Habitat selection of bats hibernating in a limestone cave

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1. Introduction

In several papers (e. g., van Nieuwenhoven, 1956 and recently Punt and Parma, 1964) attention has been drawn to the fact that cave-dwelling bats can be found anywhere in the caves at the beginning of the hibernating season, whereas they concentrate more and more near the entrance as the winter advances. The gaining of further and more detailed information about this phenomenon was the main goal of the investigation here described, which was carried out in one of the artificial limestone caves in South Limburg (The Netherlands).

This cave-complex, the „Geulhemergroeve" (number 87 in Bels' 1952 list of the South Limburg excavations), was mapped out during a preparatory investigation in the winter of 1962/63 and then visited monthly from October 1963 until May 1964. Of every twoday visit the first day was spent in systematically searching the whole cave and plotting on a map the bats thus found. On the second day temperature measurements were carried out near the bats and at several stations throughout the cave.

In the Geulhemergroeve nine species of bats were found hibernating:

Barbastella barbastellus (Schreber, 1774)
Myotis dasycneme (Boie, 1825)
Myotis daubentonii (Kuhl, 1819)
Myotis emarginatus (Geoffroy, 1806)
Myotis myotis (Borkhausen, 1797)
Myotis mystacinus (Kuhl, 1819)
Myotis nattereri (Kuhl, 1818)
Plecotus spec.: *P. auritus* (Linnaeus, 1758) or *P. austriacus* (Fischer, 1829)
Rhinolophus hipposideros (Bechstein, 1800)

One of the requirements of the investigation has been to avoid any disturbance of the hibernating animals. We did not band or even touch any bat, but only made silently notes about their positions and ambient temperatures. The necessary experience in identifying bats without handling them had been obtained during several winter excursions to the South Limburg caves under the direction of Prof. Dr. A. Punt (Laboratory of Animal Physiology, Amsterdam).

2. The cave of investigation

Topography

The Geulhemergroeve (see figure 1) is a large limestone excavation situated in the hills bordering the valley of the river Geul at the south side, in the municipality of Berg and Terblijt. The cave is connected by a narrow corridor with the much smaller "Koepelgroeve" (Bels' nr. 84), which has been dug out in a marl layer lying about ten meters below the Geulhemergroeve level. Except for this corridor the cave is practically horizontal, with a very slight slope upwards — roughly a rise of 8 meter over a distance of 600 m. — running southward from the main entrance in the north. There is not much variation in height and width of the corridors (estimated averages: height 2.50 m.; width 3.00 m.).

The Geulhemergroeve has four entrances originally, three of which were closed up by brick walls in the summer of 1963. In each of these walls small holes were kept open, especially to enable bats to fly in and out (thin arrows in figure 1). The main entrance is closed by an iron gate (fat arrow). In the Koepelgroeve one entrance was likewise closed by a wall with a bat hole, and one remained open during both seasons of investigation. Finally, there is a connection with the outside world in a vertical ventilating shaft (see figure 1), about 35 meters high, which was sunk by a former mushroom grower in the Geulhemergroeve. This shaft is only one meter across and is probably not used as an exit or entrance by the bats hibernating in the cave.

In order to facilitate the evelution of the data collected on bat distribution and temperature, we divided the whole cave — the two caves will be regarded as one and called Geulhemergroeve for the purposes of this article — arbitrarily into eight sections, numbered I—VIII (see figure 1). Of each section the total area of the corridors was determined by weighing the corresponding areas of a map (scale 1:1.000), cut out along the walls, and by dividing the values thus obtained by the weight of 100 cm² of the same paper, corresponding with 10.000 m² (= 2.47 acres). The corridor surfaces of the sections are given in table 3.

Microclimatology

Measurements of air temperature on the ground and near the roof in the corridors were taken on the second day of each visit at twenty-three stations, which are indicated in figure 1 as a — w. An NTC-thermometer as described by Punt and Parma (1964) was used. It would carry too far to give here all the data of temperatures measured. The range of variation of the temperature at each of the 24 stations and in each of the eight sections is shown in table 1.

It is not surprising that sections I and II, where the two prominent entrances are located, have the largest fluctuations in temperature, since cave conditions here are, of course, largely influenced by the weather outside. On the other hand, the rear of the excavation (section VIII, stations v, w) remains fairly constant at about 10.4° C. Sections IV and VII likewise fluctuate very little in temperature, though a bit more than section VIII. Sections III, V and VI are climatologically intermediate between these "peripheric" sections and the entrance areas. Section V, though, contains an entrance in the form of three small bat holes in a brick wall, that connect the cave with the outside world. These connections, however, influence the cave circumstances far less than a large entrance does. In 1962/63, before the brick wall was built, the range of fluctuation in section V was —1,6—7,9° C (roof) and —4—7,2° C (floor). The warming effect of the wall in 1963/64 is obvious.
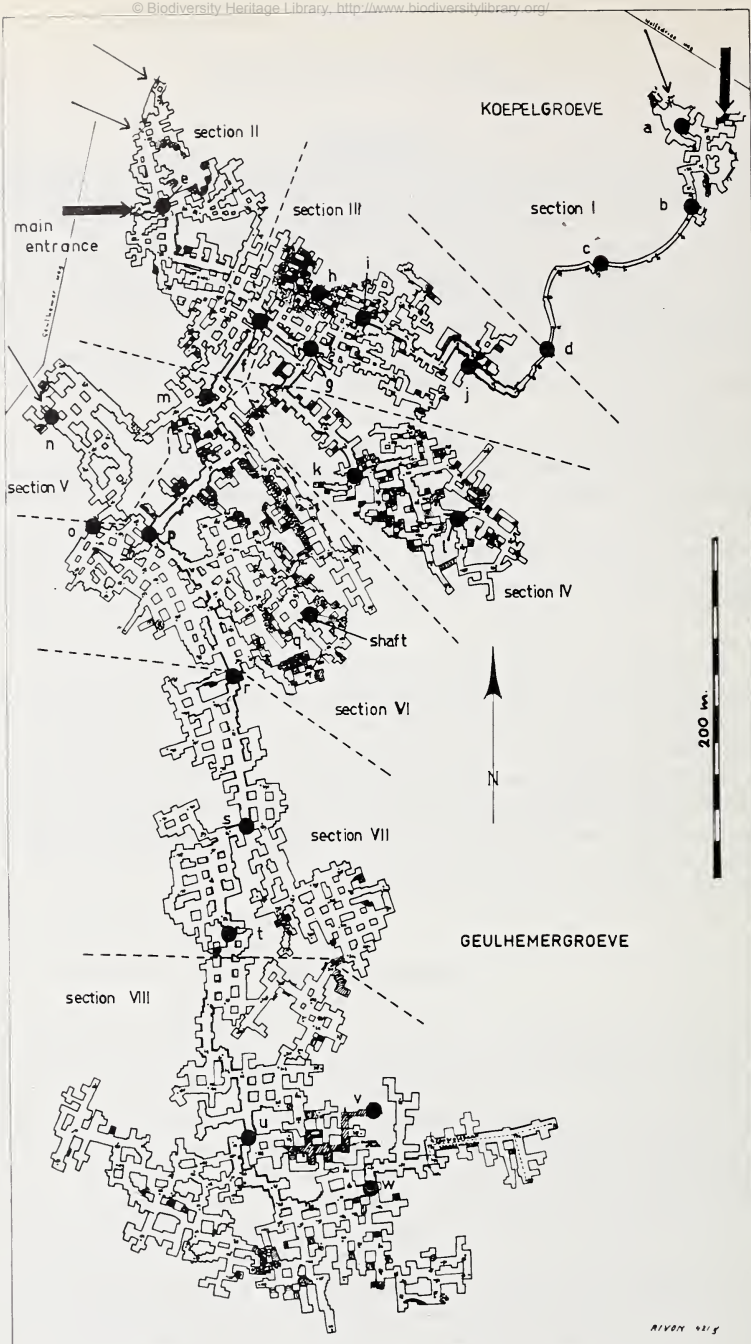
Fig. 1. Map of the excavation; entrances, sections and temperature stations are indicated. There are two main corridors: one in west-east direction, leading from the main entrance to the Koepelgroeve (stations e, f, g, i, j, d, c, b, a) and one in north-south direction (stations e, f, m, p, r, s, t, u, w). Thick arrows point to entrances, thin arrows to former entrances with bat holes

Figures 2 and 3 give an impression of the distribution of roof temperatures over the cave for one day in each season with mildly freezing weather. Again, these figures demonstrate that air temperatures were higher in 1963/64 in most parts of the cave. This difference is probably due to the prolonged periods of severe frost in 1962/63 and to the construction of walls in most of the entrances. The most drastic change came about in section V, sections I and II each having retained one entrance.

Figure 4 shows the temperatures measured along the two main corridors on October 20, 1963 and on January 4, 1964. Under the graphs the height-length diagrams of both corridors are given (please, note the different horizontal and vertical scales!). The differences in temperature between both dates are of course only striking in entrance areas (stations a, b, c, d, e, f). In the deep periphery of the cave (stations t, u, v, w) outside conditions have lost their influence. Except for the entrance, this is always the warmest part of the cave. Intermediate areas (stations f, m, p, r) are always colder than the rear, at high as well as at low outside temperature.

Table 1

Range of temperatures measured at 23 stations (see figure 1) in the Geulhemergroeve on seven days in the season 1963/64

Outside temperature ranged on these days from — 5° C (December 12) to 17° C (October 20) –

Station	Section	Roof air layer	Bottom air layer
a	I	3.0— 8.4	0— 8.4
b	I	4.1— 8.9	4.1— 8.8
c	I	5.1— 8.8	5.1— 8.8
d	I, III	6.1— 8.8	5.8— 8.8
e	II	3.2—11.7	—3.1—10.3
f	II	6.5— 9.0	5.8— 8.8
g	III	7.5—10.0	7.3— 9.9
h	III	8.4— 9.2	8.2— 9.1
i	III	8.2— 9.2	8.1— 9.0
j	III	6.5— 9.1	6.1— 8.9
k	IV	9.6—10.1	9.4—10.0
l	IV	9.9—10.4	9.9—10.4
m	V	6.7— 9.0	6.5— 8.8
n	V	7.4— 8.7	7.3— 8.5
o	V, VI	7.7— 8.4	7.5— 8.2
p	VI	8.2— 9.2	8.1— 8.9
q	VI	8.8— 9.7	8.8— 9.2
r	VI, VII	9.3— 9.7	8.9— 9.5
s	VII	10.0—10.4	9.8—10.3
t	VII	10.3—10.4	10.2—10.3
u	VIII	10.3—10.5	10.2—10.4
v	VIII	10.3—10.6	10.3—10.5
w	VIII	10.3—10.4	10.3—10.4
section	I	3.0— 8.9	0— 8.8
	II	3.2—11.7	—3.1—10.3
	III	6.1—10.0	5.8— 9.9
	IV	9.6—10.4	9.4—10.4
	V	6.7— 9.0	6.5— 8.8
	VI	7.7— 9.7	7.5— 9.5
	VII	9.3—10.4	8.9—10.3
	VIII	10.3—10.6	10.2—10.5

Moreover, the entrance section II (stations e, f) is distinguished by a great difference in temperature between roof and bottom air layers, whereas these values are nearly equal further back in the cave. This is due to thermocirculation: At low outside temperatures (in January), cold air flows into the cave along the ground, whilst along the roof there is a much warmer current in the opposite direction. In summer the situation is just the reverse: relatively cold air from the interior of the cave flows out over the ground, and relatively warm air is drawn inwards along the roof. This is usual in the so-called *static horizontal caves* (cf. van Nieuwenhoven, 1956) to which the Geulhemergroeve can largely be reckoned.

However, there are two features in the topography of the cave, which give a slightly 'dynamic' aspect to the microclimate. The first is the steep corridor connecting the Geulhemergroeve with the Koepelgroeve. In the right half of figure 4 (bottom) the temperatures measured in section I (stations a—d) show that hardly any difference exists between top and bottom air layers in this corridor, although temperature fluc-

tuation is as large here as in the entrance section II. Obviously, there is no normal thermocirculation pattern in the corridor: when the outside temperature is low, cold and dry air from the Koepelgroeve is drawn upwards rapidly through the whole corridor, as in an internal chimney. But when it is warm outside (in summer), there is a draught in the opposite direction, from the Geulhemergroeve down to the Koepelgroeve. In the corridor there is neither air stratification nor a separate movement of top and bottom layers. Wind measurements taken in 1962/63 showed us that the upward current in winter may exceed a speed of 60 centimeters per second.

More or less the same happens much more rapidly in the vertical shaft in section VI. Standing in the cave under the shaft on a hot day in summer, one can feel warm air from the outside running down. On the other hand in frosty weather a cloud of condensation above the shaft marks the upward current of damp air from within the

Fig. 2. Distribution of roof air temperatures on February 28, 1963. Outside temperature around freezing point (— 0,2° C)

Fig. 3. Distribution of roof air temperature on January 4, 1964. Outside temperature around freezing point (— 0,6° C)

cave. Generally speaking, in summer the cave has a chilling influence on the air, and a down current is established from the higher to the lower apertures. In winter, air is warmed up in the cave and — as in a stove — currents are directed upwards.

As was stated above, however, by far the largest part of the cave has been dug out at nearly one level, and in that part the normal thermocirculation pattern persists — especially in the main entrance section II, and formerly in the entrance section V as well. The summer and winter circulations in the two main corridors of the cave are diagrammed in figure 5 and 6.

Measurements of humidity were not carried out. It is a wellknown fact that the large limestone caves have a fairly high relative humidity of 95 to 100 %/0 in the deepest parts. In the entrance areas under winter conditions the air layers near the
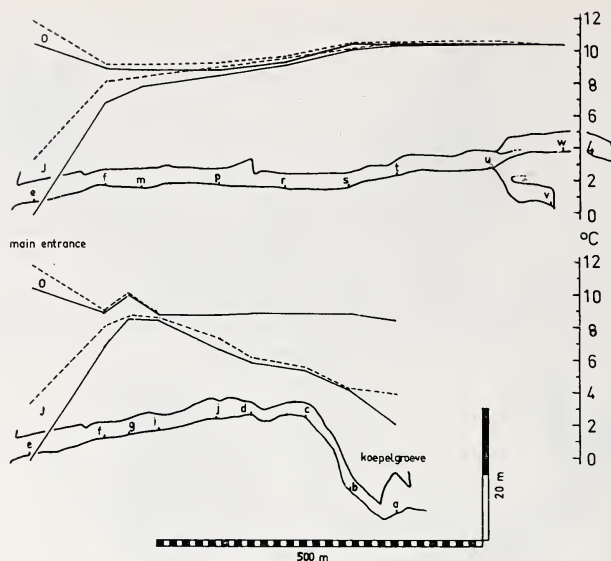
Fig. 4. Roof (dotted line) and bottom (drawn line) air temperatures along the two main corri-
dors on a warm (October 20, 1963; O) and a cold day (January 4, 1964; J). Height profiles
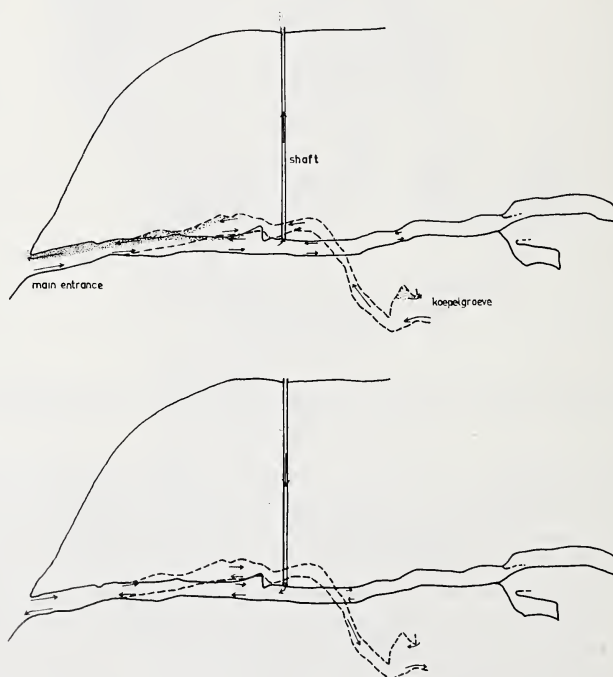of these corridors are also shown (note the different horizontal and vertical scales)

Fig. 5 (above). Winter pattern of circulation in the two main corridors and in the ventilation
shaft. Areas of condensation are dotted. Scales as in figure 4 — Fig. 6 (below). Summer pattern
of circulation in the two main corridors and in the ventilation shaft. Scales as in figure 4

roof, coming from the inside, are very damp, which often results in fog by the chilling influence of the lower air current. The latter is cold and dry. Stratification of the air layers in the entrance sections is strictly horizontal; consequently the horizontal limit of the fog in winter can be fairly sharp. The extension of this "condensation zone" in limestone caves can be defined by hanging light metal strips from the roof of the corridors and by checking after a few days if any condensation has taken place (VAN WIJNGAARDEN, in press). A standard interval between hanging and reading of the strips — e. g., two days — should be observed. After a month or more even in the farthest rear of the excavation the strips will be covered with a coat of dew.

Heavy condensation within a few days, and limited to the upper parts of the corridors occurs only in those entrance areas with thermocirculation and with a well marked difference in temperature between roof and bottom air layers. In frosty days, the condensation zone in the Geulhemergroeve covered about the sections I (except for the draughty steep corridor between the caves) and II. In 1962/63, before the entrance in V was closed up, also in V and VI a zone of condensation used to be established.

Fig. 7. Distribution of bats on October 19, 1963. Each dot represents one animal

Fig. 8. Distribution of bats on April 2, 1964. Each dot represents one animal

S. Daan and H. J. Wichers

3. "Internal migration"

During several preparatory visits in 1962/63, we had got the impression that the bat populations hibernating in the Geulhemergroeve move to the entrance parts of the cave in the course of winter. More detailed data concerning this phenomenon were collected during eight visits in 1963/64: October 19, November 16, December 14, January 3, February 5, March 8, April 2 and May 5. At each of these days the cave was investigated thoroughly, and the exact location of every bat present — as far as visible — was noted on a map of the cave.

Figures 7 and 8 summarize the distribution of the bats at two of these dates. On October 19, most of the animals were found in the southern half, in the rear of the excavation. On April 2, these "peripheric" sections had been almost completely abandoned and the bats were sleeping in large concentrations in the front of the cave.

Table 2 contains the total numbers of bats — regardless of species — found to be present during each of the visits in the various sections, and in the whole cave. Evidently, the number of bats hibernating in the Geulhemergroeve increased mainly during the months of October and November, to remain fairly constant at 98—99 specimens from December until March. In April most animals left the cave in search of their summer habitats.

The distribution of the bats over the different sections remains by no means the

Table 2

Number of bats present in each of the sections per visit

Section	Oct. 19	Nov. 16	Dec. 14	Jan. 3	Feb. 5	Mar. 8	Apr. 2	May 5
I	1	14	17	14	18	25	16	0
II	0	7	15	28	33	31	33	2
III	0	4	5	5	6	7	5	2
IV	0	3	3	2	1	1	0	0
V	1	10	26	22	26	24	15	1
VI	2	8	13	11	4	5	3	1
VII	5	8	7	9	8	3	2	1
VIII	16	13	12	8	2	3	2	2
whole cave	25	67	98	99	98	99	76	9

Table 3

Number of bats per 10 000 m² corridor surface in each of the sections per visit

Section	Surface	Oct. 19	Nov. 16	Dec. 14	Jan. 3	Feb. 5	Mar. 8	Apr. 2	May 5
I	1,600	6.2	87	106	87	112	156	100	—
II	5,200	—	13	29	54	63	60	63	3.8
V	2,600	3.8	38	100	85	100	92	58	3.8
III	5,200	—	7.7	9.6	9.6	12	13	9.6	3.8
VI	10,000	2.0	8.0	13	11	4.0	5.0	3.0	1.0
IV	4,600	—	6.5	6.5	4.3	2.2	2.2	—	—
VII	7,600	6.6	11	9.2	12	11	3.9	2.6	1.3
VIII	16,300	9.8	8.0	6.8	4.9	1.2	1.8	1.2	1.2
whole cave	53,100	4.7	13	18	19	18	19	14	1.7

Table 4

Specific composition of the cave population in each visit

Species	Oct. 19	Nov. 16	Dec. 14	Jan. 3	Feb. 5	Mar. 8	Apr. 2	May 5
B. barbastellus	—	—	1	—	—	1	—	—
Plecotus spec.	—	—	1	1	1	—	—	—
M. nattereri	—	—	3	3	5	5	3	—
M. mystacinus	2	22	24	28	29	27	21	1
M. daubentonii	6	20	30	30	23	27	21	—
M. myotis	5	6	10	10	9	8	5	1
M. dasycneme	10	8	16	14	18	19	16	1
R. hipposideros	1	3	3	3	4	4	3	—
M. emarginatus	1	8	10	10	9	8	7	6
together	25	67	98	99	98	99	76	9

same throughout the season. For instance, section VIII lodged 16 bats in October, which number steadily decreased during the winter. In the mean time, there were three sections (I, II, V) with an increasing bat population.

These entrance sections contain the largest numbers of bats. But as the sections as distinguished by us are widely different in area, these figures do not represent sufficiently the differences in bat density. Therefore, concentrations per unit of corridor surface have been calculated (see table 3). With respect to the changing densities of the bat populations the sections can be pooled in three "zones". This grouping reveals a close relation with the topographical and climatological properties of the cave areas:

Zone A consists of the sections with a very high bat density which increases during the season (in section I and II also after December, in section V only before). These are the entrance sections.

Zone B: Sections lodging small populations and showing little fluctuation in number. These sections III and VI are topographically as well as climatologically intermediate between entrance sections and periphery.

Zone C: Sections showing a steady decrease in bat density from November to March. These form together the deep "periphery" of the cave: IV, VII and VIII.

The difference between the intermediate zone B and zone C may not be as convincing as that between A and B, neither in number of bats nor climatologically. The division of the back parts of the cave into B and C is made, however, in order to enable a comparison between the two extreme zones A and C.

Summarizing, we could conclude that all species of bats taken together (see table 2 and figure 9 top left) tend to be found in the rear of the cave (zone C) in the beginning of the hibernating season (figure 7) and to concentrate in the entrance zone A in the course of the winter.

We then proceeded to check which species of bat cause this phenomenon, which has been called "internal migration". The division into three zones appeared to be useful for further analysis. In figure 9 the total numbers of bats found are given in histograms, based on table 4, in addition to the seasonal changes in percentual distribution in zones A, B and C in seven species of bats.

Four species of the genus *Myotis* evidently behave in the way described for all the bats together: *M. mystacinus, M. daubentonii, M. dasycneme* and *M. myotis* are each found mainly in zone B and C in October, while more or less rapidly — roughly in the sequence of species given here — from November onwards zone A becomes inhabited, zone C simultaneously being abandoned.
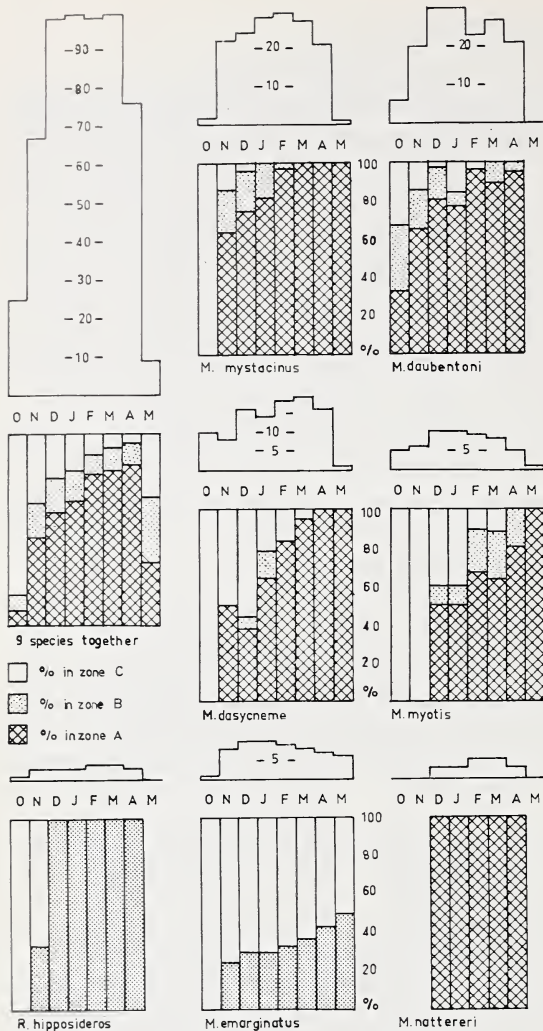
In the lower left corner of figure 9 the changing distribution of *Rhinolophus hipposideros* and *Myotis emarginatus* is shown, two species which were found exclusively in the back parts (zone B and C) of the excavation. These two figures may give some impression of migration from zone C to B, but this is hardly plausible. The number of Lesser Horseshoe Bats is too small for us to attach much value to their distribution. In *Myotis emarginatus* the steady percentual increase in B from February to May is not a real increase, but is caused by the departure of one specimen from zone C each month.

Whereas these two species were not found in any entrance section, *Myotis nattereri*, *Plecotus spec.* and *Barbastella barbastellus* were found sleeping exclusively in zone A. The latter two species are only occasionally found in the Geulhemergroeve.

As can be deduced from figure 9, the four species clearly showing "internal migration" are those which form the largest part — this is about 80 % — of the total bat population of the cave. On several occasions in the following discussions it will be necessary to take the data on these species together. In May, however, the specific composition of the bat population in the cave has changed: While nearly all other bats have then left the cave, most specimens of *Myotis emarginatus* still sleep in the back parts. The relative abundance of this species in the end of the hibernating season causes the percent of the overall population in zone A suddenly to be reduced to 33 % (against 84 % in April; see figure 9 top left). This prolonged hibernating period seems to belong to the normal behaviour of the species. Differences in the duration of the hibernating period will be discussed in a later chapter.

Fig. 9. Histograms showing the number of bats present in the cave in each visit (above) and a graphic representation of the distribution of bats over the cave zones (below)

Although the differences in behaviour of the various bat species as described here may seem rather occasional, since they rest on data obtained in only one season, observations in the literature on bat distribution in the caves support the general value of these differences. Figures given by van NIEUWENHOVEN (1956, table I) suggest that

Myotis nattereri and *M. mystacinus* show some "internal migration" in the 'Apostel-hoeve'-cave, while "*M. emarginatus, M. dasycneme* and *Rhinolophus hipposideros* stay deeper in the mountain". Punt and Parma (1964) describe how *M. mystacinus, M. nattereri* and *M. myotis* prevailed in the entrance section of the 'Kloostergroeve' in January, whereas *M. emarginatus, M. dasycneme* and *R. hipposideros* were found regularly distributed over this small excavation. Sluiter and van Heerdt (1963) found in January *M. emarginatus* occupying a rear section of the 'Sibbergroeve', whereas *M. myotis, M. mystacinus* and *Plecotus auritus* obviously preferred one entrance section. The study by Bezem, Sluiter and van Heerdt (1964), extending over several years' surveys in various caves, revealed a preference in the month of January for the outer cave regions in *M. mystacinus, M. nattereri* and *Plecotus auritus*. The species *M. emarginatus, M. daubentonii* and *R. hipposideros* preferred the 'inner regions' (more than 50 meters from the entrance). It should again be emphasized that this preference changes in the course of the season, at least in several species.

Apart from such data on the bats hibernating in South Limburg, literature on foreign caves adds to our understanding of specific differences in choice of cave sections. In the 'Sontheimer Höhle' in Southern West-Germany, for instance, *Eptesicus serotinus, Plecotus auritus* and *Myotis bechsteini* are found in the extreme front part (Frank, 1960). When going deeper into this cave, this author met a colony of *Barbastella barbastellus* first, then *Myotis nattereri, M. daubentonii* and *M. mystacinus,* and in the deepest part of the cave *M. myotis* and *R. hipposideros* hibernated.

Concerning the seasonal migration within a cave, Roer and Egsbaek (1966) recently reported on *Myotis daubentonii* assembling in the front parts of a limestone excavation near Daugbjerg (Jylland, Denmark). These animals were supposed to have been hibernating in deeper areas of the cave and hidden away in crevices.

Combined with such observations, our data from the Geulhemergroeve lead to the idea of a specific sequence in differential selection of cave areas,

Barbastella barbastellus	preferring entrance parts,
Plecotus auritus	preferring entrance parts,
Myotis nattereri	preferring entrance parts,
Myotis mystacinus	preferring rear of the cave in autumn, entrance parts in winter,
Myotis daubentonii	„ „
Myotis myotis	„ „
Myotis dasycneme	„ „
Rhinolophus hipposideros	preferring rear of the cave,
and *Myotis emarginatus*	preferring rear of the cave,

This sequence has only general value, and does not pretend to be accurate in detail. For instance, it may be true that *Myotis nattereri* performs "internal migration" in small and relatively cool excavations (e. g., the 'Apostelhoeve'-cave: van Nieuwenhoven, 1956), whereas *Myotis dasycneme* is supposed to stay in the back parts of such caves (e. g., 'Apostelhoeve' and 'Kloostergroeve': Punt and Parma, 1964). Other species, hibernating only occasionally in South Limburg caves may be located in this sequence roughly as follows:

Eptesicus serotinus	found only in entrance parts,
Pipistrellus pipistrellus	found only in entrance parts (in the 'Cannerberg', van Heerdt and Sluiter, 1961),
Myotis bechsteini	found mainly in entrance parts,
Rhinolophus ferrumequinum	found mainly in the rear, and

Plecotus austriacus:	This species, which was only recently recognized is supposed to hibernate in the deep periphery of the caves (VAN WIJNGAARDEN, 1962). VAN BREE and DULIC (1963) have called this observation in question.

4. Displacement activity

Displacements within the cave of hibernation — and to a certain extent also between separate caves (FOLK, 1940; VERSCHUREN, 1949; PUNT and VAN NIEUWENHOVEN, 1957) — occur throughout the whole winter season. In addition to bats which are found in exactly the same position for several months, there are specimens present at a certain locality at one visit only. Indications in the literature on bats hibernating in South Limburg caves suggest, however, specific differences in this behaviour. For instance, TER HORST and VAN NIEUWENHOVEN (1958) state that only *Myotis emarginatus* has a long and uninterrupted hibernation. The other species wake up from time to time, and often move to new locations.

During the investigation carried out in the Geulhemergroeve we could get an impression of the relative extent to which individual displacements occur in the various species, both in regard to the cave area and to the period in the hibernating season. As a measure of displacement activity we chose the relative number of animals, which had disappeared between two visits from their former hanging places. Instead of this number we could have used the number of bats occupying new locations in the cave, but in that case in autumn any new animals flying into the cave would be counted as well, thus confusing the information about the activity of those bats that had already started on their hibernation.

Calculation of an index Z, representing the displacement activity in the various species and months, is as follows:

Let X be the number of bats, present in the cave in a certain visit, and Y the number among X, which is still hanging in the same locations when the next visit is made,

then $\dfrac{X-Y}{X}$ is the relative frequency of animals moved between both visits.

The intervals between the pairs of visits being unequal, however, this relative frequency should be calculated for a standard interval. As such, a period of four weeks was chosen. If the actual length of the interval is i days, the standardized relative frequency Z can be calculated in the formula:

$$(1 - Z)^i = (Y/X)^{28}$$

This formula is based upon the following considerations:

Y/X = the relative number of bats still occupying their original locations after i days.

Z = the relative number of bats moved from their original locations after 28 days. Hence,

$(1-Z)$ = the relative number of bats still occupying their original locations after 28 days.

It is reasonable in the model to assume the relative number of nondisplaced bats to be an i-power function of the fraction p nonmoved after one day: If on each day of an interval a fraction $(1-p)$ of the bats occupying original locations moves, the relative number of nonmoved bats is:

after one day: p
after two days: p^2
after i days: p^i $= Y/X$
after 28 days: p^{28} $= (1-Z)$
Hence, the relation $(1-Z)^i$ $= p^{i.28} = (Y/X)^{28}$ follows.

The values of the index Z thus calculated in the various species are given in table 5. Figure 10 shows the change in Z-values during the season in each of the most generally occurring species.

Table 5

Relative frequency of displacements per period of 28 days (Z)

Explanation in text. Z-values based on $X < 5$ appear in italics

Visit:	Oct. 19	Nov. 16	Dec. 14	Jan. 3	Feb. 5	Mar. 8	Apr. 2 May 5	mean over December — March
Period: ±	October	Novemb.	December	January	February	March	April	
Interval i:	28	28	20	33	31	25	33	
Species								
B. barbastellus	—	—	*1.00*	—	—	*1.00*	—	*1.00*
Plecotus spec.	—	—	*1.00*	*1.00*	*1.00*	—	—	*1.00*
M. nattereri	—	—	*0.43*	*0.64*	0.77	0.64	*1.00*	0.62
M. daubentonii	*0.67*	0.85	0.75	0.54	0.53	0.77	*1.00*	0.65
M. mystacinus	*0.50*	0.64	0.58	0.51	0.55	0.71	*1.00*	0.57
M. dasycneme	0.90	0.62	0.86	0.44	0.25	0.51	*1.00*	0.51
M. myotis	1.00	1.00	0.51	0.54	0.41	0.54	*1.00*	0.50
R. hipposideros	*1.00*	0.67	*0.43*	*0.29*	*0.47*	*0.54*	*1.00*	0.43
M. emarginatus	*0.00*	0.25	0.14	0.09	0.20	0.14	0.16	0.14
species together	0.80	0.69	0.64	0.47	0.46	0.63	0.88	

Except for *Myotis emarginatus,* these species exhibit a common phenomenon in having high displacement activity in autumn, which decreases as the hibernating season proceeds, and increases again in March and April, up to about Z=1. This pattern is, of course, most regular in the graph representing activity in all species together. There is, however, some variation as to species. The Z-values obtained for *Myotis nattereri* in the middle of the winter are somewhat higher than for the other species, whereas *M. emarginatus* has a constantly very low activity. Specimens of the latter species can often be found hanging at one site in the cave throughout the whole season. One animal was observed from November 16 until May 5 (a period of 172 days!) occupying the same location each time. TER HORST AND VAN NIEUWEN-HOVEN (1958) reported on a specimen of *M. emarginatus* sleeping 21 weeks at a single site. Of course, one is never sure that the animals have not been awake in between, and our index Z of 'displacement activity' may therefore not represent real activity, yet some correlation between the two is tacitly understood. We presume that displacement activity depends on the specific average sleeping period.

To express the specific differences in a numerical character, the Z-values obtained for the four intervals from December to April are averaged in the last column of table 5. In this period the total population remained rather constant in number, and displacement activity was minimal and not fluctuating very much.

Apart from the relation to species and to period in the season, activity of the

Table 6

Relative frequency of displacements per period of 28 days (Z) in the populations of *Myotis daubentonii, M. mystacinus, M. dasycneme* and *M. myotis* combined, in each of the cave zones distinguished. Z-values based on X < 5 appear in italics

Period: ±	October	November	December	January	February	March	April
Interval i:	28	28	20	33	31	25	33
zone							
A	*0.50*	0.68	0.65	0.41	0.44	0.65	1.00
B	*0.50*	0.78	0.62	0.74	*0.31*	0,84	*1.00*
C	0.89	0.88	0.89	0.88	0.77	*1.00*	—
whole cave	0.83	0.75	0.70	0.51	0.46	0.67	1.00

bats depends on the part of the cave in which they are hibernating. In table 6, this is worked out for the four "migrating" and most common species together, which are not very divergent in activity nor in preference of cave areas. In the same way as in table 5, Z-values were calculated for zones A, B and C of the cave, and plotted in a graph (figure 11).

Comparison of zones A (entrance area) and C (periphery) shows that, apparently, differences in displacement activity of the bats exist in these zones. In zone C the relative frequency of displacements (per period of 28 days) is about 0.9, without much fluctuation in the course of the season. On the other hand, in zone A there is again obviously a minimum in activity in January and February. Another feature
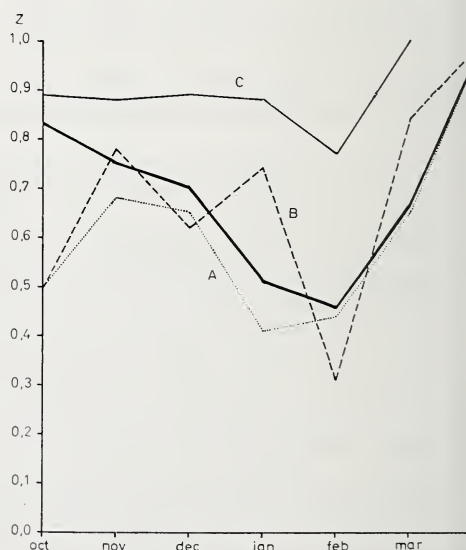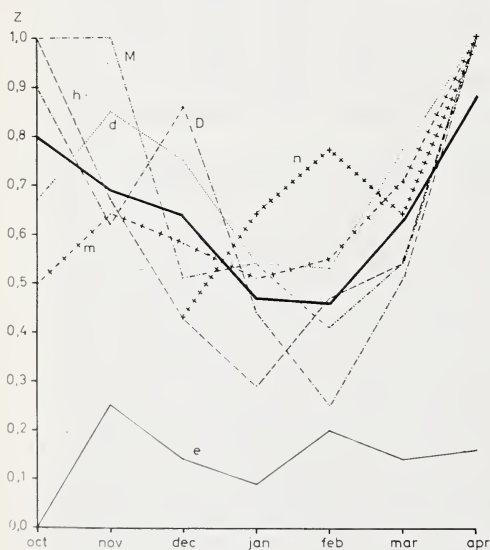

Fig. 10 (left). Displacement activity indices of each species in the course of the season — M = *M. myotis*, h = *R. hipposideros*, d = *M. daubentonii*, D = *M. dasycneme*, n = *M. nattereri*, m = *M. mystacinus*, e = *M. emarginatus*. The solid black line represents all species together — Fig. 11 (right). Displacement activity indices of the species *M. mystacinus, M. daubentonii, M. dasycneme* and *M. myotis* combined, in each of the cave zones in the course of the season. The solid black line represents animals of these species in the whole cave together

expressed in figure 11 is that the behaviour of the four populations combined in the whole cave is, in October, largely determined by the animals in zone C (the area harbouring the greatest part of the cave's population in autumn), but more and more by those in zone A as winter advances.

Summarizing, we can state that in autumn and spring all bat species taken together exhibit a high, and in the middle of the winter a low displacement activity. Such seasonal change in activity is not found, however, in *Myotis emarginatus* (hibernating in the rear of the cave, with constantly very low activity), nor in those species hibernating only in entrance parts of the Geulhemergroeve and having a high displacement activity *(M. nattereri, Plecotus* and *Barbastella)*. It is the four commonest species *(M. mystacinus, M. daubentonii, M. myotis* and *M. dasycneme)* — and in addition perhaps *Rhinolophus hipposideros* — which are responsible for the low rate of displacement in January and February. In these species this fall in activity in the middle of the winter occurs in the entrance sections only.

High displacement activity is presumably related to frequent periodical arousal. As this activity is low in the cold entrance sections in winter and high in autumn and spring as well as in the warmer zone C during the whole season, a relation with temperature is hypothetically assumed: Lower environmental temperature seems to cause a lower frequency of arousal and displacement. This agrees well with the findings of Twente (1955) in North American species of the genera *Myotis, Eptesicus* and *Corynorhinus:* "Those hibernating bats that hang in unfavorable (warm) places become irritable and move in a shorter period of time than those in cooler, more favorable places".

5. Position of the bats

Exposition

In chapter 3, the preferences of the bats have been described as to the different parts of the cave (entrance zone, transitional zone and rear sections). On the other hand it is useful to consider habitat selection within these zones: bats are found in various positions, which expose them to, or protect them against climatological variation. In the deeper parts of the cave, there is hardly any difference in conditions between exposed positions and deep crevices in the rock. In the front part, however, — the zone of strong thermocirculation in winter — the bats hanging freely in the corridors are exposed to draught, for instance, while those animals hidden in crevices are much more protected. Bezem, Sluiter and van Heerdt (1964) systematically collected data on this subject during five years in many caves in South Limburg. Their observations revealed significant differences in behaviour between the various species, as to the choice of more or less exposed positions. However, Bezem c. s. did not study this behaviour in relation with the cave area occupied. Our observations lead to some statements about this relation.

In order to work out our observations we adopted the code, used by Bezem c. s., which distinguishes between 29 positions. These authors grouped the positions in three categories, viz. 'exposed', 'moderately protected' and 'highly protected'. The data resulting from our investigations are arranged in the same way in table 7. In each zone and in each category of protection, all the positions in which bats were found throughout the season were included. Animals which were found in two or more subsequent visits at the same place, were counted only once. The data from the cave zones B and C were taken together.

The lower two lines of table 7, containing the observations for all bats together, show that animals hanging freely in the corridors ('exposed') are more frequent in

Table 7

Positions of bats observed in the Geulhemergroeve in the winter of 1963/64, pooled into three categories of protection, according to Bezem, Sluiter and van Heerdt (1964)

Entrance area (zone A) and back parts of the cave (zones B and C) are distinguished

Species	Cave area	„Exposed"	„Moderately protected"	„Highly protected"	Sum
B. barbastellus	A	—	—	2	2
	B+C	—	—	—	—
Plecotus spec.	A	—	2	1	3
	B+C	—	—	—	—
M. nattereri	A	—	—	13	13
	B+C	—	—	—	—
M. daubentonii	A	5	7	74	86
	B+C	3	—	23	26
M. mystacinus	A	21	20	43	84
	B+C	7	3	4	14
M. myotis	A	6	1	5	12
	B+C	20	2	—	22
M. dasycneme	A	5	7	25	37
	B+C	14	1	12	27
R. hipposideros	A	—	—	—	—
	B+C	9	3	—	12
M. emarginatus	A	—	—	—	—
	B+C	10	4	—	14
species together	A	37	37	173	247
	B+C	63	13	39	112

the back parts of the cave, while highly protected positions are abundant in the entrance area. As shown by the data worked out per species, this phenomenon is caused in the first place by differences in specific composition of the bat populations of zone A and B+C. Barbastella, Plecotus and M. nattereri, encountered exclusively in the front parts, were never found in exposed positions, while R. hipposideros and M. emarginatus nearly always hung freely from the roof in the rear of the cave. Secondly, however, the more common "migrating species" tend to hang freely in the rear of the cave and to prefer protected positions near the entrances. This is clearly

Table 8

Relative frequency of highly protected positions in the cave zones A and B+C

In the right column the frequencies calculated by Bezem, Sluiter and van Heerdt (1964, table 17) are entered

Species	zone A	zone B+C	whole cave	data Bezem c. s.
M. nattereri	1.00	—	1.00	0.75
M. daubentonii	0.86	0.88	0.87	0.58
M. dasycneme	0.67	0.44	0.58	0.42
M. mystacinus	0.51	0.29	0.48	0.41
M. myotis	0.42	0.00	0.15	0.14
M. emarginatus	—	0.00	0.00	0.10
R. hipposideros	—	0.00	0.00	0.00

expressed in table 8, giving the relative frequency of the highly protected positions in both cave areas (A and B+C) and in the whole cave. The frequencies calculated by Bezem c. s. for a large number of caves together are likewise reproduced in this table. The specific sequence in the relative frequency of highly protected positions is shown to be the same in the data resulting from both investigations. Evidently, we may conclude without statistical treatment that real specific differences in behaviour are responsible. Highly protected positions are more frequent in our investigation than in the counts made by the Utrecht group. This is presumably due to more intense searching.

Ambient temperatures

In order to get precise information about the microclimatological circumstances to which the bats are exposed during hibernation, measurements of the air temperature near the animals were taken electrically. This was done every second day of the visits to the Geulhemergroeve (except in the March and May visits). The device used has been described by Punt and Parma (1964). The present paper is only a preliminary attempt to study these conditions in detail in South Limburg caves. In future, the investigations will probably be extended to measurements of wind velocity and humidity at the bats' locations.

In table 9, the average air temperatures near the locations of the hibernating bats are shown. In October, most animals were hanging in air of slightly more than 10° C. In the course of the winter, the average air temperatures gradually fell to about 6° C for most species. This phenomenon is in direct relation to the "internal migration" described in chapter 3: In October many bats are found in the rear of the excavation, where the air temperature is very stable at about 10.5° C; in the course of the hibernating season, however, this part of the cave is abandoned by the majority, and the much cooler entrance sections become populated. The tendency in the entrance sections to hide away in crevices, discussed above, is not related to temperature: in such crevices, temperature fluctuation may be less than in the exposed hibernating positions, but our observations did not show any significant absolute difference in temperature.

The slight decline in average air temperatures at the locations of Lesser Horseshoe Bats and *M. emarginatus* is not a result of "internal migration" but of a slight

Table 9

Air temperatures at the hibernating locations

(in ° C)

Species	20. X.	17. XI.	15. XII.	4. I.	6. II.	3. IV.	Mean	Range	Range (Kowalski, 1953)
					Average air temperature per visit				
B. barbastellus	—	—	(0)	—	—	—	(0)		0 — 4
Plecotus spec.	—	—	5.2	(0)	5.3	—	3.5	(0) — 5.3	0 — 7
M. nattereri	—	—	6.4	6.8	5.9	5.6	6.2	3.3 — 8.1	
M. mystacinus	10.1	8.9	6.6	5.9	6.2	6.8	6.8	(0) — 10.3	2 — 4
M. daubentonii	9.2	8.9	7.0	6.8	6.5	6.4	7.2	2.2 — 10.4	
M. dasycneme	10.2	9.4	8.5	7.0	6.4	5.6	7.5	3.7 — 10.6	
M. myotis	10.2	10.2	8.4	8.5	7.5	6.5	8.5	3.7 — 10.6	2 — 7
R. hipposideros	10.4	9.7	8.2	8,3	7.9	7.5	8.4	6.4 — 10.4	6 — 7
M. emarginatus	10.3	9.9	9.7	9.5	9.5	9.4	9.5	8.1 — 10.4	7 — 8

influence of outside conditions on the air temperature in the transitional sections (III, VI) of the Geulhemergroeve.

In table 9, averages of ambient temperatures are also given for the whole season. These figures can of course never represent specific preference temperatures, because such different data as obtained in October and April, for instance, are included. Still they give an impression of specific differences in behaviour as to the choice of colder or warmer parts of the cave. When comparing our results to the data given by KOWALSKI (1953) concerning bats hibernating in Polish caves, we see an obvious resemblance in the specific order. Presumably, real specific differences in the selection of hibernating locations are responsible.

6. Length of the hibernation period

In a comparison of the bat species as to several aspects of their hibernating behavior in winter quarters it seemed useful to get an idea of the amount of time the animals spend in the caves. It is impossible to collect exact data about the duration of the whole hibernation period by means of the sample investigations in South Limburg: individuals cannot be followed during a whole season from their first entering the cave until the day they leave for the summer habitats.

The only way to obtain information in this matter was for us to trace in the literature and in working reports — as far as these deal with the South Limburg bat populations — for each species the earliest date of observation in a cave in autumn, and the latest date in spring. The number of days between these two dates is by no means an estimation of the average hibernating period, yet it may serve to compare the species. In table 10, the data collected on extremely early and late observations are summarized.

On comparison of table 10 to the specific order in cave area selection given in chapter 3, the rough conclusion may be drawn that those species which were found to prefer outer regions of the cave *(Barbastella, Plecotus* and *M. nattereri)* generally tend to have a short stay in the caves in the middle of the winter, while species like *R. hipposideros* and *M. emarginatus*, hibernating in the rear of the caves, may enter them in early autumn and do not leave before spring, the Lesser Horseshoe Bat leaving considerably earlier than *M. emarginatus*.

Table 10

Earliest and latest observations of bat species in South Limburg limestone caves

Species	Earliest observation		Latest observation		Days
	Date	Cave	Date	Cave	
B. barbastellus	14. XII. 63	Koepelgroeve	8. III. 64	Koepelgroeve	84
Plecotus spec.	4. XI. 63	Barakkengroeve	1. IV. 59	Dolekamer[3]	138
M. nattereri	23. X. 54	Apostelhoeve[1]	6. IV. 56	Apostelhoeve[1]	165
M. mystacinus	9. X. 54	Apostelhoeve[1]	5. V. 64	Geulhemergroeve	208
M. daubentonii	9. X. 54	Apostelhoeve[1]	23. IV. 56	Apostelhoeve[1]	196
M. myotis	9. X. 54	Apostelhoeve[1]	5. V. 64	Geulhemergroeve	208
M. dasycneme	26. IX. 58	Dolekamer[2]	5. V. 64	Geulhemergroeve	221
R. hipposideros	26. IX. 58	Dolekamer[2]	11. V. 56	Apostelhoeve[1]	227
M. emarginatus	9. X. 54	Apostelhoeve[1]	2. VI. 58	Apostelhoeve[4]	236

[1] VAN NIEUWENHOVEN (1956) — [2] BONGERS (unpubl.) — [3] OVERMEER & ROOS (unpubl.) — [4] TER HORST and VAN NIEUWENHOVEN (1958).

7. Discussion

"Internal migration"

The phenomenon of "internal migration", exhibited in our investigation by four bat species in one cave during a single season (see chapter 3), is probably far more common. Outside the Dutch literature incidental indications of the phenomenon have been given for North American species (e. g., *Myotis lucifugus:* GUTHRIE 1933; *M. velifer:* TWENTE, 1955 and *Corynorhinus rafinesquei:* PEARSON c. s., 1952). In various South Limburg caves, with their specifically complex bat populations, such seasonal migration has been observed (VAN NIEUWENHOVEN, 1956; PUNT and VAN NIEUWENHOVEN, 1957; TER HORST and VAN NIEUWENHOVEN, 1958; PUNT and PARMA, 1964; BONGERS, unpubl.).

It is not assumed that the changing distribution of the bats in the cave is caused exclusively by animals which migrate from the rear of the excavation to the entrance parts. The fact is that the population as we observe it is subject to a certain inconstancy in composition. There is a continuous turnover in two directions:

In the first place, exchange of animals takes place with other quarters of hibernation. The literature contains many data on incidental displacements outside the winter quarters (see VAN NIEUWENHOVEN, 1956). By means of banding, several authors (e. g., BELS, 1952; DE WILDE and VAN NIEUWENHOVEN, 1954; MUMFORD, 1958; KRZANOWSKI, 1959) traced a considerable amount of turnover. In these investigations, however, the disturbance inherent in the fixing and reading of the "rings" probably caused overestimation. Also, the increase in number of the population sampled during the winter — in our investigation lasting from October until December — is a result of bats flying in from outside the cave. In other South Limburg caves the largest numbers are counted usually in February and March. This has also been reported of the North American *Myotis lucifugus* (GUTHRIE, 1933; FOLK, 1940).

Secondly, exchange takes place with a "reservoir" *within* the cave: A number of bats, hidden in deep crevices, are unavoidably overlooked. PUNT and VAN NIEUWENHOVEN (1957) traced this reservoir by providing all the bats in the "Flessenberg"-cave with radioactive rings. In several subsequent countings by means of a Geiger-Müller counter, 20 to 45 % of the animals banded were found to hide in invisible locations. Except for these data, based on a small total number of bats, nothing is known about the extent to which turnover takes place to both "invisible reservoirs", one within and the other outside the cave.

The mobility of the population makes the term "internal migration" somewhat speculative. It is not acceptable that all animals accumulating in the entrance areas after December have been hanging in the periphery before: some have arrived directly from outside the cave. This does not imply, however, that the possible causes of the changing distribution cannot be examined. In some of the literature as well as in several unpublished working reports on the subject speculative explanations have been developed, usually favouring microclimatological conditioning of the bat behaviour. We will try to summarize here the possible factors which may be responsible for "internal migration". Arguments will mainly arise from our own investigation in the Geulhemergroeve.

"Internal migration" is a result of changes in habitat selection during the winter. The only environmental conditions inside the cave that regularly modify in the course of the season are climatological. Therefore, it is not illogical to suppose internal migration to be based on responses to climatological circumstances. In respect to these circumstances, the rear of the cave — the area covered by zone C in the Geulhemergroeve — remains constant throughout the year. In entrance areas, on the contrary,

outside conditions modify those within the cave; this influence steadily decreases from the entrance towards the deeper parts. As shown in chapter 2, entrance sections I and II in the Geulhemergroeve undergo a regular alteration in climate. When we assume that it is a response to environmental circumstances which gives rise to internal migration we are bound to conclude that, in early autumn, these conditions in zone A are not suitable for the bats to start hibernation and force them to look for a temporary place deeper in the cave, until winter has improved conditions in zone A and made these preferable to those in zone C.

In the climatology of the caves, three properties can be emphasized: draught, humidity and temperature. Their seasonal changes in zone A, and their likeliness as possible factors to which the bats respond, will be discussed separately.

Circulation in large horizontal static limestone caves has been described in chapter 2. Wind velocity is relatively high in zone A, in summer as well as in winter, and almost zero in the rear of the caves. Thus, the behaviour of the bats — avoiding entrance sections in the beginning of the hibernating season, and preferring them in winter — cannot be related directly to wind velocity. Moreover, any presumed preference for strong air currents would be contradicted by the choice of position of the bats. The so-called protected positions — which are climatologically different from the exposed positions only in respect to wind velocity, are more frequent in zone A than in C (see chapter 5). This points to avoidance of locations exposed to relatively strong air currents. We have not the impression, however, that the bats do avoid draughty corridors — for instance, the tunnel between Geulhemergroeve and Koepelgroeve, where very high wind velocities were common, nearly always harbours several specimens — but when found in such places they are very often well hidden away in crevices. VAN NIEUWENHOVEN (1956) found the same phenomenon in the draughty entrance corridor of the "Apostelhoeve"-cave. A higher rate of evaporation may very well be the disadvantage of exposed positions in entrance sections and other draughty parts of the excavations.

In *humidity* as well as in other climatological respects, zone A changes in the course of the season. Throughout the summer and early autumn a relatively dry warm air current from outside the cave flows in along the roof, while near the floor a damp cold draught goes out. Thus, the upper half of the corridors in A, where nearly all bats will find locations later on in the season, is probably fairly dry in the beginning of the hibernating period. Even the porous limestone and the crevices in it may to some extent have dried out during summer, though no data to affirm this supposition have been collected yet. In winter, however, when the outside temperature is generally below 7° C, and the thermocirculation has turned, fairly saturated air from deeper parts of the cave flows out along the roof through the entrance section. Thus, in zone A, humidity in locations near the roof is low in October and November, and will become at least as high as in the constantly humid rear of the excavation in winter.

In order to relate this to the changing bat distribution, we might suppose that a tendency to avoid dry surroundings — the disadvantage of which may be the increased rate of evaporation again — could force the animals to concentrate in the periphery (zone C) in autumn. But, as far as is known, there is no large difference in humidity between A and C which could be responsible for their preference for zone A in winter.

It has been suggested (PUNT and PARMA, 1964) that a preference for the "condensation zone" which in winter develops in the entrance areas might force the animals to move there. The advantage of hanging in this zone would be that the animals become covered with dew, protecting them from any evaporation and providing a supply of water, to be licked directly after arousal or perhaps even by reflex action in hibernating lethargy as has been incidentally observed in *Myotis emarginatus*. How-

ever, only such individuals as hang free from or against the walls and the ceiling are sometimes found to be covered with pearls of dew. As we saw in chapter 5, many animals hide away especially in zone A. This would seem to contradict a supposed preference for areas with condensation. Indeed, only few — 12 to 17 % — of all the bats present during the winter months are actually covered with dew.

Also in *temperature* zone A is largely influenced by outside conditions, but there is no complete turnover as in humidity: If we leave the extreme entrance part (up to about twenty meters from the entrance) out of account, the area directly behind is shown in chapter 2 to be the coldest part of the cave as well in summer as in winter. The same has been found in the huge excavations of the Pietersberg (van Schaik, 1942). The periphery of the cave is always warmest, at a constant temperature of about 10 to 11° C. Therefore, an assumed preference for cold areas might be responsible for concentration of the bats in zone A in winter, but would not explain why the animals occupy the warmer areas when entering the cave in October and November. We may readily presume that a low temperature, when not dropping below zero, is advantageous for hibernating bats as body temperature, metabolism, and perhaps even periodical arousal activity (see chapter 4) keep pace with the environmental temperature. Low functional activity requires less dipping into the reserves stored in the body.

Summarizing, we may state that "internal migration" cannot easily be related to responses to any single climatological factor. Reaction to draught is probably limited to a tendency to creep away in crevices in those corridors where there are relatively high wind velocities. In respect to this behaviour, however, considerable specific variations exist, as shown by the investigations of Bezem, Sluiter and van Heerdt (1964). The only hypothesis which could reasonably be defended at present is a combination of presumed responses to temperature and relative humidity:

If "internal migration" — as performed in the larger South Limburg caves at least by the most numerously occurring species, viz. *Myotis mystacinus*, *M. daubentonii*, *M. myotis* and *M. dasycneme* — has anything to do with climatological preferences, we can conceive of, firstly, a tendency to avoid dry circumstances — as are present in available locations in the entrance parts in autumn — forcing the bats to remain for a short time in the rear of the excavation; secondly, a tendency to prefer lower temperatures in the entrance zone in winter, when the reversed thermocirculation has made the important upper half of the corridors in this zone suitable in respect to humidity. This hypothesis is going to be a starting point of future investigations.

There is one aspect in habitat selection of the bats which makes conclusions extremely hypothetical. From his banding investigations, Bels (1952, p. 34) has drawn the following conclusion: "If a bat returns to the caves to hibernate, it chooses by preference the one where it has been hibernating before". The same tendency to return to former hibernating locations is probably active in habitat selection *within* the caves. It has often been observed that the same location is occupied by an animal of the same species in several subsequent hibernating seasons. In the Geulhemergroeve, for instance, a specimen of *Myotis emarginatus* was found hanging in a narrow hole, located about seven hundred meters from the entrance, in five subsequent years (1963—67). Such incidental observations give us amazing impressions of an extraordinarily developed memory in bats.

The tendency to return to formerly occupied locations is probably largely responsible for the high concentration of bats observed in section V of the Geulhemergroeve in the winter of 1963/64 (see table 3). This section had been a really cold entrance area in previous seasons, — also in 1962/63 high concentrations of bats were found there — but had grown warmer by the raising of walls in the entrances in 1963 (see chapter 2). That the bats still preferred this section was at first a rather unexpected

S. Daan and H. J. Wichers

feature. However, one of us continued counting the cave population in January of the years 1965, 1966 and 1967, and observed a steadily continuing depopulation of section V, while the other entrance section (II), where outside influences had not been eliminated, apparently remained attractive to many bats (Daan, 1967).

Such after-effects of previous habitat selection present a great difficulty in studying the bats' behaviour by means of experimental interference in natural circumstances.

Specific hibernation behaviour

Bezem, Sluiter and van Heerdt (1964) have formulated the important general rule: "The tendency of a (bat) species to penetrate into the interior of the caves increases as the northern boundary of its distribution area shifts to the south." This conclusion was based upon five yearly samples of data concerning several characteristics of hibernating locations, taken during visits in January of subsequent years to a great number of caves in South Limburg.

In a working report describing the investigation in the Geulhemergroeve in 1963/64, we arrived at a similar conclusion. Although our data are based upon a much smaller total number of bats than Bezem c. s. could study, they cover an entire hibernating season, and therefore have led to some statements about the seasonal changes in penetrating behaviour ("internal migration"). In addition, several other phenomena in hibernating behaviour were discovered to show specific differences which also suggest some relation to the distribution area in Europe. These phenomena are: activity during hibernation (chapter 4), duration of stay in the caves (chapter 6), mean air temperature at the bats' locations and, to a lesser degree, exposedness of the positions (chapter 5). The nine species studied in the Geulhemergroeve have some characteristical sequence in respect to these various features, as is shown in table 11. The exact

Table 11

Survey of several characteristics of the bat species studied

Species	a	b	c	d	e	f
B. barbastellus	entrance areas	—	—	(1.00)	84	5
Plecotus spec.	entrance areas	3.5	—	(1.00)	138	2 *(auritus)*
M. nattereri	entrance areas	6.2	1.00	0.62	165	4
M. mystacinus	migrating from rear to entrances	6.8	0.48	0.57	208	1
M. daubentonii	migrating from rear to entrances	7.2	0.87	0.65	196	3
M. dasycneme	migrating from rear to entrances	7.5	0.58	0.51	208	6
M. myotis	migrating from rear to entrances	8.5	0.15	0.50	221	7
R. hipposideros	rear of cave	8.4	0.00	0.43	227	8
M. emarginatus	rear of cave	9.5	0.00	0.14	236	9

a = Area in the Geulhemergroeve where the bats were mainly found to hibernate. — b = Mean ambient air temperature (from table 9; in ° C). — c = Relative frequency of "highly protected positions" (from table 8). — d = Relative frequency of displacements per period of four weeks in winter (from table 5). — e = Number of days between earliest and latest date of observation in South Limburg caves (from table 10). — f = Specific sequence in northward extension of the distribution area in Europe (from Bezem, Sluiter and van Heerdt (1964), amplified for *B. barbastellus* after van den Brink [1955]).

data in this table may have little general value, but for reasons of comparison they are quite suitable.

In chapter 5, it has been concluded that the exposed positions occur more frequently, with bats of the "migrating" species, in the rear of the excavation than in the entrance parts. It is therefore not astonishing that the tendency of species to prefer protected positions decreases in general with growing tendency to penetrate further into the cave, roughly in the order *Barbastella barbastellus . . . M. emarginatus. (M. daubentonii* seems to make an exception). Also, it is obvious that the mean air temperature is directly in relation to the area in the cave preferred by the species. Therefore, in table 11, columns a, b and, to a lesser extent, c represent dependent phenomena. Activity during hibernation (d) and length of the hibernating period (e), however, are different characters. Still, these exhibit about the same specific sequence. Finally, comparison with column f where the sequence in northward extension of the distribution areas in Europe is indicated, shows that the relation between characters in a, d, e and f is evident; at least in the four southernmost species, *(M. emarginatus, R. hipposideros, M. myotis* and *M. dasycneme)* which in the South Limburg cave area are not far from their northern boundary.

These relations may be formulated in an extension of the rule of Bezem, Sluiter and van Heerdt:

The tendency of a species to hibernate in the warmest, climatologically most constant rear of the excavations in South Limburg is less as the northern boundary of its distribution area lies more to the north, a shift which is accompanied by an increase in activity during hibernation and by a shorter hibernating period.

The relation of these phenomena leads to the speculation that it is a matter of thermoregulatory adaptation, that determines several aspects in the hibernating behaviour and, on the other hand, limits the distribution of the various species to the north.

Summary

An Investigation in one of the larger artificial Dutch limestone excavations, the "Geulhemergroeve", is reported. This cave can roughly be reckoned to the static horizontal caves. Nine species of bats were found hibernating in the Geulhemergroeve. In their behaviour during the hibernation season these species exhibit variations that have some rough relation to their geographical distribution. Species like *Myotis emarginatus* and *Rhinolophus hipposideros* which reach their northern boundary in the South Limburg area arrive early in the caves, and stay in the warmer back parts of the caves during the whole season. *M. emarginatus* tends to have very long and uninterrupted sleeping periods well into the month of May. The species *M. dasycneme, M. myotis, M. daubentonii* and *M. mystacinus,* of which the geographical distribution reaches farther north, together make up about 80 % of the bat population in the cave. They usually arrive in October, November, and occupy the rear of the cave, moving, however, to the colder entrance areas as the winter advances. They tend to prefer exposed positions in the back parts — where climatological fluctuation is very little — and to select more protected positions (crevices etc.) in the entrance areas (perhaps as a reaction to draught). The problem remains how much "trial-and-error" and how much direct preference there is in habitat selection. Concentration of the bats in the entrance areas may very well be the result of a preference for favourable low temperatures. In autumn a low relative humidity in these areas might interfere with this preference, and force the bats to look for a place of temporary stay in the warmer rear of the cave. The relative frequency of displacements is high (0.9 per period of four weeks) in this zone (probably as a consequence of a higher frequency of arousal, in relation with higher environmental and body temperature and metabolic activity), but decreases as soon as the bats assemble in the colder entrance sections. At last there are three species, *Barbastella barbastellus, Plecotus* spec. and *Myotis nattereri,* which occur only in very small numbers in the cave of investigation. These were found only in protected positions in the entrance areas. They are supposed to stay shorter in the caves than the other species and to have a somewhat higher rate of arousal and displacement. The described variations in habitat selection within the cave of hibernation seem to depend more or less on thermoregulatory adaptation.

Zusammenfassung

Es wird berichtet über die Fledermäuse in der künstlichen niederländischen Kalkhöhle „Geul-hemergroeve". Man kann die Höhle praktisch zu den statischen horizontalen Höhlen rechnen. 9 Fledermaus-Arten überwintern in ihr und zeigen dabei Unterschiede, die in gewisser Beziehung zu ihrer geographischen Allgemeinverbreitung stehen. Arten wie *Myotis emarginatus* und *Rhinolophus hipposideros*, die in Süd-Limburg ihre Nordgrenze erreichen, erscheinen früher in den Höhlen und verweilen während der ganzen Saison in den wärmeren rückwärtigen Teilen der Höhle. *M. emarginatus* neigt zu einer ununterbrochenen Schlafperiode bis in den Mai. *M. dasycneme*, *M. myotis*, *M. daubentonii* und *M. mystacinus*, deren geographische Verbreitung weiter nach Norden reicht, machen zusammen ca. 80 % der Fledermaus-Bevölkerung in dieser Höhle aus. Sie treffen gewöhnlich im Oktober, November ein und besetzen zunächst den inneren Höhlenteil, rücken aber mit fortschreitendem Winter weiter gegen den kälteren Eingang. Sie scheinen in inneren Höhlenteilen — wo nur geringer klimatischer Wechsel stattfindet — im allgemeinen freie, ungeschützte Schlafplätze zu bevorzugen, während man sie in der Eingangsregion meistens in Spalten usw. versteckt findet. Es verbleibt die Frage, wieviel bei der Wahl der Überwinterungsstelle auf Versuch und Irrtum, und wieviel auf direkter Bevorzugung beruht. Die Konzentration der Fledermäuse in der Eingangs-Region könnte sehr wohl auf Bevorzugung der dortigen niedrigen Temperaturen beruhen. Im Herbst mag eine niedrige relative Feuchtigkeit dieser Region einen negativen Einfluß ausüben und die Tiere zwingen, zunächst für vorübergehenden Aufenthalt ins dann noch feuchtere, aber auch wärmere Innere der Höhle zu ziehen, wo dann auch relativ häufig noch ein Platzwechsel vorgenommen wird.

Barbastella, *Plecotus* und *Myotis nattereri* überwintern in dieser Höhle nur in geringer Zahl, und zwar nur an geschützten Stellen der Eingangs-Region. Es wird angenommen, daß sie sich nur kürzere Zeit in der Höhle aufhalten als die anderen Arten, auch unruhiger sind und zu häufigerem Platzwechsel neigen. Die dargestellten Unterschiede der Platzwahl in der Überwinterungshöhle scheinen mehr oder weniger auf thermoregulatorischer Anpassung zu beruhen.

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Gefangenschaftsbeobachtungen an Zwergfledermäusen

Verfasser hatte Gelegenheit, eine größere Zahl von Zwergfledermäusen, *Pipistrellus p.
pipistrellus* (Schreber, 1774) über einen längeren Zeitraum in Gefangenschaft zu halten.
Es handelte sich um 47 Tiere, die Anfang März aus dem Winterquartier in einer Kirche
geborgen wurden, weil das Bauwerk renoviert werden sollte. Dabei wurde der Mauer-
spalt verputzt, in dem die Tiere gesessen hatten. Nach Abschluß der Bauarbeiten wur-
den die Fledermäuse wieder freigelassen, um sich in den umliegenden ausgedehnten
Klosteranlagen ein neues Quartier zu suchen.

Die Tiere setzten bis Anfang April bei entsprechenden Temperaturen ihren Winter-
schlaf fort und wurden dann vier Monate lang in Gefangenschaft gepflegt und von
Hand ernährt. Es waren 13 ♀♀ und 34 ♂♂. Diese Zahl spiegelt aber nicht das natür-
liche Geschlechterverhältnis wider; denn es konnten in dem etwa 75 cm tiefen, stark
zerklüfteten Mauerspalt nicht alle Exemplare gefangen werden. Außerdem hatte ein
Teil der ♀♀ das Winterquartier wahrscheinlich schon verlassen.

Die Fledermäuse waren während ihrer Gefangenschaft verschiedenen natürlichen,
gefangenschaftsbedingten und zu Versuchszwecken vorgenommenen Belastungsproben
ausgesetzt. Diese forderten folgende Opfer: 1 ♂ erwachte nicht aus dem Winterschlaf.
1 ♂ war so geschwächt, daß es trotz Aufnahme der angebotenen Mehlwürmer nach
48 Stunden starb. 1 ♂ verweigerte beharrlich die angebotene Nahrung und war nach
3 Tagen tot. 2 ♂♂ starben, nachdem versuchsweise 6 Tage lang die Luftfeuchtigkeit
herabgesetzt und das Trinkwasser entzogen war. 2 ♂♂ verendeten unter typischen
Vergiftungssymptomen, als der Holzkasten, der den Tieren als Unterkunft diente,
gegen Ektoparasiten mit einem Kontaktinsektizid ausgestäubt wurde. Diese „Versuchs-
bedingung" war nicht vorgesehen; denn der Kasten wurde anschließend gelüftet, und
die Tiere kamen erst nach 24 Stunden wieder hinein. 2 ♂♂ starben ohne erkennbare
Ursache.