Lemförde (G)	190	S. E.
2638	♀	15. 8. 68	Sloten	8. 3. 69	Menden (G)	250	S. E.
1987.[1]	—	23. 7. 58	Kollum	26. 4. 69	Lemförde (G)	190	S. E.

[1] As the last figure of the band number has not been recorded, no sex is known.

near Warstein, Antfeld, and Menden (Ruhr area) at circa 250 km from their place of banding.

Conclusions

ad a.   These three instances indicate that part of the pond bats which have their summer haunts in Friesland do hibernate in the dutch-belgian cave area.

ad b.   From this result it may be concluded that the majority of the same frisian population migrates to other hibernating quarters which are situated near the N. W. margin of the german central hilly region. Most probably, these roosts are caves also.

Discussion

Summarizing the paragraphs 3.3.2. and 3.3.3., we are inclined to suggest that the total summer population of pond bats living in the northern parts of the Netherlands is divided in two sub-populations by the Ijssellake (fig. 7): one living in the province of N. Holland which hibernates mainly in the dutch-belgian cave area (fig. 5), and the other living in Friesland which hibernates mainly in the german area (fig. 6). Differences in population size (cf. table 10), however, seem to disagree with this hypothesis: the very rich population of the dutch-belgian caves is supposed to correspond with summer haunts in N. Holland where only one nursing roost has been found, whereas the rather poor population of the german cave area should be able to populate nine nursing roosts known in Friesland.

We cannot explain these contradictions, but we are inclined to think that a number of nursing roosts and some hibernating caves must have escaped the attention of the investigators. This view is acceptable if it is realized that bats may hibernate in caves inaccessible to man and may roost in double brick-walls which are very difficult to locate in the summer haunts concerned here.
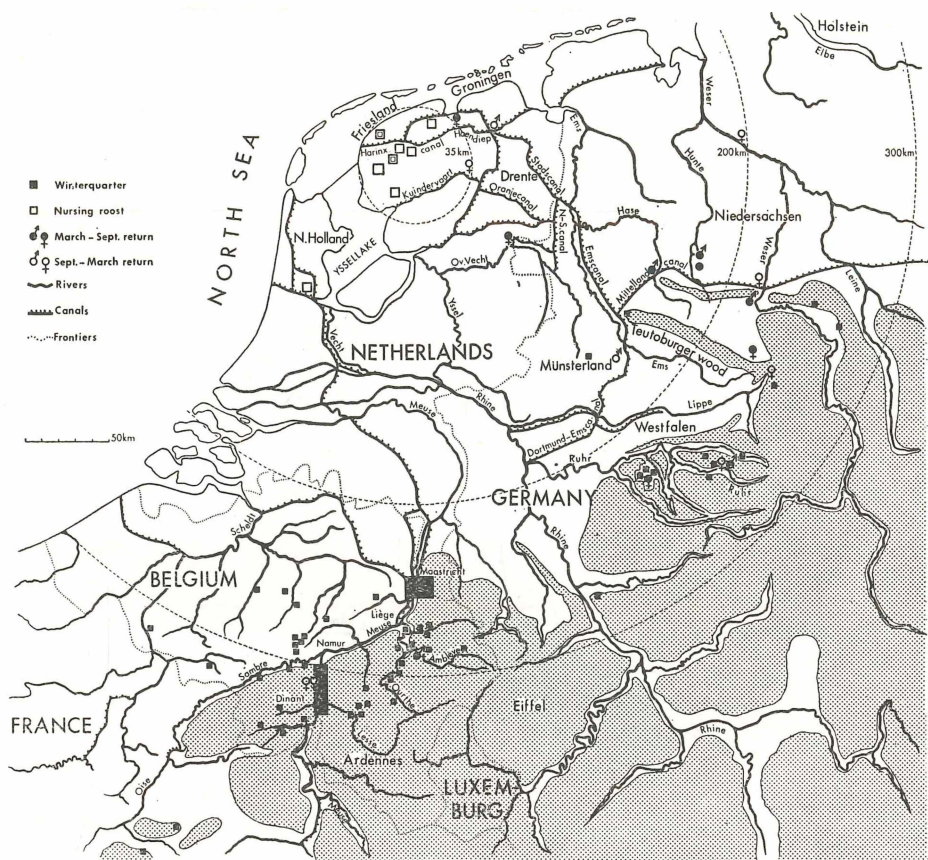
Figure 6. All foreign returns of 1139 pond bats banded in nursing roosts (open squares) in Friesland (cf. table 12). The places of recovery are indicated by ♂ and ♀ symbols. Hilly regions are dotted. Black squares refer to all caves, where pond bats have been found hibernating.

3.3.4. Behavioural aspects of migration

Direct observations on migrating behaviour are lacking completely. We can only try to reconstruct it as good as possible from circumstantial evidence.

In 1964, we have started to observe summer behaviour of pond bats roosting on church lofts in Friesland. Results of this investigation will be published elsewhere; we will restrict ourselves here to recording preliminarily some observations which might be relevant to migrating behaviour also. Many times we have seen more than a hundred pond bats leaving their roost after sunset, in order to go out feeding somewhere in the wide land around. The first thing they do is to join a canal bordered by reed and follow it, flying one by one, closely above the water, over several kilometers in one direction. In one case where canals are absent in the vicinity of the roost (at Beetgum), we have seen them taking roads bordered by scrubs and trees instead. We have got the impression that it is not only their insect fauna that makes canals attractive to pond bats, but also their course leading to favourite feeding places and back home.
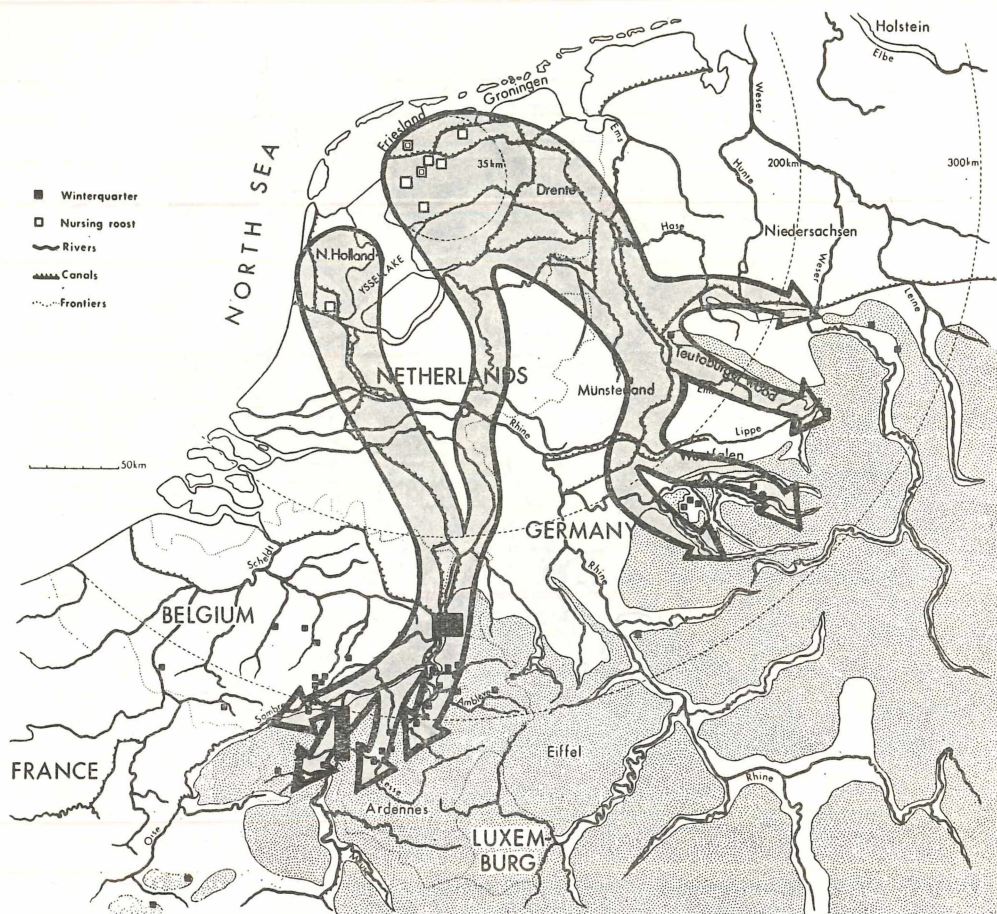
Figure 7.   Schematical illustration of the distribution area of two subpopulations of the pond bat, one having its summer haunts in N. Holland, the other in Friesland.

The habit to follow water ways as guiding lines is very likely to be an essential component of the basal congenital behaviour pattern which regulates migration in pond bats. As we will show below, the banding results we recorded above appear to agree with this habit.

In addition, bats are known to have a remarkable capacity to remember places where they have been a rather long time ago. This too may help them to learn how to find their way to special traditional winter and summer roosts.

3.3.5. Migration routes

It has been shown in a previous paragraph (3.3.3.) that pond bats which spend the summer in Friesland scatter in all directions, except in those leading to sea, in order to reach winter roosts (fig. 6). Therefore, the assumption that they are guided only by a congenital compass sense for a single direction of migration is not very plausible. It seems much more likely that pond bats follow beaconed migration routes
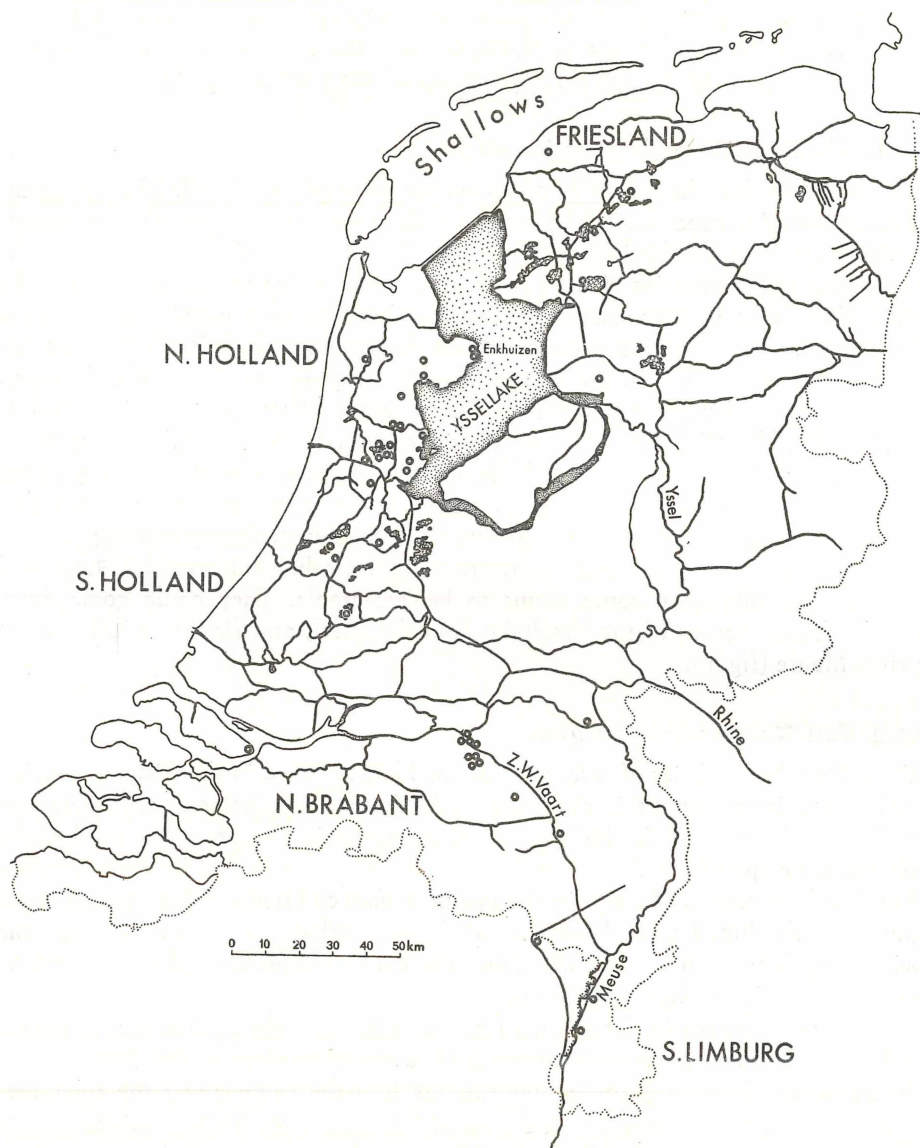
Figure 8. Map of the Netherlands showing the topographical relation between the sites of recovery (○) of pond bats banded in winter quarters (cf. fig. 5), and the main dutch waterways and lakes.

which may lead to different places on the map, but always to caves at one end, and to their traditional summer haunts at the other.

In this paragraph we will deal with additional arguments to support this hypothesis, and with a description of routes which could be relevant to it. The description will be based on four main points:

a. The localities of the known summer and winter roost areas of the species.
b. The localities of recoveries of banded specimens between these areas.

c. The pronounced preference of the pond bat to fly along water ways (cf. 3.3.4.).
d. The natural course of rivers in N. W. Europe, the artificial course of its main canals (cf. fig. 6 and 7), and the topography of dutch lakes (fig. 8).

3.3.5.1. The north ⇆ south migration route

Fig. 8 shows that the localities of recoveries of pond bats banded in the dutch-belgian hibernating area (cf. 3.3.2.) mark clearly a migration route which is related to water ways from the beginning to the end. Starting from the belgian caves this route follows the tributaries of the river Meuse in the Ardennes, passes through the dutch limburgian cave area, and switches from this river to a canal, the s. c. Zuid Willemsvaart. The latter cuts it short through the province of N. Brabant, and leads to a dense network of rivers, canals and lakes in the province of S. Holland. There, it passes through a wide low polderland which is rather similar to the typical summer biotope of pond bats (cf. 3.2.2.2.), and continues west of the IJssellake to the head-land of Enkhuizen in the province of N. Holland. The occurrence of a nursing colony at Oostzaan near Amsterdam (cf. fig. 3) proves that at least a part of the pond bats that migrate along this route in spring stays in this province during summer.

For frisian pond bats that want to hibernate in dutch-belgian caves (cf. 3.2.2. and 3.3.3.) another migration route seems to be acceptable. They could come down along the frisian border of the Ijssellake, join the Ijssel, and finally switch over to the river Meuse (fig. 8).

3.3.5.2. East ⇆ west migration routes

Regarding the localities of recoveries of pond bats, banded in the frisian nurseries, we will try again to design migration routes. As these recoveries are much less nume-rous than in the case of the N-S route, the routes which we are going to describe below are more speculative.

Starting from summer haunts in the northern part of Friesland (fig. 6), the route begins with the broad van Harinxma canal, and probably continues through the provinces of Groningen and Drente along the canals Hoendiep and Stads-canal to the eastern frontier of the Netherlands.

Starting from haunts in the southern part of Friesland, the canals: Kuindervaart, Oranje-canal and N-S canal respectively lead to the same place at this frontier.

In Germany, these W-E routes immediately join the canal along the river Ems which may lead the bats straight to the tip of the longest westward reaching tongue of the central german hills which is known as the Teutoburger Wald. From there, they can reach along various waterways the caves which are scattered in the foot hills from Niedersachsen to Westfalen (fig. 6). If they fly along the Mittelland canal, they may reach caves in the valley of the river Weser. If they continue along the river Ems to its origin, they may reach the hills at a more southern point. As a third possibility, they could cross Munsterland along the Dortmund-Ems canal and reach the Rhine at the point where the Ruhr joins this river. The Ruhr would bring them to the caves near Warstein, Antfeld and Menden where frisian specimens have been recovered hibernating (cf. 3.3.3.).

In support to our suggestion that frisian pond bats prefer hibernating roosts in the german cave area (cf. 3.3.3.), we point to the fact that the general course of water-ways (fig. 6) almost invites them to do so.

Summarizing the paragraph 3.3.5., it may be said that many relevant waterways are available for pond bats to migrate along, if they would like to do so.

In our description of possible migration routes, canals play a dominating role, even when rivers are also present, and seem to provide an alternative route. We have chosen canals as the most favourable waterways for pond bats for two reasons. First, the bats are probably used to be guided by canals when feeding in their frisian summer haunts (cf. 3.3.4.) Secondly, the canals are usually straight lines leading in the right direction, while rivers often would make the route longer by taking many detours.

Finally, we admit that the majority of the caves where pond bats are found hibernating are not situated direcly along any waterway, meaning that the bats must be able to find these caves over land also. It seems acceptable, however, to believe that they may be guided by dry valleys to the entrance of a cave, as we saw them take roads as well in one instance where waterways were not present in the vicinity of their summer roost.

3.3.6. Times of departure and arrival

Some information exists on the dates of departure from and arrival at summer and winter roosts of pond bats in N. W. Europe.

Through the kind intermediary of Mr. Serge DAAN from the Laboratory of Animal Physiology of the University of Amsterdam, we are allowed to publish here some data gathered by this laboratory in two caves in S. Limburg during the winter of 1967/68. It concerns circa 30 pond bats in total. These specimens were counted every other day from September till May. At the other end of the migration routes, in the nursing roost at Berlikum, we observed during the same time the population size of this colony by means of an infrared-ray-photocel combination placed at the entrance of the church loft. According to these observations, the following preliminary idea can be given of the traveling scheme of migrating pond bats.

3.3.6.1. Spring migration

In the middle of March, the first pond bat leaves for spring migration. Numbers keep decreasing steadily till the end of April, when all specimens have left the hibernating caves concerned here. The first pond bat arriving at Berlikum in 1968 has been registered on March 30. From then, the nursing colony grew gradually till the end of April to more than a hundred specimens. Consequently, the mean time the bats need to cover at least 300 km along this south-north migration route in spring is about a fortnight. This implies a mean speed of at least 20 km pro night. We have observed pond bats on feeding flights to cover much more kilometers in one summer night as a rule.

3.3.6.2. Autumn migration

The Berlikum colony begins to decrease in the middle of July again, as soon as the first born young have become weaned. The bats had left the church almost completely at the end of August 1968.

In addition, an inspection of the nurseries at Oosterend, Sloten, Goutum and Beetgum on August 12—14, 1968, yielded a decrease of almost 50 % of the sample,

if compared with the mean sample sizes we got at the end of July of the preceding three years at the same nurseries (cf. table 1). The mean time for leaving a nursery may be estimated about mid-August. The invasion of pond bats in the two hibernating caves mentioned above started in the second half of October 1967. Early November the hibernating number was complete.

According to these data, the mean time between departure from the nursing roost and arrival at the hibernating cave may be roughly estimated as about ten weeks. This is eight weeks longer than the mean time we estimated above to be needed to fly from hibernating roost to nursery in spring (cf. 3.3.6.1.). There is, of course, no reason to retreat towards hibernating quarters in full summer. Their departure from the nurseries may be connected with the circumstance that mating begins in August. We are inclined to think that adult females use to join adult males during this month in the summer roosts of these males which are not known to us. The juveniles do not stay in the nurseries either. They disappear also during the period between the beginning of August and half October. In our opinion, migration to hibernating quarters does not really start before the end of September.

3.4. Historical development of distribution and migration in the Netherlands

It is generally accepted that the habit of migration has developed under influence of an unfavourable trend in the climatological situation. The critical phase in this respect for pond bats eventually living in N. W. Europe may have been reached at some time after the last glacial period. According to KOWALSKI et al. (cited from HANAK & GAISLER 1965, p. 125), pond bat skulls are known from central Europe in geological deposits since the Pliocene. Unfortunately, there is no evidence at all which proves that the pond bat has occured in N. W. Europe before it was described as a species by BOIE in 1825, as fossil specimens have never been found in this region. Bat remnants are not likely to have been fossilised at all in the Netherlands.

The only sensible thing left to do is just to regard some relevant aspects of the various ecological situations during the Holocene, and to ask oneself how pond bats could have lived in these situations, taking as a standard the biotopes which they prefer to live in nowadays (cf. 3.2.). These speculations will be mainly based on the recent review given by HAGEMANN (1969) on the holocene stratigraphy and climate in the western parts of the Netherlands.

3.4.1. Development of dutch landscapes

The development of these parts of the Netherlands during the Holocene depends on two main factors. First, a considerable and almost continuous rise of the sealevel. Secondly, the formation of a coastal barrier during the mid-Atlantic (approx. 4000 years B. C.), at about the place where it still exists.

At the end of the Pleistocene, some 8100 years B. C., this region consisted of a vast and mainly sandy plain. During the early Holocene it was invaded by a rising sea causing a wide landstrip along the transgressing sea to be drowned by a break of the ground water equilibrium. A freshwater backswamp area came into being for the first time then. As the sea went on rising, the backswamp moved upward towards the east. Peat growth in the western part of the coastal area started during the late Boreal (approx. 6000 B. C.), whereas in the eastern part the appearance of this „basis peat" layer has to be placed in the second half of the Atlantic (approx. 4000 B. C.).
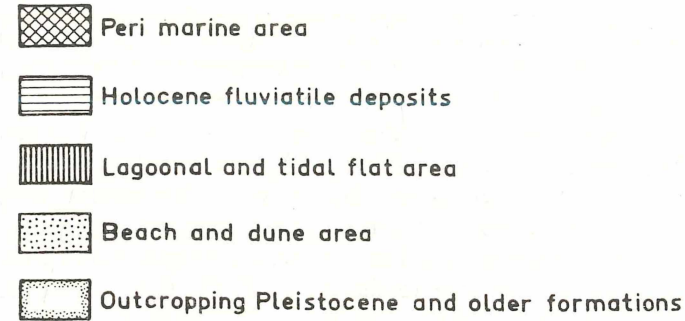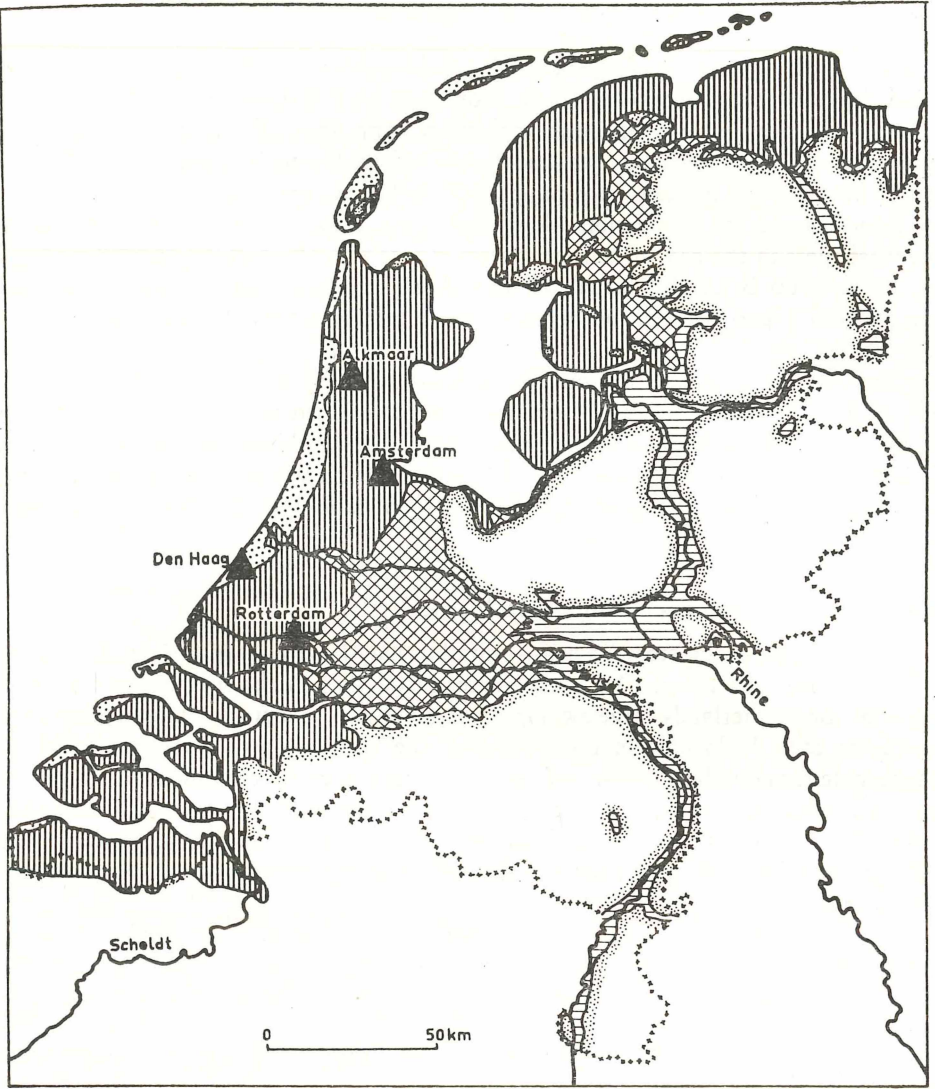
Map labels: Akmaar, Amsterdam, Den Haag, Rotterdam, Rhine, Scheldt

0   50 km

Legend:

- Peri marine area
- Holocene fluviatile deposits
- Lagoonal and tidal flat area
- Beach and dune area
- Outcropping Pleistocene and older formations

Figure 9. After HAGEMAN (1969): development of the western part of the Netherlands during the Holocene.

In the mid-Atlantic a l a g o o n a l   a n d   t i d a l   f l a t   a r e a developed be-
hind the coastal dune barrier (fig. 9). From then on untill the mid-Subboreal (about
1800 B. C.), marine sedimentation took place four times (the „Calais deposits") in
this area, which covered the basis peat. After that, the main layer of the „Holland
peat" developed in a practically completely freshened lagoon.

Renewed marine aggression along the coast caused new transgression at the
weakest spots in the coastal barrier system. These s. c. Dunkirk transgressions began
at about 1500 B. C. and lasted till 800 A. D. at least. They created the present
situation of superficial marine deposits in the former lagoonal area, as is shown in
fig. 10.

Towards the east, the lagoonal area is bordered by a   p e r i m a r i n e   a r e a
(fig 9). Here, marine or brackish sediments are absent, but peat growth was indirectly
favoured by the relative sea level movements causing the freshwater level to rise.
It is characterized by the occurrence of backswamp and fluviatile areas. In the latter,
clay layers alternate with peat layers cut by fossil sand-filled gulleys from the rivers
Rhine and Meuse.

3.4.2. Pond bat biotopes during the Holocene

In our opinion, the story of peat formation may be the story of former pond bat
habitats. From the above (3.4.1.) it is concluded that in the western and northern
parts of the Netherlands large swamp areas must have occurred almost permanently
since the early Holocene. In these swamps, the biotope must have been extremely
favourable for pond bats. Most probably, they have been covered by a rich vegetation
of reed, sedge, and many water plants leaving room only for river branches and a
network of narrow strips and pools of open water. On the east side, many of these
swamps were bordered by woods of oaks and other big trees, growing on pleistocene
formations.

A relatively warm and very humid climate may have allowed pond bats to live
there in all seasons. During summer, there must have been a rich insect fauna to feed
on. Plenty of hollow trees to roost in are likely to have occurred locally along the
eastern borders of the swamps. Probably, the winters have been so mild that hollow
trees may have given sufficient shelter to serve as hibernating roosts as well. Conse-
quently, migration would not have been needed at all in these times.

3.4.3. Development of migration

The last period of geological history, the Subatlantic (700 B. C. — Present), is
characterized by lowering of temperature. Some time during this period, conditions
in the supposed pond bat habitats in the western and northern parts of the Nether-
lands must have grown subliminal for hibernation, as temperatures in tree roosts
have begun to fall below zero then. Accordingly, pond bat populations living in
these regions would have been obliged either to emigrate, or to develop the habit
of seasonal migration to and from caves, in order to survive. Regarding their be-
haviour today (cf. 3.3.5.), it seems likely that they preferred to evacuate along the
rivers that passed their haunts, keeping near to the water all the time. Doing so,
they are guided almost automatically into the vicinity of caves which are found near
the origin of these rivers. Equally relevant to this purpose may have been several
branches of the Rhine, including the Vecht and the Ijssel leading to southern natural

cave areas, either via the Rhine itself towards the Eiffel, or via the Meuse to the Ardennes. The rivers Ruhr, Lippe, Overijsselsche Vecht, Ems and Hase could have guided them to natural caves in Westfalen and Niedersachsen (cf. fig. 6).

In spring, the absence of a suitable summer biotope in these cave areas may have forced them to follow the same rivers in the opposite direction, in order to reach again the presumed original habitats near the sea coast.

3.4.4. Development of synanthropy

In more recent times, activities of man have changed the pond bat haunts in the provinces of N. Holland and Friesland a great deal too.

On the one hand, man has changed biotopes by digging almost all peat using the soil for agriculture and meadows afterwards, and by cutting down trees. On the other hand, he probably saved these haunts for the pond bat population of N. W. Europe by impoldering and by digging canals and ditches, most of them becoming bordered by marsh vegetation. As substitutes for tree roosts which were cut down, he built church lofts and double brick-walls (cf. 3.2.2). Of course, the pond bats themselves have played an important role in this story too, by having shown a remarkable adaptability to these new situations.

In addition, man happened to create better migration routes for them by digging long and straight canals leading in all directions to the old hibernating areas (cf. 3.3.5.). He improved the number and the quality of hibernating roosts a great deal by excavating corridors in the limestone areas of dutch S. Limburg and Belgium (cf. 3.2.1.).

3.4.5. Explanation of the present locations of summer haunts

Since swamp areas have practically disappeared, pond bat summer haunts are found in wide polderland, where meadows grow on subatlantic marine deposits in a moderate and humid climate. This land is traversed by man-made reed-bordered canals (cf. 3.2.2.). A biotope like this one is found in almost every dutch coastal province, and in adjoining parts of Belgium and Germany.

As we have shown above (3.2.2.1.), the known pond bat nursing roosts, however, are confined to and remarkably concentrated in rather small habitats situated in N. Holland and Friesland. In our opinion, an explanation of this phenomenon may be found in the geological history of these habitats.

The habitat in N. Holland, due north of Amsterdam, belongs to the former lagoonal and tidal flat area. This part of the area remained free from the subatlantic marine transgressions (fig. 10). So, peat formation could go on in this habitat without interruption since about 1800 B. C. The same can be said from adjoining parts of the province S. Holland; but here, the relevant biotope has probably been spoiled for pond bats by the activities of an extremely dense human population living there today.

The frisian haunts, being the most important ones at present, are located due west of or in the former perimarine area where no marine transgression has taken place at all during the Holocene. In addition, peat formation has never been interrupted by fluviatile sedimentation in the frisian part of the perimarine area (fig. 9). Woods growing on nearby pleistocene and older formations may have provided tree roosts for pond bats at the very borders of these backswamps. In more recent times, the
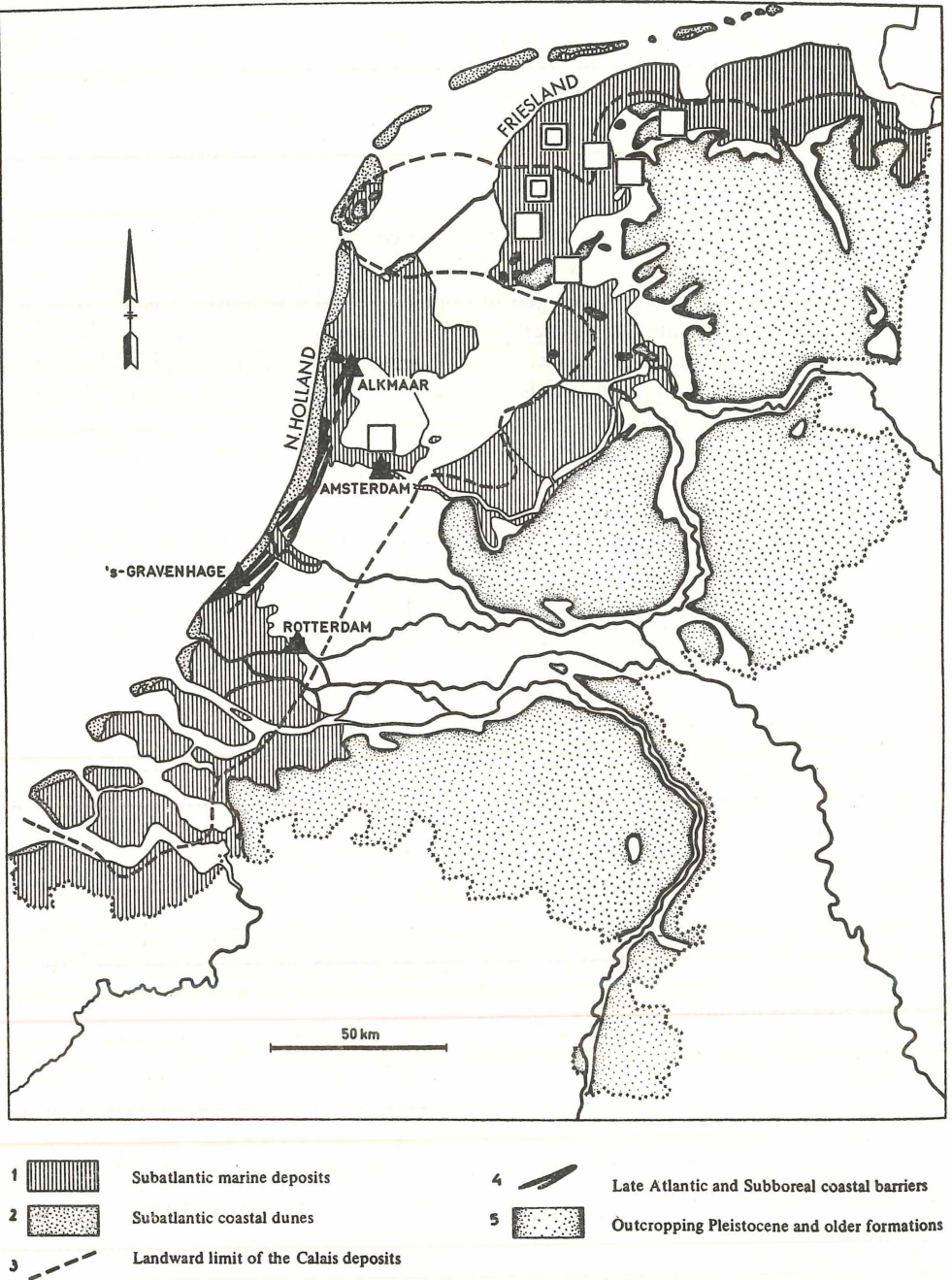
Figure 10. After HAGEMAN (1969): development of the western part of the Netherlands during the Holocene. In addition, the locations of recent nursing roosts (open squares) of the pond bat are drawn in this map.

frisian part of the perimarine area has been transformed into a lake district, which is evidently not preferred as a haunt by the pond bats (cf. fig. 3). Most of them may have retreated westward into nearby parts of the former lagoonal area where they can feed above and along canals and can roost on church lofts and in double brick walls.

Taking into account these historical considerations, the striking preference pond bats show for the present habitats in Friesland as well as in N. Holland might be caused by old traditions.

4. General discussion

The aim of this chapter is to compare the population biological features of the pond bat that we described in the foregoing pages, with the same particulars of the other bat species ranging commonly in the Netherlands.

4.1. Populations

4.1.1. Definitions

In our chapter on quantitative population data (2.) the word „population" has been used in the sense of a colony: a group of individuals of one species roosting together at the same places during the major part of the summer. Places are in case of the pond bat: nursing roosts on one or two church lofts located within the home range of the population concerned. Unfortunately, this definition holds only for females with their young, as the adult and subadult males and part of the subadult females do not live in a nursing roost. These bats are supposed to roost either individually or in small groups, their roosts being dispersed over a much wider area in the same region. Genetically, however, many of them must be members of the population under observation. Similar difficulties arise with regard to the populations of most bat species living in the temperate zone.

Regarding the annual behaviour cycle of these species, some additional difficulties have to be faced in defining a bat population. After weaning of the young ones, the members of a summer colony usually leave the place and disperse over a number of other roosts which are not known to the investigators. Most probably, the mature females among them join the males then, before they depart for hibernating quarters.

Formation of a colony during winter is common in *Nyctalus noctula* and *Pipistrellus pipistrellus*; it has also been observed in *Myotis myotis* and in rhinolophids. But usually specimens of both sexes, of all ages, and of different species are found roosting individually and mixed all over a winter quarter. If we try to define such a winter population in the same way as we did above, we have to reconsider our ideas on the place of occurrence of a population. During summer, this place may be confined to the home range around one or two nursing roosts of a colony, but during winter we are obliged to think in terms of a large number of individually hibernating specimens dispersed over either a cave or a cave area, a town, a province, or even a country. In addition, members of different summer populations may become united in a winter population of the same species, but having a quite different composition as to individuals. From the genetical point of view, this phenomenon might have a survival value, if many mature female bats should not be inseminated before they reach their hibernating cave. According to STRELKOV (1962), in the northern

parts of Russia the majority of them is, in fact, not yet inseminated then. This phenomenon has not been investigated in N. W. Europe, as far as we know.

4.1.2. Composition

A nursing roost of bats is populated for the greater part by adult females and their young. In pond bats, like in most other dutch species (cf. GAISLER 1966), this population is completed by a relatively small number of subadult females.

Regarding the adult and subadult females the question arises whether the specimens found in a given year are the same individuals as those which populated the roost the year before. According to a definition given before (SLUITER et al. 1956, p. 66) each banded bat recovered at the place of banding at least once during a period of investigation of several years is considered to have belonged to the population of this place all the time of this period. This allows emigration for one or more years provided that it is followed by reimmigration. In our opinion, temporary emigration from a nursing colony especially during the second year of life may occur in about 50 % of the female pond bats (cf. 2.1.2.2.). Permanent emigrants from a pond bat nursing colony are supposed to be males only (cf. 2.1.1.).

In other bat species, evidence on emigration of females from dutch nurseries is only observed in *Nyctalus noctula* (SLUITER & VAN HEERDT 1966).

4.1.3. Parameters

In the foregoing pages, population parameters like sex ratio (2.1.1.), survival rate (2.2.2.), and population size (2.2.4.) have been estimated in a summer population of pond bats.

It could be observed that s e x   r a t i o at birth is almost fifty-fifty, and is approximately equal to this rate observed in hibernating quarters. Though numbers of males and females of some other species suggest them to have a different sex ratio when hibernating (BEZEM et al. 1960, p. 528), it seems most probable that this ratio at birth is fifty-fifty in these species too (BEZEM et al. 1960, p. 534).

The estimate of the s u r v i v a l   r a t e obtained in a summer colony of pond bats may be compared with the same rate of 5 other species hibernating in the same caves as the pond bat (table 13).

This table suggests some variation around a mean value of 0.71. It is concluded that the survival rate of the pond bat is quite normal if compared with this rate in other bat species ranging in the Netherlands.

Table 13.   Estimates of survival rates of 6 bats species.

Species	Survival rate	Author
M. daubentoni	0.80	
M. mystacinus	0.75	
M. emarginatus	0.70	BEZEM et al. (1960, p. 524)
M. dasycneme	0.67	
Rhin. hipposideros	0.57	
M. dasycneme	0.70	SLUITER et al. (1970) (par. 2.2.2)
Plec. auritus	0.75	STEBBINGS (1966, p. 60)

Population sizes of different nursing colonies of the pond bat in the Netherlands vary from 50 to 300 individuals. Total sample sizes recorded in table 1 may be divided by the number of years of investigation and be multiplied by the factor 3 (2.1.2.1.), in order to get a rough estimate of the mean annual population size. All together the populations of 8 nursing colonies (10 roosts) which are known now in the Netherlands number approximately 1300 individuals of the pond bat annually. For *Pipistrellus pipistrellus* similar values for individuals in one dutch colony have been found recently; for *M. myotis* and *Nyctalus noctula*, the maximum of about 300 has only been scored in the past (BELS 1952), whereas for other species a nursing colony of 50 individuals is almost the maximum scored in our country. Nursing colonies numbering more than 300 individuals, however, are known of *M. myotis*, *Rhin. ferrumequinum* and *Pip. pipistrellus* in regions abroad.

The pond bats of the nursing colony at Kollum have been scared away and gone to unknown new summer roosts. During the period 1954/63, sample sizes have shown no trend indicating a change in population size of this colony (cf. table 6). As far as we can judge, the same may be said of other summer colonies of the pond bat known in the Netherlands at present. Between 1940 and 1957, the population size of pond bats hibernating in the limburgian cave area showed — like those of *M. emarginatus*, *M. myotis* and *Rhin. hipposideros* — a decrease of approximately 10 % annually (BEZEM et al. 1960, p. 535). Since 1958, this decrease has come to a standstill. Winter populations of *M. mystacinus* and *M. daubentoni*, on the contrary, have shown no trend to decrease during the same period.

In order to give an impression of the relative abundance of the pond bat compared with the other limburgian bat species during the period of five years following 1958, we have made the estimates recorded below. They are based on sample sizes which have been published before (SLUITER & VAN HEERDT 1964, p. 165). This time, the number of individuals of each species is given as a percentage of the total number of 7 species combined: *M. mystacinus* 30 %; *M. daubentoni* 19 %; *M dasycneme* 15 %; *M. nattereri* 14 %; *Rhin. hipposideros* 8 %; *M. emarginatus* 8 % and *M. myotis* 6 %.

It is concluded that the pond bat has taken a medium position as to relative abundance in S. Limburg during the period of investigation.

The rate of capture (2.2.3.) is not an unbiased biological parameter, as it depends partly on the effort and the skill of the investigator. On the other hand, the bats may influence this rate by hiding away more or less, and by temporary emigration towards roosts which are not known to, respectively are not visited by, intruders. These habits, which may have a considerable survival value (cf. 2.2.5.), are somehow reflected in the value of the rate of capture too. For the pond bat, this rate (0.17) may be called average, if compared with other species hibernating in the same caves. According to BEZEM et al. (1960, p. 524), these values vary from 0.13 (*M. mystacinus*) to 0.23 (*Rhin. hipposideros*).

4.2. Biogeography

In this chapter we will discuss some ecological factors which tend to determine the geographical distribution of dutch bats. They are: thermophily, selection of roosts, feeding biotopes, and survival value of migration. Distribution in the Netherlands will be placed against the background of distribution in Europe.

4.2.1. In the Netherlands

If this discussion is restricted to the biogeography in a very small country like the Netherlands, the factor thermophily may be almost neglected, as mean temperatures do not differ so much in most parts of this country.

The relevant data concerning habitats, roosts, feeding biotopes, and migration are summarised in table 14 according to the following definitions:

WINTER HABITATS: parts of the Netherlands where winter roosts occur.

W i n t e r r o o s t s : hiding places where bats hibernate.

T r o g l o p h i l i c : in caves and subterranean quarries. In the Netherlands, these are found in the utmost south (S. Limburg) only.

O i k o p h i l i c : in subterranean parts of buildings (cellars) including fortresses and ice cellars. Sometimes, also draft courses in double brickwalls, for instance in case of *Eptesicus serotinus* and *Pipistrellus pipistrellus*, are relevant.

D e n d r o p h i l i c : in tree cavities and nest boxes which are fixed on trees.

SUMMER HABITATS: parts of the Netherlands where summer roosts occur.

S u m m e r r o o s t s : hiding places where bats roost during daytime in summer.

T r o g l o p h i l i c : in caves and subterranean quarries. The occasions that dutch quarries provide summer roosts, which are favourable as to the factors temperature, light and disturbance, are rather rare.

O i k o p h i l i c : in and under roofs (lofts); in holes, crevices, and draft courses in walls of buildings; behind window shutters.

D e n d r o p h i l i c : in tree cavities and nest boxes which are fixed on trees.

FEEDING BIOTOPE: ecological features of places where the bats feed.

MIGRATION: a genuine migration, i. e. a regular shifting between summer and winter habitats (cf. 3.3.).

O b l i g a t e : if summer and winter habitats are found in different regions; „long distance" means that these habitats are from 150 to 300 km apart.

F a c u l t a t i v e : if summer and winter habitats overlap completely, whereas a genuine shifting between summer and winter roosts either occurs or not; „short distance" means that these roosts are from 20 to 150 km apart. For instance, the population of *Myotis myotis*, hibernating in the cave area of S. Limburg has been observed to split up in two parts in spring. One part stayed in this area building a nursing colony in a cave, but the other migrated over 100 km to a church loft at Berlicum (prov. of N. Brabant) in order to settle there for the summer (cf. BELS 1952).

N o n e : if summer and winter habitats overlap completely, whereas individual winter and summer roosts are situated from 0 to 20 km apart.

Table 14. Habitat selection of bats living in the Netherlands (cf. text par. 4.2.1.).

Species	M. das.	M. myotis M. emarg.	M. myst. M. daub. M. natt.	Ept. ser. Pip. pip.	Plec. aur.	Rhin. f. e. Rhin. hipp.	Nyct. noct.
WINTER HABITATS	S. Limburg	S. half of Netherlands	everywhere	everywhere	everywhere	S. Limburg	everywhere
Winter roosts	troglophilic	troglophilic, (oikophilic) [1]	troglophilic, oikophilic	oikophilic	troglophilic, oikophilic	troglophilic	dendrophilic
SUMMER HABITATS	Friesland, N. Holland	S. half of Netherlands	everywhere	everywhere	everywhere	S. Limburg	everywhere
Summer roosts	oikophilic	oikophilic, troglophilic	oikophilic, dendrophilic	oikophilic (dendrophilic) [2]	oikophilic, dendrophilic	oikophilic, troglophilic	dendrophilic
FEEDING BIOTOPE	canals in polderland	no special	no special	no special	no special	wooded hills	woods, parks
MIGRATION	obligate, long distance	facultative, short dist.	facultative, short dist.	none	none	none	none

[1] For M. myotis only.
[2] Pip. pip. has been found either single or in small groups in nest boxes.

According to its pure troglophily during winter, a dutch winter habitat of the pond bat has to be located in S. Limburg. In the other dutch species — except *M. emarginatus* and both rhinolophids — habitats (winter and summer) are not limited in this way, as these species may roost in buildings and/or trees which may be found almost everywhere in the Netherlands.

A similar conclusion may be drawn on the relation between feeding biotopes and dutch habitats. Summer habitats of the pond bat are likely to exist only in the coastal provinces where their own feeding biotope exists. Species which have no special demands in this respect may feed almost everywhere. As woods and parks are widely spread over the Netherlands, the noctule bat belongs to the latter group also.

The location of winter and summer habitats (cf. table 14) completely explains why the pond bat is the only obligatory migrating dutch bat species.

4.2.2. In Europe

From our own experience and from the relevant literature, we have got the general impression that most ecological features, as described for a number of dutch bat species in table 14, are not much different when these species are ranging elsewhere.

Regarding Europe, however, the factor thermophily can be no longer excluded from our discussion on biogeography. As before (BEZEM, SLUITER & VAN HEERDT 1964), we will take the northern boundary of the range of a species as a measure of its thermophily. In order to give an impression of the variability of this factor, we have roughly drawn these northern boundaries (according to VAN DEN BRINK 1968) for the bat species which commonly occur in the Netherlands, adding the July isotherms for 10, 15 and 20 degrees centigrade, in figs. 11 and 12. The latter have been chosen, as bats which are able to hibernate in frost-free roosts are supposed to depend mainly on summer temperatures.

Six dutch species appear to be less thermophilic than the pond bat (fig. 11): *M. mystacinus, Plec. auritus, M. daubentoni, Pip. pipistrellus, Nyct. noctula* and *M. nattereri*. For the former three, being the most northern ones, not only the average July temperature, but also the shortness of the summer and the persistence of light during the summer nights may be limiting factors (RYBERG 1947, p. 22).

Five dutch species are ranging south of the northern boundaries of the pond bat (fig. 12): *Ept. serotinus, M. myotis,* both rhinolophids, and *M. emarginatus.* The latter four have the northern boundaries of their range mainly south of the Netherlands; for all five of them thermophily seems to be the main limiting factor.

Western boundaries of bat ranges in Europe are limited by sea generally. An exception to this rule is the pond bat, as this species has not been found in the major part of France (cf. MENU 1965). The lack of suitable feeding biotopes in the middle west of Europe located within about 300 km from a suitable hibernating habitat is likely to be the limiting factor for the pond bat.

4.2.3. Historical development of geographical distribution

According to our historical review in par. 3.4., the s. c. „pond" bat must have been a „swamp" bat originally which has developed into a „canal" bat in the Netherlands. In the swamps where it is supposed to have been living in former times, hollow trees must have been the only roosting places available for bats. Hence, the pond bat is thought to have been purely dendrophilic originally in these regions.
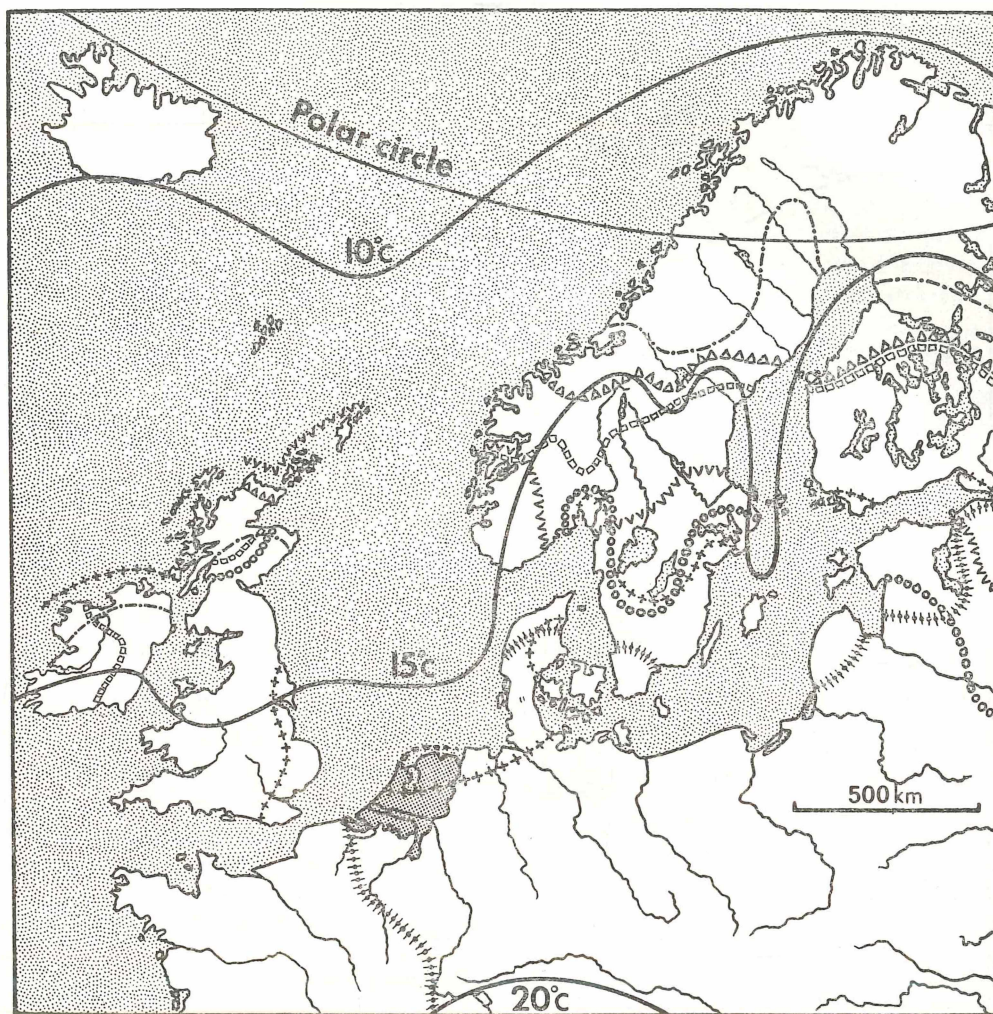
Figure 11. Northern boundaries of the european ranges of *Myotis dasycneme, M. daubentoni, M. mystacinus, M. nattereri, Nyctalus noctula, Pipistrellus pipistrellus* and *Plecotus auritus*, compared with the July-isotherms of 10, 15 and 20 degrees centigrade.
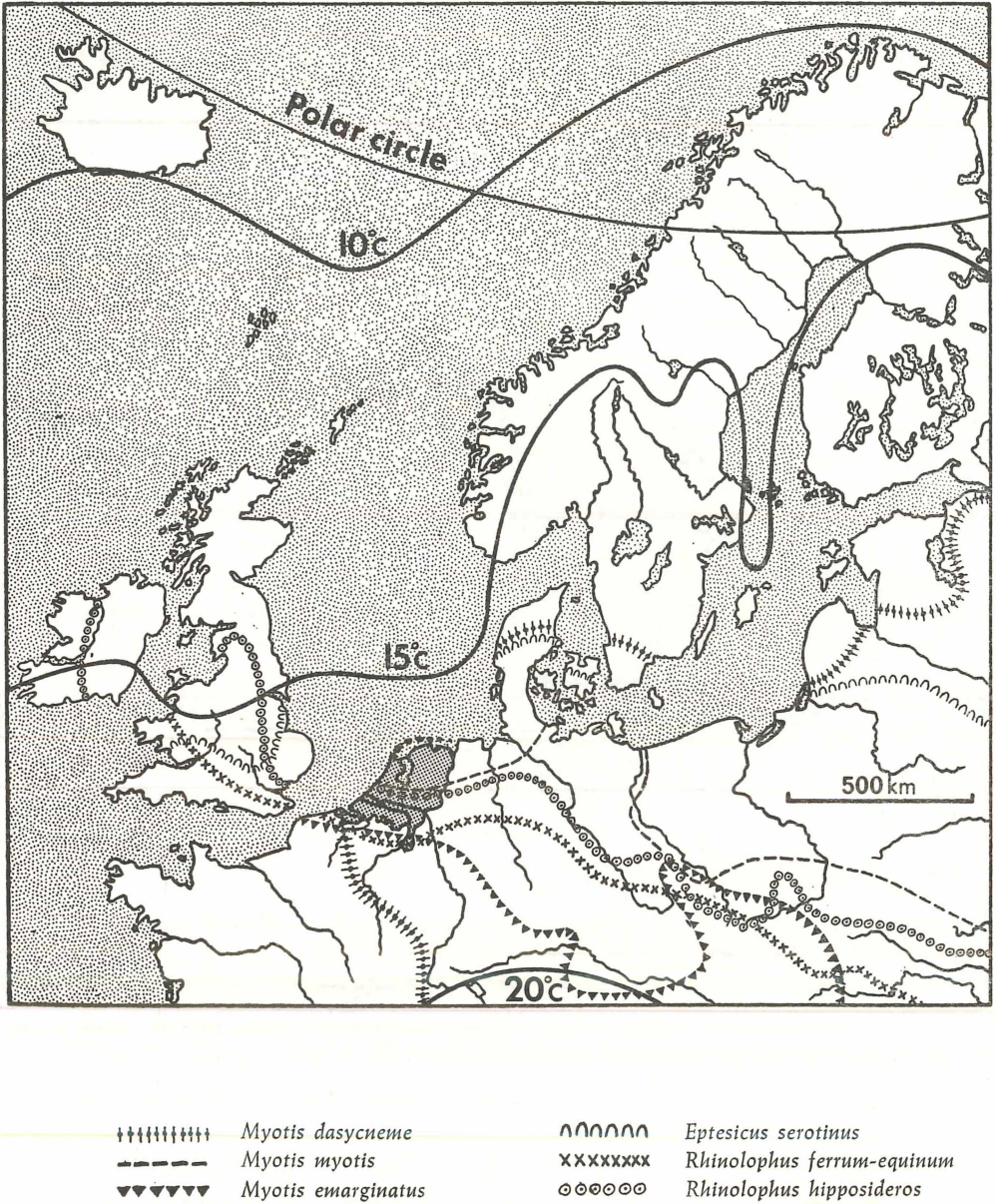
Figure 12.   Northern boundaries of the european ranges of *Myotis dasycneme*, *M. emarginatus*, *M. myotis*, *Eptesicus serotinus*, *Rhinolophus ferrum equinum*, *Rh. hipposideros*, compared with the July-isotherms of 10, 15 and 20 degrees centigrade.

The troglophily which it shows today only during winter, must be an adaptation for finding new hibernating roosts, as the climate became unfavourable. Accordingly, it must have necessarily developed its migrating habits. The oikophily which it shows today during summer, must be an adaption for the occupation of new summer roosts, as hollow trees failed to be present in or near their special feeding biotope.

The four bat species which reach their northern boundary in the southern half of the Netherlands at present *(M. myotis, M. emarginatus,* and both rhinolophids), on the contrary, most probably are troglophilic originally, for two reasons. First, they show a strong troglophily when hibernating at present, while they are roosting often in caves during summer. Secondly, in former times their population centres probably have been located in regions south of the Netherlands, where plenty of suitable caves must have occurred at all times. In accordance with this, their present populations in W. Europe still largely increase in density towards the south. Oikophily is likely to be an adaptation which has enabled these species to extend their range of occurrence towards the north into regions where temperatures are too low to allow for troglophily during summer.

A discussion on the prehistorical whereabouts of the remaining dutch species has to be still more speculative, as no evidence on present nor on former special population centres exists. As far as they were dendrophilic, they may have lived also in the woods which formerly existed in the eastern and southern parts of the Netherlands on outcropping pleistocene and older formations (fig. 10). Oikophily is doubtless one of the main adaptations allowing most of them both to hibernate and to spend the summer in regions where caves and hollow trees are scarce or completely lacking. If combined with a rather low degree of thermophily and no demands for special feeding biotopes, this may have enabled some of them to extend their range of occurrence considerably more northward (cf. fig. 11: *M. mystacinus, Plec. auritus,* and *M. daubentoni)* than the pond bat has been able to do.

Entering a cave in winter, one may find specimens of several bat species hibernating together. It is a remarkable thing to realize that the way in which they have become troglophilic may be different for several of them.

5. Summary

From 1954 till 1969, eight nursing colonies of the pond bat were found in the Netherlands, numbering almost 1300 individuals all together. They were distributed over ten roosts: one in the province of N. Holland, nine in the province of Friesland. Eight roosts were located on church lofts, two in the draft course of a double brick wall of a house.

A quantitative study of one of the largest colonies revealed that the population size was constant from 1955 till 1962, numbering approximately 220 individuals each time at the end of July. The composition of a pond bat nursing colony may be roughly estimated in fractions as follows: adult males 0.02, adult females 0.45, subadult females 0.08, juveniles 0.45. The sex ratio of the juveniles was almost fiftyfifty. The survival rate of adults was 0.70. Accordingly, the mean life expectation of this part of the colony was 2.8 years, the life span 13 years. The rate of capture of adults was estimated as about 0.25. The females born in this colony are presumed to have returned to the same roost each summer after they had become adults; almost 50 % of them temporarily emigrated to other summer roosts as long as they were

subadults. Ring damage to the wing membranes occured more frequently to bats banded in nursing colonies (28 %) than to those banded in hibernating quarters (10 %).

The following biological particulars of the pond bat came out of ecological observations and results of banding. In the dutch summer roosting places, 1139 specimens were banded procuring 19 foreign returns. These results were added to those of almost 3000 bandings formerly made in winter quarters located in the southern Netherlands, in Belgium, and in W. Germany. The pond bats ranging in these regions appeared to depend on a special feeding biotope with reedbordered canals, as it is found around their present summer roosts, and on caves (subterranean quarries included) when hibernating. Accordingly, they are obliged to migrate twice a year over a distance of from 200 to 300 km which separates their summer and winter quarters. This distance was covered in about a fortnight on average. Doing so, they most probably find their way by following waterways (especially canals) which happen to connect these quarters.

The results summarized above explain almost completely the present geographical distribution of the pond bat in N. W. Europe. It is tentatively suggested that this population has been concentrated formerly in swamp areas which are known to have occurred in the Netherlands from the early Holocene on. The changing climate during the Subatlantic may have forced them to become troglophilic during winter. Accordingly, they had to populate relevant cave areas in Belgium and W. Germany. But their presumed traditional bonds with the location of two former swamp areas in the Netherlands have not been broken, as their present summer haunts were still found only there.

Our assumption that they formerly were living only in swamp areas implies that they must have been purely dendrophilic originally. The oikophily which they show at present during summer must have developed, when man cut down the hollow trees growing in and near their feeding grounds. In addition, these pond bats have had to accept and to profit by the consequences of several other human activities, like peat digging in and impoldering near their summer habitats, as well as quarrying in their winter habitats. Especially the digging of canals may have considerably improved their feeding biotope as well as their migration routes.

The difficulties in defining a bat population in connection with their annual behaviour cycle are discussed in the last chapter. Furthermore, population-biological features of the pond bat are compared with similar particulars of the other bat species ranging commonly in the Netherlands. No striking differences are found concerning composition of a nursing colony and population parameters like sex ratio, survival rate, and size. Regarding biogeographical data, however, the pond bat appears to be a rather exceptional species as to distribution of habitats, special demands for feeding biotopes and hibernating roosts (cf. table 14). In consequence of this, the pond bat is found to be the only obligatory migrating bat species in the Netherlands.

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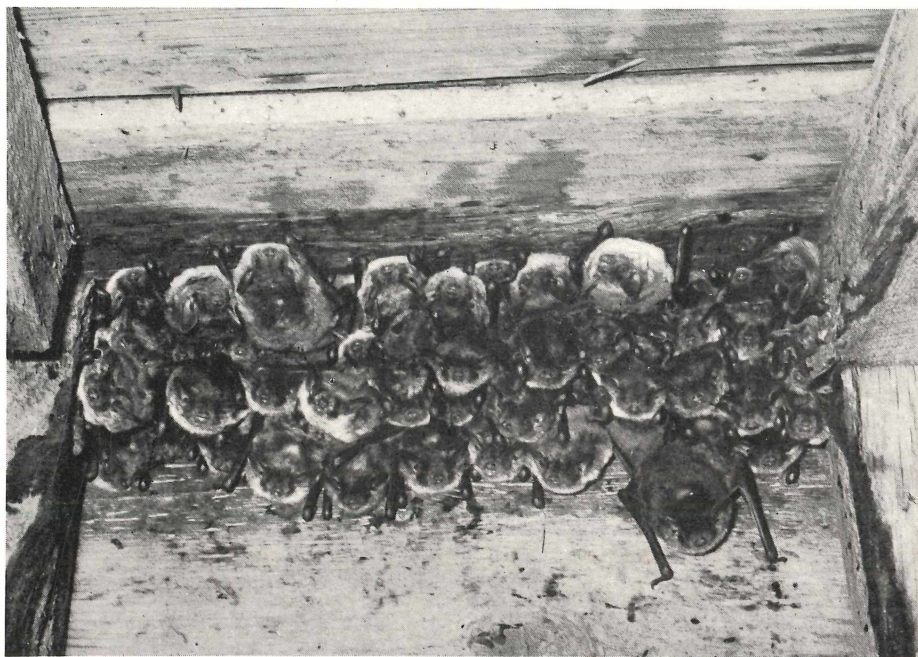
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Plate I.   A nursing colony of pond bats roosting on a church loft at Beetgum (no ridge-pole) in the apex of the roof. Photo Unfi.