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A CONTRIBUTION TO THE POPULATION ECOLOGY OF NYCTALUS NOCTULA (MAMMALIA: CHIROPTERA)

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Abstract

From March to October colonies of *Nyctalus noctula* were found in hollow trees where also the reproduction takes place; winter colonies in trees are evidenced by oldish material. In buildings these bats were found throughout the year with the exception of June and July, and they do not reproduce there. One winter colony was found in a crack in a rock. According to the authors' material and according to data in literature the relation of different components of populations to different types of shelters is evaluated as well as the behaviour of *N. n.* in their hunting grounds. In Central Europe all females and most of the males mature at the age of about 3 months, *i. e.*, immediately after finishing their growth. Most females older than 1 year have 2 young and the average number of young per one grown-up female is 1.8. The sex ratio at birth is 1 : 1 and is probably also maintained later on. The young are born from mid-June till early July and nursery colonies disintegrate in August. Old females as well as those born in that year move to mating quarters to territorial old males. The males of that year do not mate and in juvenile colonies they gradually exceed the females in number. In October at the latest the summer shelters are left till March or April. Males prevail in all winter samples from Western and Central Europe; the possible causes of this phenomenon are being discussed. The average population density in the summer season, found in two areas of the optimum habitat, is 0.32 individuals per ha. Although originally a forest species, *N. noctula* has managed to adapt to the civilization pressure and in places it exhibits a trend towards a hemisynanthropic way of life.

Contents

Introduction

Nyctalus noctula (Schreber, 1774) (hereinafter, *N. n.)* occurs in Europe south of approximately the 60th parallel, being frequent in woodland or park landscapes of lowland regions. It is a species with considerable migratory activity, covering distances up to 1,500 km (Strelkov 1969, Roer 1971). Its ecology has been dealt with by a number of authors, particularly Löhrl (1936), Ryberg (1947), Kuz'akin (1950), Meise (1951), Blackmore (1963), Cranbrook & Barret (1965), Sluiter & Heerdt (1966), Stratmann (1968), Pan'utin (1963, 1970) and Sluiter, Voûte, Heerdt (1973). Despite the fact that the number of papers devoted to this species is considerable, many aspects of its ecology have remained obscure. It is above all the fact that there are few quantitative data concerning the populations; also the yearly life cycle and reproduction have been studied only in part.

In the present paper we therefore summarize our observations carried out in the western part of Czechoslovakia (Bohemia and Moravia) in the course of the last 20 years. The main objective of the paper is the analysis of the occupation of shelters all the year round, the evaluation of important aspects of the population, such as the reproduction process, and the estimation of the structure and density of the summer population in the optimum habitat. The share of the individual authors is as follows: The third author dealt with reproduction. The second author obtained most of the material from Bohemia and elaborated the chapter on population. The first author obtained most of the material from Moravia and elaborated the remaining chapters, preparing the paper for print.

For the assistance in obtaining our material we wish to thank numerous persons, above all, our students and colleagues; extraordinary help was given by Dr. I. Horáček and Mr. V. Bejček (both from Prague). We also thank Dr. I. Flasar from the Museum at Teplice for supplying us with material of a great thanatocolony of the species studied. Dr. V. Hrabě, CSc., from the Institute of Vertebrate Zoology, ČSAV (Brno), has our thanks for carrying out the cross-sections through the teeth of the noctules. And, last but not least, we wish to thank the heads of our workplaces for enabling us to carry out the research, and the reviewers for valuable comments.

Material and methods

The region of the research is situated between 50°15′ and 48°40′ northern latitude and 13°10′ and 18°15′ eastern longitude. The period of the research lasted from 17 Sept., 1955, to 15 July, 1977. Altogether, 1,383 individuals were caught, out of which there were 963 grown-up and 420 juvenile individuals. Most of those individuals were banded and released. For studying the reproduction 18 grown-up males and 24 grown-up females were killed. Besides this material about 400 skeletons or mummies were found. In the above sample those individuals flying away before their sex could be established and those observed in flight in the hunting grounds are not included.

Owing to the fact that *N. n.* is one of the most frequent bats in Czechoslovakia (Hanák 1967) and in Central Europe in general, we do not give a list of collecting stations. The main regions of collection were: the south Bohemian pond basin (about 50 % of the sample), central Bohemia, including the City of Prague, and southern Moravia including the southern part of the Českomoravská vrchovina Highland and the City of Brno. A detailed description of the main region under investigation in southern Bohemia is given in the chapter dealing with the density of the summer population. The stations studied are situated at elevations from 150 to 500 m.

For catching *N. n.* from hollow trees we most often used cages according to Bels (1952) which, in the course of time, were variously modified. We found

out that the probability of the whole colony flying out was increased by decreasing the compactness of the cage walls, particularly that opposite the opening of the cavity. It is not even necessary that the cage should be completely closed, as far as the wall opposite the opening safeguards knocking off or sliding of the outflying bats into a plastic bag fastened instead of the bottom of the cage. The type used at present, suggested by the second author, has a frame made of a strong wire and only a slanting roof consisting of silon fibres stretched at the distance of 1 cm from each other (Pl. II, left). The cage can be folded and the catching bag removed, so that a large number of such devices can be transported. Another catching device are telescopic dural rods 8 m in maximum possible length in which the cage can be put and lifted to hollows situated at a major height. In the systematically followed region, next to the known holes there are permanently hammered hooks on which the catching cages are hung up.

The catching device was placed before the entrance holes about one hour before the sunset and removed after finishing the catching. When working with cages of the older type (all walls made of wire netting and a fabric bag instead of the bottom) it sometimes happened that only some of the individuals flew out, but others stayed in the cavity from where they uttered sounds. If they were grown-up individuals (the young can be distinguished according to the sounds), the cage was left in place for several hours, twice even for the whole night. In spite of this it happened several times that part of the colony evidently remained in the hollow; those cases are excluded from the calculation of the size of the colonies. If the individuals flew quickly one after another and no sounds were heard after the last one had left the hollow, the catch was considered quantitative.

From hiding places in buildings the bats were taken out with hand or with a long forceps or caught with a hand net. Such catches could not often be quantitative. A small sample described in the chapter on hunting grounds was mist-netted. At the beginning of the research several individuals were shot dead in their hunting grounds (they could not, however, be included in the material for studying the reproduction); besides we were several times given individuals caught in various environments, often unable to fly. Skeleton remains or mummies were, as a rule, found in building adaptations of houses.

The above sample of 1,383 individuals was classified according to sex and further into juvenile and grown-up individuals. As for the grown-ups we tried to classify them into yearlings and old ones, but the identification of yearlings is not quite reliable, as described below. We should like to stress the fact that yearlings cannot be synonymized with subadult individuals, as our study of the reproduction has shown that the existence of the subadult stage in *N. n.* is questionable. The terms used in the paper are to be understood as follows: juveniles = young individuals at the stage of rapid growth, from the end of June to the end of September; grown-ups = all individuals older that juveniles; yearlings = individuals older than the young and younger than one year, from October to May, sexually mature as a rule; the old = all individuals older than the yearlings, from June of the year following the year of birth, sexually mature (adult).

In the material of 42 specimens used for the study of the reproduction the following were determined: body mass, coloration of pelage, the stage of upper limb metacarpal and finger ossification, the dry mass of the eye, and the degree of dentition abrasion. Genital organs were dissected and preserved. In males the right testis, the right epididymis and the vesicular gland were weighed; smears and histological sections of testes and epididymides were carried out. In females the size of nipples was estimated, the width of vaginal fissure measured as well as the length of uterus and the presence of embryos or sperms in the uterus established – the latter in the smear of the cut right uterine horn. Further, histological sections of ovaries, uteri and vaginae were made. In randomly selected specimens (7 males, 11 females) transversal sections through the right lower canine were made.

The ossification of long bones of the wing is well visible macroscopically in juvenile individuals when the light is passed through the wing; this has been known in bats for a long time (Barrett-Hamilton 1910). The cartilaginous zone of cartilago epiphysaria appears white in passing light, the newly formed primary bone is reddish brown and the permanent, secondary bone is gray. The growth zone is more or less macroscopically visible in yearlings in October and under a dissection microscope also in November. The later distinction of yearlings from older individuals was carried out according to the dentition with fine sharp points and darker hairs. In the material used for the study of reproduction where further criteria were available the distinction of yearlings is reliable, but in the sample under investigation of living animals in the field the distinction of yearlings is rendered difficult by subjective error taken into account in the evaluation.

The dry mass of the eye was ascertained instead of the usual dry mass of lens (*cf.*, Giles 1971) on the assumption that with progressing age the dry mass of different eye parts increases, such as of sclera and the lens. The right eye was fixed for 7 days in 10 % formaldehyde, then dried at 80 °C. for 36 hours and immediately weighed. On the canine sections the increment zones of dentin were followed by means of the Klevezal' & Klejnenberg (1967) method. The teeth were decalcified in 7 % nitric acid for 6 hours, rinsed in running water for 5 minutes, cut on a freezing microtome and stained with the Mayer haematoxyline. Histological sections of the genital organs were processed by current technique; they are not reproduced in the paper, as they agree with published materials on bats with a similar reproduction cycle.

Results

Shelters

As in other countries of Central Europe, *N. n.* in Czechoslovakia was most often found in trees and, from time to time, in buildings (Gaisler & Hanák 1969, Hůrka 1973). In our material ($n = 133$ finds of living individuals or colonies) 72.8 % fall to tree cavities, 21.8 % to buildings, and 5.4 % to remaining finds.

Trees. As shown in Fig. 1, *N. n.* was found in tree cavities from March to October. The average abundance in one shelter was the highest in July. In hollows we found individuals, pairs as well as colonies (for the definition of a bat colony, *cf.* Gaisler 1966). In Tab. 1 we distinguish 5 types of colonies according to their composition. Their number varies from 3 to 53 individuals, on the average the strongest colonies were those of grown-up females, found from March to June. The data in the table are distorted by the fact that they do not include the young incapable of flight which remained in the cavities

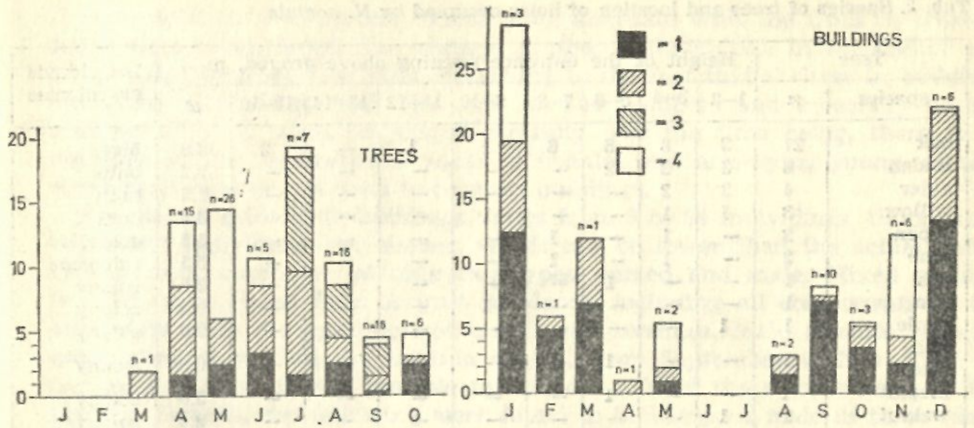


Fig. 1. Composition of samples obtained in the two main types of shelter in the course of the year. Explanations: ordinate, the average number of individuals per shelter per month; abscissa, months; 1, grown-up males; 2, grown-up females; 3, juveniles; 4, sex and age not determined; *n*, number of finds per month.

Tab. 1. The size of colonies in tree holes

Type of aggregation	Period	Number of individuals in a colony						
		3–10	11–20	21–30	31–40	41–50	51–60	$\bar{x}$
grown-up males + females	May–Oct.	9	5	3	–	–	–	11.7
grown-up males	May–Sept.	7	–	–	–	–	–	6.9
grown-up females	March–June	6	2	3	–	1	1	19.5
nursery	July–Sept.	4	4	4	1	1	–	18.6
juvenile	Aug.–Sept.	11	2	–	–	–	–	6.5
not stated	May–Sept.	2	1	3	–	–	–	16.5
total	March–Oct.	39	14	13	1	2	1	13.4

and thus could not be caught. According to sound utterances and individual finds of quite small young the births of *N. n.* take place from mid-June to early July in the region under investigation. The first flying young were found on 12 July. The number of members of nursery colonies is – particularly in the first half of July – substantially higher than that stated in Tab. 1, these colonies being in fact numerically strongest aggregations of the species studied in the summer season. Later on, their numbers drop because, starting from mid-August, the nursery colonies begin to disintegrate, as will be described in the chapter on population. By the number of members the smallest are the colonies of males and the juvenile colonies, the latter type being more frequent. A small number of grown-up males can be found in female and nursery colonies. Besides the data summarized in Tab. 1, in the cavities of trees individual males were found (3×), a pair of males (1×), and a male and a female (2×).

The colonies of *N. n.* were found in trees from March to October, individuals or pairs from June to October. There are no finds in trees during the winter season in our material. In the collections of the National Museum in Prague there are specimens labelled as found in hollow trees in Prague in January and in "winter"; as far as could be established, the respective colonies were discovered in the cavities of a mighty lime-tree and a beech; their number,

Tab. 2. Species of trees and location of holes occupied by *N. noctula*

Tree		Height of the entrance opening above ground, m									Individuals or colonies
species	*n*	1–2	3–4	5–6	7–8	9–10	11–12	13–14	15–16	*x*	
oak	27	3	8	5	6	2	1	–	2	6.2	both
linden	8	3	3	2	–	–	–	–	–	3.2	both
alder	4	2	2	–	–	–	–	–	–	2.5	both
willow	3	1	1	–	–	1	–	–	–	4.8	both
aspen	2	–	1	–	1	–	–	–	–	5.5	colonies
pine	2	–	1	–	1	–	–	–	–	5.5	colonies
ash	1	–	–	1	–	–	–	–	–	5.5	colony
elm	1	–	–	–	–	1	–	–	–	9.0	colony
apple	1	1	–	–	–	–	–	–	–	2.0	colony
false acacia	1	–	–	1	–	–	–	–	–	5.5	colony
maple	1	–	–	1	–	–	–	–	–	5.0	colony
walnut	1	1	–	–	–	–	–	–	–	2.0	colony
spruce	1	1	–	–	–	–	–	–	–	1.5	ind. male
total	53	12	16	10	8	4	1	–	2	5.1	both

however, is not exactly known (Gaisler 1956, Hanák, Gaisler, Figala 1962). Hůrka (1973) published a find of 1 male behind the bark of a big oak in Plzeň on 4 Dec. There are some more reports about winter finds of *N. n.* in hollow trees by wood workers which, however, cannot be verified.

Tab. 2 summarizes those finds in which the species of tree is known and the height of the entrance measured or estimated. Those bats were found in 13 species of trees, most frequent of them being the oak (50.9 % of cases). In the table each hollow is counted only once; the average frequency of oak would be still increased if repeated finds in the same hollows were considered. The height of the entrance varied between 1 and 16 m, the accuracy of the estimate dropping with increasing height. The average height of the aperture is 5.1 m, but more than a half (53.8 %) of the occupied hollows was at the height of 1 to 4 m. As to a possible objection that the occupation of higher situated cavities can be registered less easily than in cavities situated lower, we should like to note that the summer colonies of *N. n.* utter loud sounds during daytime (*cf.*, Stratmann 1968), and according to our measurements those utterances can be well heard up to the distance of 20 m. Thus, the probability of discovering higher situated hollows will not be substantially lower than in the hollows near ground. Exceptions are cold days particularly at the beginning and at the end of the period of occurrence of *N. n.* in trees; it is, however, improbable that at that very time the bats should seek higher situated hollows. Only single individuals can be missed, because they utter sounds only under special circumstances. This methodological error, pertaining to many analogical population studies on bats, cannot be eliminated so far.

Besides cavities in trees, *N. n.* was found in bat boxes hung up on trees in two stations: the Velký Tisý Pond, southern Bohemia, and the reserve Pod Trlinou, northern Moravia. In one case they were 4 males; in another case, 1 female; and in two cases 1 male, all of them being old individuals. The last mentioned case was a bat hidden between the back wall of the box and the tree trunk. In other tree shelters we did not find these bats, but Dr. Balát (Brno) informed us on his observation of 4 individuals behind loose bark of a pine tree.

Buildings. Finds in buildings fall into the period from August to May

(Fig. 1) so that, to a certain extent, they alternate with the finds in trees as far as time is concerned. The average number of individuals in one shelter was highest in December and January. Owing to the fact that shelters in buildings are often difficult to find, the data on the numbers and especially on the missing of *N. n.* must be judged carefully. For the time being, there is no evidence of the occurrence of suckling females and non-flying young, so that nursery colonies do not seem to occur in buildings.

The size of colonies in buildings varies from 3 to 54 individuals, the average being 10.7 individuals per shelter, which can be lower than the actual value. The colonies found are of only two types: mixed and male. Mixed colonies ($n = 13$) were found from August to March, including all components of the population with the exception of non-flying juveniles. Male colonies ($n = 10$) are known only from the autumn season, from September to November. In further 6 colonies it was possible to find out neither the composition nor the number. Besides, the following were found in buildings: 1 male in three cases, 2 males in 4 cases and once 1 female; the finds are from April, May, September, October, and November, respectively.

The highest number of finds ($n = 29$) is from prefabricated houses of a new housing estate in Prague, Zahradní Město (= Garden City). The flats there are equipped with an inbuilt recess in the kitchen connected with the outside through a narrow ventilation shaft, partitioned from inside by removable metal sheet. The bats hide most frequently in that shaft which is heated in winter. The occurrence was evidenced from the first to the ninth floor, most often on the third and on the sixth foors of houses. The total situation is shown in Pl. I.

Further evidence is from a family house at Roztoky near Prague where a colony of *N. n.* was hiding in the space between the ceiling of an unoccupied room and a flat roof with an entrance slot over the window. We got to the place only after the owner had closed the aperture; we obtained 2 emaciated males, the other individuals had probably perished. There is some evidence from the City of Brno. According to sound utterances a winter colony was hiding in a bay under the roof of a four-floored building of the Medical Faculty, at least from October to January for five successive winters. Another supposed colony inhabited a space above the ceiling of a room on the first floor of a house, according to unverified statements of local people "for the whole year". Evidence to this are droppings fallen out of the entrance and, besides, a male *N. n.* which flew into the room below the shelter in August. Besides, three times there were found individual males creeping on the ground in Brno: In October, January, and April. Another find of a winter colony was reported by Z. Rumler (Olomouc). The shelter was a narrow fissure between the wooden panelling and the wall of a window recess on the second floor of the castle building at Šternberk (northern Moravia). On 11 Feb., 1976, 413 individuals of *Pipistrellus pipistrellus* were found there, 1 female *Vespertilio murinus* which, in captivity, bore 2 young (for details *cf.*, Rumler 1977) and 22 male and 10 female *N. n.* And, finally, we were supplied with two individuals of *N. n.* from villages: a dead male found in May in the hall of a farmer's house at Pozďatín (the Českomoravská vrchovina Highland) and a living female which, in October, flew out of the stove of a recreation cottage at Čeladná (the Beskydy Mountains).

Large series of skeletal remains (thanatocolonies) were found in Prague and at Teplice (northern Bohemia). In building adaptations of the former abbey Na Slovanech in Prague, more than 200 skeletons of *N. n.* were found in a bricked-up recess high in the attic turned towards the Vltava River. In the castle at Teplice, 166 skeletons of *N. n.* were discovered behind a metal sheet cover of the roof cornice. Both cases were most probably winter colonies. Besides we found or were given mummies of individual specimens which had lain in lofts or towers of various buildings.

Other shelters. The most remarkable shelter, evidencing the occurrence of *N. n.*, is a crack in a vertical rock wall near Srbsko (central Bohemia), about 50 m above the water level of the Berounka River. According to sound utterances, a colony stays there at least from November to January, probably during the whole period of hibernation. The crack is not normally accessible; with the kind assistance of mountaineers, 2 females of *N. n.* were caught there in November. The situation is shown in Pl. II (right). The last find was made by dr. K. Hudec (Brno) in a reed stand of Prostřední rybník Pond (southern Moravia). In May, he found there a pregnant female hung up at a cluster of *Typha* stalks 1 m above the water level. The individual, which we could examine, did not show any symptoms of disease and was able to fly.

Flight activity, hunting grounds

N. n. belongs to bats having a very characteristic outline (Gaisler 1959) and way of flying. The characters distinguishing this species in the field were very instructively described by Klawitter & Vierhaus (1975). In this chapter we only summarize those observations when the determination of the species is beyond doubt; in several instances it was verified by shooting, catching from cavities or netting. Flying (hunting) individuals were observed from April to October. From April to September, we noted the beginning of the flight activity 16 times according to the moment of leaving the shelter, mostly a tree cavity. In all cases the bats flew out only after the astronomical sunset; the difference with respect to the sunset was + 2 to + 39 min., on the average + 19 min. In culminating summer, the bats seem to leave the shelter relatively later, but due to a small number of observations we do not consider this observation conclusive.

In five cases, we observed hunting individuals of *N. n.* at daytime in full light: once in April (10 Apr., 1973), once in September (8 Sept., 1972) and three times in October (14 Oct., 1973, 13 and 19 Oct., 1974). In the last two cases mentioned uninterrupted observations were carried out from 12 to 14 h, using a 7×50 fieldglass. Throughout the observation, 10 to 12 individuals of *N. n.* were flying over the station (ponds and surrounding small woods near Lednice, southern Moravia). The height of the flight was estimated to be 20 m. During the night of 12/13 Oct. there had been a heavy rain; during the night of 18/19 Oct., the temperature was as low as −2 °C. During the observations there was sunny weather with temperatures of 4 to 8 °C. Due to the fact that the station is regularly visited by student excursions at the beginning of October, observations of this kind were also carried out in subsequent years but in spite of using stronger telescopes, the result was negative.

Hunting individuals were observed in 35 stations. Most of them (62.9 %) fall to ponds and their immediate surroundings; they are both ponds situated in woods as well as those between fields and woods, in castle parks and at the outskirts of towns (Prague, Záběhlice – Krč). The majority of such observations can also be the result of the orientation of our research. We further observed *N. n.* flying over the edges of woods, wood clearings and roads, old lanes and

fields. Inside the built-up areas of the towns hunting *N. n.* have not been observed so far, although a systematic research of urban chiropterofaunae is in progress at present.

In our study area, we netted bats in 9 stations (altogether 92 net-nights), but in only one station did we also get hold of *N. n.* The station is the pond Hlad near Studenec (the Českomoravská vrchovina Highland), where nets were put on the shores and in the surroundings of the pond. In 1968 and 1969, altogether 17 males and 2 females of *N. n.* were netted, always in the same net placed across the pond shore in such a way that 1 m of the net was on shore and 5 m above the water. In close surroundings there was a willow-tree with a hollow in which 3 times a male colony of *N. n.* was found, counting 6 to 9 individuals. At the time of successful netting, the cavity was mostly empty but banding proved that 3 males that had been hiding in the hollow were netted later on. Nettings and indirect observations showed that round the willow-tree there was a regular flight route at the height of 1 to 3 m above the water surface of the pound. In all other stations, hunting *N. n.* were observed at least 4 m above ground, as a rule 10 to 20 m high.

Reproduction

Description of reproductive organs. Since we did not find detailed descriptions of the morphology of genital organs of *N. n.* in literature,

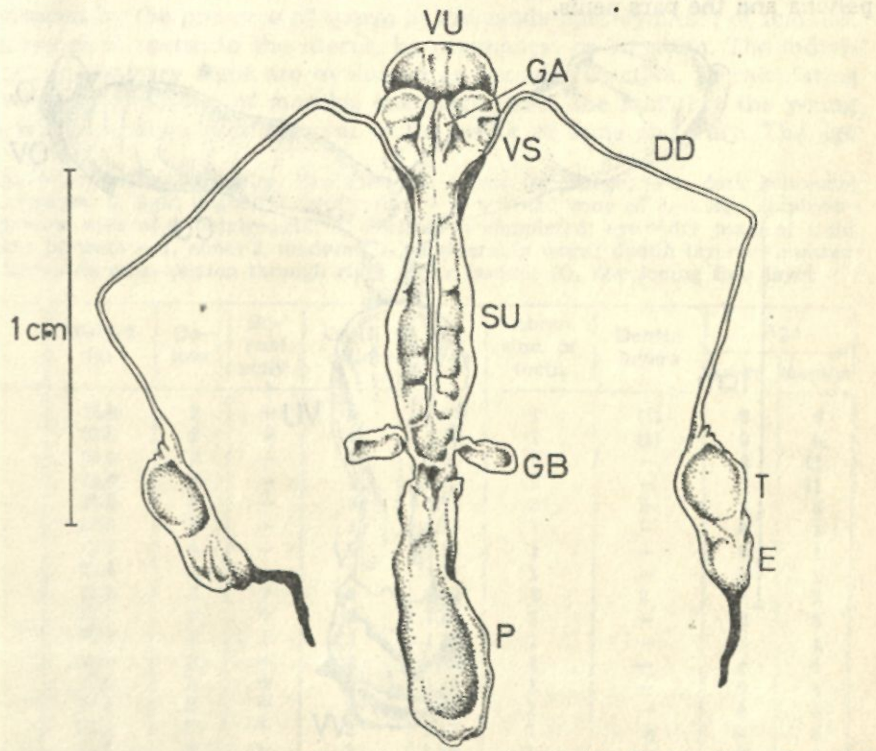


Fig. 2. Reproductive organs of the adult male in June, dorsal side. Explanations: T, testis; E, epididymis; DD, ductus deferens; VS, vesicular gland; GA, ampullary gland; VU, vesica urinaria; SU, sinus urogenitālis; GB, bulbourethral gland; P, penis.

we give their description here (Figs. 2, 3). The penis of the male is covered with hairs up to the tip, it is slightly flattened and pointed at the end, without a preputium. Inside the big glans penis there is a rod-like os penis. The scrotum is formed only in the functional period in dependence of the descent of the abdominally positioned testes and the increase in the volume of epididymides. Both halves of a sac-like scrotum are symmetrically adjacent to the root of the tail, resting firmly in the uropatagium, where they are easy to see ventrally. In the non-functional period only the caudae epididymidis are situated in that position.

The testis is of the usual bean shape and the caput epididymidis is attached to its cranial part. The ductus epididymidis penetrates in numerous loops both the caput and the considerably long cauda epididymidis, which is attached to the caudal part of the testis. Ductus deferens is long and conspicuous when full of sperm in the functional period, similarly as cauda epididymidis. Before opening into the sinus urogenitalis, the former forms a pars glandularis ductus deferentis (ampulla ductus deferentis). In this part of the male reproductive tract, three anatomically and histologically distinct glands are situated dorsal of the bladder. The most conspicuous paired accessory glands are considered to be the vesicular glands; the smaller paired glands are considered to be the ampullary glands. The gland situated medially at the neck of the bladder, thus not seen in Fig. 2, is the prostate. Glandulae bulbourethrales (Cowper's glands) are situated more distally at the root of the penis, at the boundary of the pars pelvina and the pars penis.

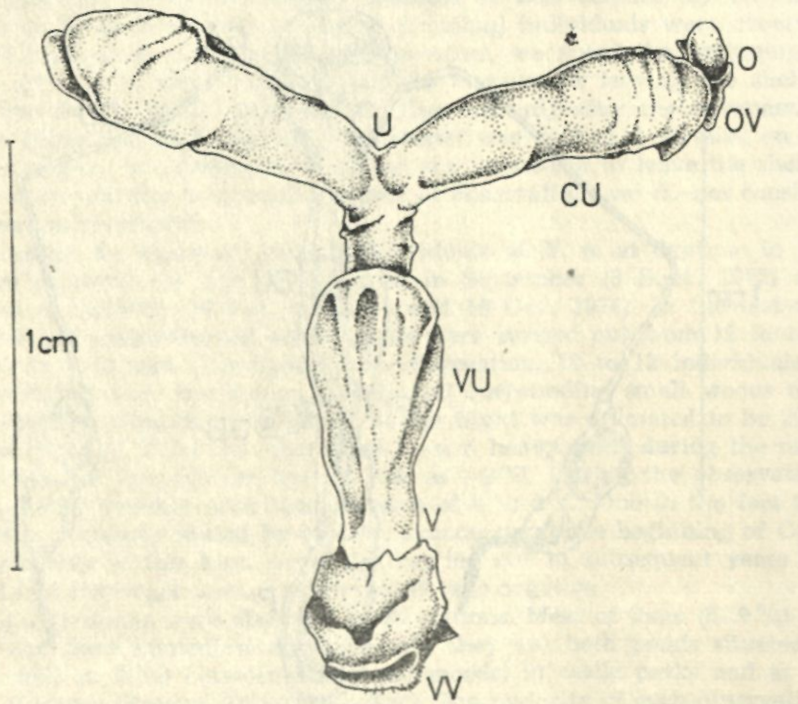


Fig. 3. Reproductive organs of the adult female after copulation in September, ventral side. Explanations: O, ovary; OV, oviductus; CU, cornus uteri; U, uterus; VU, vesica urinaria; V, vagina; VV, vulva and vaginal fissure.

The female has a transversal opening of the vulva, a shortened and flattened clitoris, an inconspicuous mons veneris; the labia are missing and the post- and circumanal fold is indistinct. In the width of the vaginal fissure there is a clear difference between nulliparous and multiparous females; the border between the two groups is 1.5 mm. The vagina is an elongated thick-walled organ into whose lumen protrudes the cervix uteri. The uterus is of the bicornis type, formed by the corpus uteri and the cornua uterina. Both horns are morphologically as well as functionally equivalent and the length of either of them in non-pregnant adult females is 6.0 to 7.0 mm. The left and the right ovary are of the same size, in adult females they measure 1.5 mm on the average. The oviducts are short and coiled. The sperm is stored in uterine horns and the oviducts.

An important additional criterion for judging whether the females take part in the reproduction process are the nipples, papillae mammae, placed near the lateral edge of the superficial part of musculus pectoralis major. In multiparous females the nipples are much cornified on the surface, elongated and hairless. In nulliparous females, both juvenile and adult, the nipples resemble those of males, with no signs of cornification, they are point-like and covered with fine hairs. Their length is difficult to measure, but the difference is macroscopically wel perceptible.

A g e a n d s e x u a l m a t u r i t y. The criteria used for the determination of age are sumarized in Tabs. 3 and 4. The sexual activity of males is considered to be evidenced by the presence of sperm in the cauda epididymidis; of females, by the presence of sperm in the uterus, by pregnancy, or lactation. The individuals showing contrary signs are evaluated as sexually inactive. In calculating the age with the precision of months, one starts from the fact that the young are born within a short time interval at the break of June and July. The age

Tab. 3. Age determination of males. Explanations: colour (of pelage) — 1, dark ochreous; 2, glossy ochreous; 3, light ochreous; ossification — 1, a broad zone of cartilago epiphysaria; 2, a narrow zone of c. epiphysaria; 3, ossification completed; eye = dry mass of right eye; abrasion of teeth — 1, none; 2, medium; 3, considerably worn; dentih layers = number of dentin layers on cross-section through right upper canine; (1), developing first layer

Date	Weight (g)	Colour	Sexual activ.	Ossification	Eye (mg)	Abrasion of teeth	Dentin layers	Age	
								years	months
13 Jan.	24.0	2	+	3	1.28	1	(1)	0	6
13 Jan.	21.0	2	+	3	1.32	1	(1)	0	6
12 June	23.5	3	—	3	1.66	3	—	2	11
12 June	25.0	3	—	3	1.52	3	—	2	11
10 July	27.0	3	—	3	1.70	3	5	5	0
6 Aug.	22.0	1	—	1	1.14	1	—	0	1
6 Aug.	22.8	1	—	1	1.18	1	—	0	1
9 Aug.	22.5	1	—	1	1.17	1	—	0	1
10 Sept.	31.2	3	+	3	1.42	2	2	2	2
10 Oct.	27.0	3	+	3	1.68	3	—	3	3
25 Oct.	28.0	2	+	2	1.11	1	—	0	4
25 Oct.	26.0	2	+	2	1.20	1	—	0	4
25 Oct.	27.0	2	+	2	1.10	1	—	0	4
12 Nov.	26.0	2	+	2	1.18	1	—	0	4
12 Nov.	23.5	2	+	2	1.13	1	0	0	4
12 Nov.	24.0	2	+	2	1.20	1	0	0	4
18 Dec.	22.0	2	+	3	1.12	1	—	0	5
18 Dec.	19.0	2	—	3	1.09	1	(1)	0	5

is rounded down; thus an individual caught on 12 Nov. which, according to the age criteria, is significantly younger than one year, has lived minimally from mid-July, and is therefore evaluated as 4 months old.

From five age criteria used three can be ascertained when handling living individuals in the field. For the shortest time one can use the ossification of long bones which is finished at the age of about 4 months, like in other bats (R y b á ř 1971). The difference in the coloration of young individuals and the absence of dental abrasion can be observed approximately up to the end of the first hibernation, *i. e.*, up to the age of about 8 months. From May onwards (material from April is missing), the coloration of young and old individuals is the same. Dental abrasion in the yearlings after the first hibernation can be smaller than in some old individuals, but this sign is not reliable. In Tab. 4 there are 6 females from May to July in which medium abrasion was found (degree 2). These females are of varying ages, from 10 months to almost 4 years. Also this conclusion corresponds to information concerning some other bats (*cf.*, B a r b o u r & D a v i s 1969). Thus, according to outer signs, the age of *N. n.* can be exactly determined at most till the spring of the year following the year of their births.

Tab. 4. Age determination of females. Explanations as in Tab. 3.

Date	Weight (g)	Colour	Sexual activ.	Ossification	Eye (mg)	Abrasion of teeth	Dentin layers	Age	
								years	months
13 Jan.	21.0	2	+	3	1.11	1	(1)	0	6
9 March	19.0	2	+	3	1.16	1	(1)	0	8
12 May	30.0	3	+	3	1.58	2	4	3	10
12 May	26.5	3	+	3	1.58	2	3	2	10
12 May	25.0	3	+	3	1.43	2	2	1	10
12 May	23.0	3	+	3	1.10	2	1	0	10
12 May	27.0	3	+	3	1.42	2	3	2	10
10 July	22.5	3	−	3	1.36	2	1	1	0
10 July	28.5	3	+	3	1.52	3	3	3	0
6 Aug.	20.9	1	−	1	1.17	1	—	0	1
6 Aug.	22.4	1	−	1	1.20	1	0	0	1
9 Aug.	19.0	1	−	1	1.20	1	—	0	1
9 Aug.	29.0	1	−	1	1.01	1	—	0	1
10 Sept.	31.0	3	+	3	1.41	3	—	2	2
10 Sept.	28.0	3	+	3	1.51	3	—	3	2
10 Sept.	30.0	3	+	3	1.45	3	—	2	2
10 Sept.	28.0	3	+	3	1.35	3	—	1	2
10 Sept.	33.0	3	+	3	1.31	3	—	1	2
10 Sept.	28.0	2	+	2	1.19	1	—	0	2
10 Sept.	25.3	2	+	2	1.20	1	0	0	2
13 Oct.	16.0	2	+	2	1.28	1	—	0	3
25 Oct.	26.0	2	+	2	1.35	1	—	0	4
12 Nov.	25.0	2	+	2	1.19	1	—	0	4
8 Dec.	24.0	2	+	3	1.21	1	—	0	5

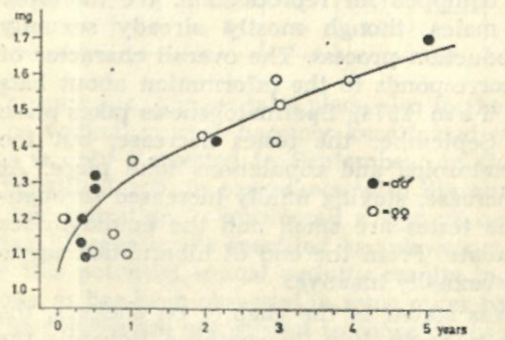
The remaining two criteria can only be used in the laboratory at autopsy. As far as we are informed the mass of the lens has hitherto been used to determine the age groups only in *Tadarida brasiliensis* (P e r r y & H e r r e i d 1969); this sign alone does not enable one to recognize the age in years. The number of the increment layers of dentin was first used by C h r i s t i a n (1956) in *Eptesicus fuscus* and later by K l e v e z a l' & K l e j n e n b e r g (1967) in several species of the fauna of the U.S.S.R., including *N. n.* The latter

two authors published a number of microphotographs of transversal as well as longitudinal sections of the canines of *N. n.* of different ages whose minimum age had been known in advance according to the results of banding. According to further information (R a c h m a t u l i n a, in litt.), the method was verified by Soviet researchers on ample material and it was established that the number of dentin layers gave the age in years.

In our material (Tabs. 3, 4) there are 4 specimens in which no increment layer of dentin was found. According to all criteria and the date of catching, their maximum age is about 4 months. In further 5 specimens one forming layer of dentin was found. Their age — again according to all criteria — is 5 to 8 months. One distinct layer of dentin was found in 2 females; according to the date of catch, the first of them is 10, the other 12 months old. The remaining 7 specimens have 2 to 5 dentin layers. According to other signs their ages cannot be estimated, with one exception, *viz.*, that they are older than 1 year. Besides the material used for the study of reproduction we obtained an individual whose minimum age was known thanks to banding: the male had been banded on 23 Jun., 1969 and found recently dead on 11 May, 1971. According to the date of banding its age must have been at least 11 months, but most probably 1 year, so that at the time of death its age was almost 3 years. In the section through its canine there are three distinct increment layers of dentin.

All the above fact prove that the number of layers of dentin is, for the time being, the most reliable criterion of bat age. That is why we used it to verify the last criterion, the dry mass of the eye, as shown in Fig. 4. The graph includes also specimens in which tooth sections have not been made, but whose age is unquestionable — altogether young animals. The graph shows that the scatter of the values of dry eye mass is great, particularly with the youngest specimens, but the overall trend of mass increment is in correlation with age. This sign can, therefore, be used as an auxiliary one in specimens older than one year, where tooth sections could not be made.

Since the combination of all criteria enables one to determine the age of the whole sample with great probability, we have reliable data available to follow



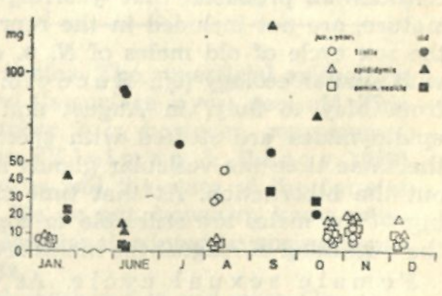


Fig. 4 (left). Correlation between the mass of dry eye (ordinate) and age determined according to the date of collection and the number of dentin layers on section through C_1 (abscissa).

Fig. 5 (right). Sexual activity of males in the course of the year according to the mass of the testes, epididymides, and vesicular glands (= semin. vesicle). In comparison with Tab. 3 one old male obtained later was added in January.

sexual maturation. As shown in Tab. 3, the sexual activity of males — according to the presence of spermatozoids in the cauda epididymidis — was found out as early as at the age of 4 months. Also the descent of the testes and the formation of the scrotum was well perceptible at that time. The above sings of sexual activity were observed in yearlings also during hibernation. An exception is a male found in December (last in Tab. 3) which, according to all signs, was sexually inactive and thus immature. Out of 10 male yearlings 90 % were mature (= adult) and 10 % immature (= subadult?).

In young females spermatozoids were found in uterine horns as early as the first half of September, when they were only 2 to 3 months old. All yearling females examined in the course of the first hibernation had been inseminated. The degree of development of their Graafian follicles did not differ from that of females older than 1 year. It can be judged that females mature together with the end of their bodily growth, thus passing straight from the juvenile into the adult stage. There is, however, a question whether all yearling females bear and successfully rear their young. In our material there is only one evidently pregnant yearling female with a normally developed embryo in May. Another female examined at the beginning of July, about one year of age, had a thread-like uterus without any signs of pregnancy and an unusually narrow vaginal fissure. It is questionable to evaluate her as immature (= subadult?, *cf.*, Tab. 5), since we do not know whether she mated the preceding year. Due to the fact that all yearling females examined from September to May were inseminated, we consider it probable that sexual maturity in this age group is 100 %, but the share in the population increment smaller than in older females.

M a l e s e x u a l c y c l e. The changes in the size of the testes, epididymides, and vesicular glands in the course of the year are given in Fig. 5. The highest mass of the testes in adult males was found in June, in the males passing from the juvenile into the adult stage in August. Also the development of the vesicular glands and the filling of the epididymides with sperm in younger males is evidently retarded. In old males the mass of both epididymides and vesicular glands was the highest in September and even in October it was about 3 times as high as in the yearlings. The graph shows clearly that the males over 1 year of age are better equipped for reproduction. We therefore consider it probable that yearling males, though mostly already sexually mature, are not included in the reproduction process. The overall character of the sex cycle of old males of *N. n.* corresponds to the information about bats with similar ecology (*cf.*, R a c e y & T a m 1974). Spermatogenesis takes place from May to July, in August and September the testes decrease, but the epididymides are stuffed with spermatozoids and copulations take place. At the same time the vesicular glands increase, staying mildly increased throughout the hibernation. At that time the testes are small and the epididymides big — the males are still able to copulate. From the end of hibernation up to the beginning of August the males are sexually inactive.

F e m a l e s e x u a l c y c l e. As was stated in the chapter on shelters, the females of *N. n.* bear from mid-June to early July. In southern Bohemia the last pregnant females were found on 4 July. From southern Moravia there is one young of 10 July which weighed 7 g, was hairless and the eyelids of which were almost fused. According to the hitherto knowledge of the postnatal development of the species (K l e i m a n 1969), the female was born between 2 and 5 July. Other characteristics of the female sex cycle can be seen from

Tab. 5. All females irrespective of age, examined from September to March, were inseminated, so that they had probably mated at the beginning of September or as early as at the end of August. Besides the presence of sperm, a sing of copulation having taken place is the widening of the uterus and particularly of its horns which are filled with sperm. This change is the most conspicuous in females of that year whose uterus is still thread-like in August and in September it does not differ from that of females older than one year. As evident from the table, the total length of the uterus remains almost unchanged.

Tab. 5. Reproductive activity of females. Explanations: nipples — L, lactating: +, large, not lactating; —, small; vagina = width of vaginal fissure (mm); uterus = length of uterus (mm); sperm = the presence of sperm in uterus

Date	Age		Nipples	Vagina	Uterus	Sperm	Embryo (s)	Reproductive	
	years	months						condition	activity
13 Jan.	0	6	—	1.3	11.0	+	—	yearling	active
9 March	0	8	—	1.1	12.0	+	—	yearling	active
12 May	3	10	+	2.5	17.0	—	2	adult	active
12 May	2	10	+	2.5	15.5	—	2	adult	active
12 May	1	10	+	3.0	16.0	—	2	adult	active
12 May	0	10	—	1.4	19.0	—	1	yearling	active
12 May	2	10	+	2.9	17.0	—	2	adult	active
10 July	1	0	—	0.8	12.0	—	—	subad. ?	inactive
10 July	3	0	L	2.2	12.0	—	—	adult	active
6 Aug.	0	1	—	0.9	12.0	—	—	juvenile	inactive
6 Aug.	0	1	—	0.9	9.0	—	—	juvenile	inactive
9 Aug.	0	1	—	1.2	12.0	—	—	juvenile	inactive
9 Aug.	0	1	—	1.5	12.0	—	—	juvenile	inactive
10 Sept.	2	2	+	3.5	13.2	+	—	adult	active
10 Sept.	3	2	+	2.2	12.1	+	—	adult	active
10 Sept.	2	2	+	2.5	13.0	+	—	adult	active
10 Sept.	1	2	+	3.8	12.5	+	—	adult	active
10 Sept.	1	2	+	3.0	13.4	+	—	adult	active
10 Sept.	0	2	—	1.2	13.5	+	—	yearling	active
10 Sept.	0	2	—	1.0	11.1	+	—	yearling	active
13 Oct.	0	3	—	1.0	11.0	+	—	yearling	active
25 Oct.	0	4	—	1.5	14.0	+	—	yearling	active
12 Nov.	0	4	—	1.2	12.0	+	—	yearling	active
8 Dec.	0	5	—	1.3	11.0	+	—	yearling	active

Conspicuous changes take place also in the vagina. The superficial epithelium of the vaginal mucosa becomes keratinized and its surface layers peel off. This state is only suggested in September; in October it is, however, conspicuous, lasting till March. In accordance with literature (K l e i m a n & R a c e y 1969) the keratinization is considered a sign of oestrus and the state of the females during hibernation is specified as suboestrus. We do not, however, know whether this potential sexual activity results in occasional winter or spring copulations, as has been observed in some other bats.

The ovaries are not subject to conspicuous changes in size and mass. The gradual change of primary follicles into secondary ones begins in juvenile females shortly after birth and before entering the hibernation the ovaries of all females show foundations of tertiary Graafian follicles. In the period from October to the beginning of March, these follicles do not continue to develop. We did not observe ovulation, as we have no material from 10 Mar. to 11 May.

All females examined in May ($n = 5$) had the corpora lutea graviditatis and macroscopically perceptible embryos in their uteri. In females older than 1 year there were 2 embryos, one in each of the uterine horns. In the only yearling female, 1 embryo was implanted in the right uterine horn. This female had still very small nipples and a narrow vaginal fissure.

The exact determination of the length of pregnancy and lactation is not possible from the sample in Tab. 5. According to observations in the field, mainly in southern Bohemia, pregnancy lasts about 3 months and lactation 4 weeks. The reconstruction of the whole sexual cycle in males and females, based on our own as well as the literary data (for references, see the discussion), is given in Fig. 9.

Population

S e x r a t i o. Information showing the sex ratio of the whole sample is given in Tab. 6. Among juvenile individuals a balanced sex ratio was found in July; later on the number of males increases. Their predominance in August is statistically still insignificant, but in September it is already highly significant. In the whole sample of juveniles the males constitute 60 % and their predominance is significant. The sample of yearlings is comparatively small ($n = 177$) and therefore it was not divided according to months. In fact, those individuals must have been more numerous but, owing to lack of reliable field criteria (see above), part of them was evidently classified among old individuals. The sex ratio among yearlings is balanced, a small predominance of males is statistically insignificant.

Tab. 6. Sex ratio in the population samples of different age classes with respect to the time of year

Age class	Period	n	% ♂	% ♀	x^2	P
juveniles	July	91	51.6	48.4	0.10	>0.50
	August	221	55.7	44.3	2.82	>0.05
	September	108	77.8	22.2	33.33	<0.01
	total	420	59.8	40.2	16.01	<0.01
yearlings	total	177	54.8	45.2	1.63	>0.20
old individuals	Jan.–Febr.	65	64.6	35.4	5.55	<0.02
	March–Apr.	143	23.1	76.9	41.46	<0.01
	May–June	254	32.3	67.7	31.89	<0.01
	July–Aug.	127	36.2	63.8	9.64	<0.01
	Sept.–Oct.	82	82.9	17.1	35.56	<0.01
	Nov.–Dec.	73	58.9	41.1	2.31	>0.10
	total	744	42.2	57.8	18.09	<0.01

The sample of old individuals must be evaluated with respect to the fact that it also includes yearlings, especially from March to May. Quite certainly the sample is constituted solely by old individuals in the period from June to October, when the yearlings are absent from the population or when they can be safely distinguished (October). The material has been divided according to periods of two months. As shown by the table, males prevail from Septem-

ber to February, females from March to August. The predominance of males in November – December is statistically insignificant, in all other cases the prevalence of either males or females is highly significant. Females prevail in the pooled sample of old individuals.

The evaluation of old disproportionate sex ratio meets with problems current in the ecology of bats. The part of the population bound to colonial aggregations is expressed relatively well, while the components living a solitary life or in small groups are included only partly and therefore underestimated. This explains, above all, the predominance of old females in the sample from April to August when most old males live outside the female aggregations. As for the predominance of old males in the winter season, this phenomenon is also known to occur in some other species of bats; it has often been discussed (*cf.*, G a i s l e r 1975) but still not satisfactorily explained. The most frequent consideration is that taking into account the differential preference of shelters by the two sexes. In the case of *N. n.*, our material of which comes exclusively from buildings, it can be theoretically judged that females are more frequent in winter tree shelters. Other alternatives are that part of the females emigrate to hibernating quarters situated more to the south, or that part of the males immigrate to our hibernating quarters from the north. This will be dealt with in the discussion.

For the time being, a realistic sex ratio seems to be that found in the juveniles in July and in the whole sample of yearlings. The prevalence of males in the total sample of the young found in this species previously (G a i s l e r & K l í m a 1968) is due to the inclusion of samples from August and September. At that time, the probability of coming across male and female young differs in the connection with mating, as will be described when evaluating the structure of the summer population.

S t r u c t u r e o f t h e s u m m e r p o p u l a t i o n. Both population structure and density can be dealt with in detail only in the sample from the growing season, as the winter sample is relatively small and most of it comes from one station and one type of shelters (dwelling houses in Prague). In the summer population we have at our disposal the results of systematic studies in a geographically well defined region of southern Bohemia. The south Bohemian pond basin is particularly suitable for the research of the ecology of *N. n.*, as the species is very frequent there and – with the exception of human settlements – in the summer season it prevails over all other bat species. The basis of our research was systematic sampling of colonies from hollow trees which, in that region, are the only known shelters of the species. Positive finds were made from April to October; occasional attempts at getting hold of the species outside this period were unsuccessful. There have been no reports on the hibernation of the species in southern Bohemia.

As shown in Fig. 6, the spring population sample consists of grown-up individuals, the most numerous of them being old females, followed by yearling females, yearling males, and the least numerous are old males. There is a ratio of 1 old female to 1.7 yearlings. This number is apparently somewhat higher than in reality, which is again due to lack of exact age criteria that could be used in the field. A certain predominance of the young of the preceding year compared with old females is nevertheless possible, considering the fact that most females bear 2 young.

Another sample is from the last ten days of June and the whole of July. Yearlings have become old individuals; there appear juvenile individuals, or population increment. Old females form 36 %, juveniles 59 % of the sample, so that there are 1.6 juveniles per 1 old female. This number is appreciable, considering that part of the young have not been found, as they had not yet flown out of the hollows. This witnesses a population increment unusually high for bats, which is in accordance with the fact that females older than one year had 2 embryos each.

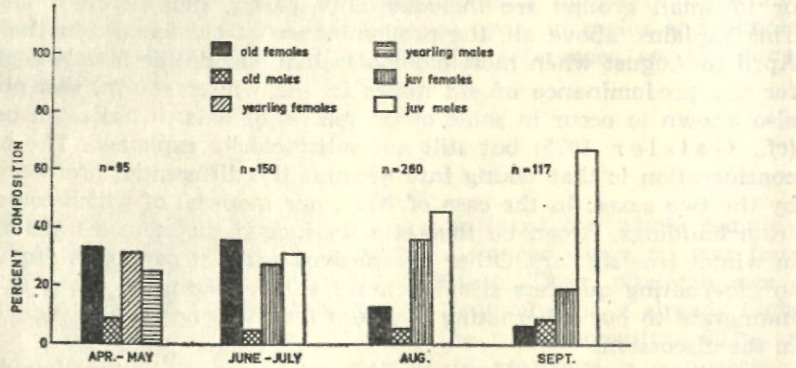


Fig. 6. Composition of the sample of the south Bohemian population durin the growing season.

In the August sample the juvenile component constitutes as much as 82 %, 6.1 juveniles falling to 1 old female. In the sample of juvenile individuals there appears a clear predominance of males for the first time. In September the juveniles constitute 86 %; to 1 old females there fall as many as 14.2 young. In the sample of juveniles there are about three times as many males as females. For the first time old males prevail over old females in September; otherwise old males were the least numerous component of the samples, their percentage representation varying between 5 and 9 %.

The quantitative relations found can be explained if we take into consideration the above information concerning the shifts in shelters, the course of reproduction, as well as information taken from literature, particularly the behaviour of *N. n.* in August and September (Pan'utin 1963, Sluiter & Heerdt 1966). The whole picture is probably as follows: Grown-up females, 1 year old or older, produce 1.8 young on the average. The sex ratio among the young is balanced or the males predominate slightly. The same sex ratio remains also among the yearlings and the old individuals. In summer most of the old males live in shelters which are difficult to discover by the observer. From August onwards, old females start to leave the nursing colonies and move to shelters of solitary old males with which they mate. After the disintegration of the nursing colonies the young form juvenile colonies; they are therefore easier to locate and in the sample they thus prevail over old females. In late August and in September the juvenile (maturing) females move to old males with which they also mate. The males of that year, however, remain in the juvenile colonies; they do not participate in the mating and in the sample they gradually exceed the females.

This pattern can still be modified by the migration taking place at the beginning and at the end of the growing season. For the time being, it cannot even approximately be estimated what the share of the transmigrating individuals is in the composition of local populations; their presence particularly in April is, however, highly probable, as shown by catches to calculate the population density (see below, Tab. 7). The population studied appears the most stable in June and July, when old females are pregnant or lactant and are strictly bound to colonial aggregations. If we add to this population component an adequate number of old males and newborn young, we get a realistic picture of the population structure.

Density of the summer population. In the population of southern Bohemia which was systematically followed, an estimate of the population density was carried out in 1976 and 1977. Several observation seasons preceded the census proper. The search for cavities was performed by a group of observers in spring when the trees were not yet covered with leaves and the openings of the cavities well visible. The terrain was walked through systematically several times and all the holes found were marked visibly on the tree trunks. During the growing season the cavities were investigated as for their population by *N. n.*, both visually (dark fringes of the entrances) and by listening. Those „listening" actions were performed on warm days in the afternoon hours. Suitably situated „suspicious" cavities were occasionally provided with catching cages even if the listening was negative. We should like to point out the fact that thit method can serve for estimating the population density of *N. n.* only in a landscape which is perfectly known, easy to observe, and which has been investigated for several years.

For the census, two quadrat plots were delimited, each having a side of 1.5 km, *i. e.*, two areas of 2.25 km^2 each. The experimental plots were situated at the northern limit of the Třeboň basin, in horizontally diversified landscape with numerous ponds between the towns of Veselí n. Lužnicí and Třeboň (49° 03′ to 49° 10′ n. lat. and 14° 40′ to 14° 50′ e. long.) at the elevation of 430 to 450 m. The two areas were about 10 km apart to prevent overlapping of hunting ranges and decrease the possibility of movements during the census.

Plot A (Fig. 7) includes a region of small woods and wet meadows between two large south Bohemian ponds, Horusický and Švarcenberský. It is characterized by a large number of old deciduous trees (mostly oaks) at the edges of woods, on the dams of ponds and along canals and, particularly, along roads. Towards the west the area touches a similar type of landscape, in all other directions there prevail field habitats. Before the census proper, the area had been followed systematically for 8 years; out of the total of 48 known tree cavities, 13 had been populated by bats (and registered).

Plot B (Fig. 8) was delimited in a group of medium-sized ponds north of the village Klec, district Jindřichův Hradec. Besides a considerable area of open water surface of the ponds, it includes a network of pond dams with lanes of old oaks and, to a lesser extent, fringes of small woods and small areas of meadows. The western part of the area is flown through by the Lužnice River bordered by a narrow band of mead wood. In the north and in the ... th characters of the adjoining landscapes are similar; in the south-w... is a village with a large area of fields. Before the census proper, t... been systematically followed for 5 years, 30 tree cavities registere... of them a periodic occurrence of bats noted.

On the two plots, *N. n.* is the most frequent bat. Colonies in ... sometimes mix with those of *Myotis daubentoni* and rarely even ... duals of *Nyctalus leisleri*. Besides, *M. daubentoni* forms independe...

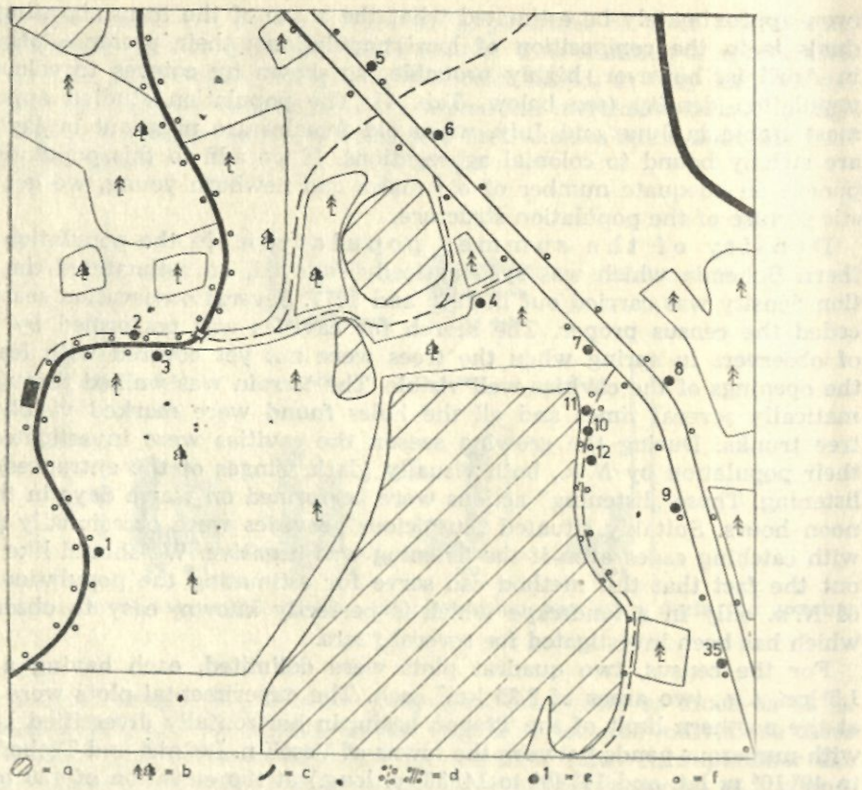


Fig. 7. A schematic map of experimental plot A. Explanations: a, ponds; b, small woods; c, running waters; d, roads with lanes of old trees; e, periodically populated tree cavities; f, other solitary old trees.

both trees and buildings and on the whole it is the second most frequent bat. On the plots or in their close neighbourhood, we also found summer colonies of *Myotis mystacinus* and *M. nattereri* (in lofts of houses) and individuals of *Plecotus auritus*, *Pipistrellus nathusii*, and *P. pipistrellus*.

The basis for the calculation of the population density of *N. n.* was the number of individuals caught on the experimental plots during several nights in succession. For catching, we used the cages described above (Pl. II, left), the individuals caught were banded and immediately released. The banding served, besides other purposes, also for counting each individual only once during each census. In applying this method we start from the assumption that the plots include typical stations of the region under investigation, where populations of tree bats are distributed in approximately the same way as in the surrounding landscape. In that case it is not necessary to consider the foraging home ranges of the individuals caught, since, in the same way as the population of the area utilizes the neighbouring habitats, there appear individuals from the neighbourhood hunting in the territory of the study plots.

The results are summarized in Tab. 7. Owing to technical difficulty it was not possible to carry out the census quite regularly and within one year (1976); important July values were completed in 1977. From the facts described in the

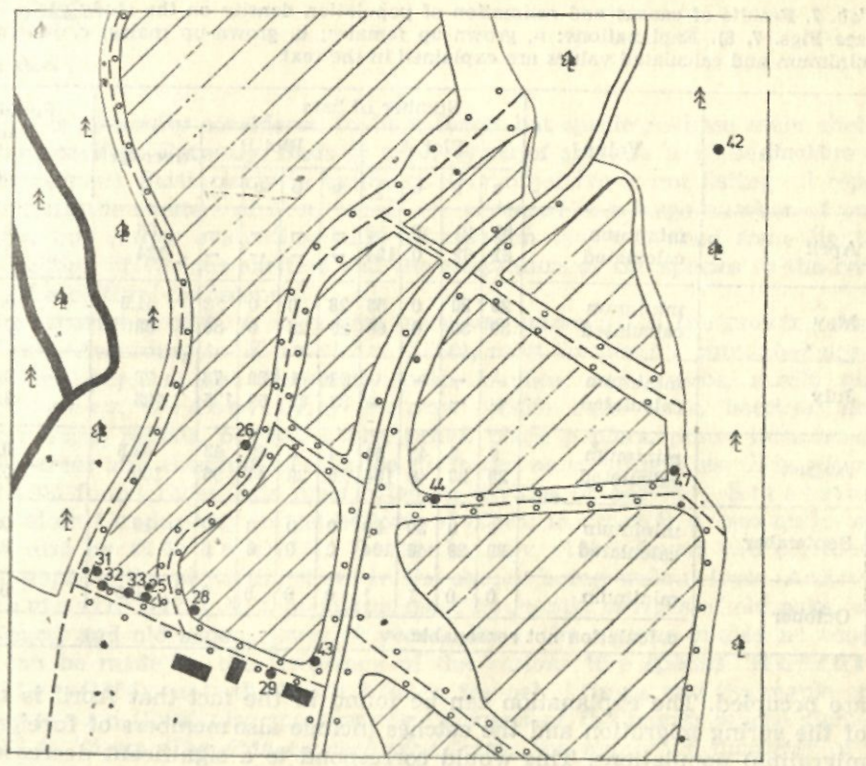


Fig. 8. A schematic map of experimental plot B. Explanations as in Fig. 7.

preceding chapters it is evident that the quantitative data obtained represent minimum values. To approach the actual situation we add the „calculated" values of the abundance and population density. Those were obtained by increasing each sample by that part of the population which is supposed to be in the area though not recorded. Namely the number of grown-up individuals was so adapted as to make the number of males equal to that of females. Furthermore, the number of juvenile females in August and September was increased so as to equal the number of juvenile males. Lastly, the ratio of old females and the young was adapted in such a way as to yield 1.8 young per 1 female in July, 1.7 young in August, and 1.6 young in September. These theoretical assumptions need not always be fulfilled, *e.g.*, the number of old males hiding in the area of both study plots need not tally with the number of old females. That is why we think that the real population density of *N. n.* will be somewhere within the range of minimum (= actually found) value and the calculated (= estimated) value.

From Tab. 7 it is apparent that although the values found do vary throughout the year, they do not differ in the order; nor are there any substantial differences between the two plots. If we evaluate the population density in the course of the year, the high values in April (minimum = 0.37 ind. per ha, calculated = 0.55 ind. per ha) are conspicuous. This state is perceptible even in a cursory inspection of the field, as at that time almost all cavities used

Tab. 7. Results of census and estimation of population density on the study plots A and B (see Figs. 7, 8). Explanations: a, grown-up females; b, grown-up males; c, juveniles; the minimum and calculated values are explained in the text

Month	Value	Number of bats									Population density
		Plot A				Plot B				average	
		a	b	c	Σ	a	b	c	Σ	Σ	*n*/ha
April	minimum	62	21	0	83	–	–	–	–	83	0.37
	calculated	62	62	0	124	–	–	–	–	124	0.55
May	minimum	25	30	0	55	28	0	0	28	41.5	0.18
	calculated	30	30	0	60	28	28	0	56	58	0.26
July	minimum	–	–	–	–	33	1	39	73	73	0.32
	calculated	–	–	–	–	33	33	59	125	125	0.55
August	minimum	9	2	43	54	4	0	39	43	48.5	0.21
	calculated	28	28	48	104	26	26	44	96	100	0.44
September	minimum	0	0	30	30	0	0	0	0	15	0.06
	calculated	29	29	46	104	0	0	0	0	52	0.23
October	minimum	0	0	1	1	0	0	0	0	0.5	0.002
	calculation not reasonable										

are occupied. The explanation can be found in the fact that April is the time of the spring migration and the catches include also members of foreign (transmigrating) populations. This would correspond to a significant decrease in the population density in May (minimum = 0.18 ind., calculated = 0.26 ind.), even if we must take into account the possible influence of the disturbance of bats due to the preceding catches. The most conclusive are considered the values of July 1977 (minimum = 0.32 ind., calculated = 0.55 ind.), as in that year the bats were not disturbed in the hollows before the action, and July being the time of the smallest shifts in the population. The August values (minimum = 0.21 ind., calculated = 0.44 ind.) keep roughly on the expected level, particularly in relation to the May values, which are from the same year of study (1976). In September there is already a conspicuous drop (minimum = 0.06 ind., calculated = 0.23 ind.) and in October the emigration of *N. n.* from the area is almost finished. An increase analogical to the situation in April does not manifest itself, so that foreign populations either do not pass through the territory under investigation or at least they do not stop there in autumn.

If October is excluded, then the average population density from all actions will be: minimum = 0.23 ind. per ha, calculated = 0.41 ind. per ha. The average of the two values, 0.32, is considered a very realistic approximation. The number of individuals of *N. n.* living in the region under investigation can thus be estimated to be about 3 individuals per every 10 ha.

Discussion

Shelters

N. n. is generally considered to be a forest bat species, whose main shelters are tree cavities. Recently, finds in other types of shelters have been more and more frequent, particularly in buildings. Our objective is not listing all reports concerning the shelters of *N. n.* which are scattered in a large number of publications, but rather evaluating such information that can shed some light on the selection of various shelters and the adaptation of the species to the conditions of a cultural landscape.

The occurrence of *N. n.* in hollow trees was evidenced in the growing season as a rule. According to Kuz'akin (1950), most frequently populated are old limes and poplars; less frequently oaks, birches, and aspens, rarely pines. Abelencev, Pidopličko, Popov (1956) state oaks, beeches, hornbeams, limes, aspens, birches, ashes, pears, black poplars, pines, false acacias, walnut-trees and chestnut-trees to be preferred as roosting sites. Blackmore (1963) found those bats most often in cavities of beeches; Stratmann (1968) almost exclusively in the hollows of pines; in pines *N. n.* was quite often found also by Hůrka (1973). Bojšebajev (1966) found two colonies in silver poplars, the prevailing trees in the station being walnut-trees. According to Pan'utin (1970), *N. n.* populates most frequently cavities of old oaks (over 100 years) and old aspens (over 40 years). From the sources quoted no conclusion can be made on the frequency of the various tree species. Heerdt & Sluiter (1965) quote the beech 7 times, the oak 6 times, and the maple once. Stratmann (1968) also specifies the thickness of the trunks whose diameter was 32 to 75 cm. The data concern pine trees; the maximum diameter of the inhabited deciduous trees is greater as a rule.

Most finds of *N. n.* in hollow trees are from lowland or slope regions, only the station described by Bojšebajev (1966) in Kirghiz is situated at the elevation of 1,600 m. Even without a detailed phytocenological analysis is it evident that the preference of trees is, as a rule, correlated with the frequency of occurrence of the respective tree species in the regions where the various authors worked. Besides, the bats prefer trees standing at the edges of woods, in lanes, on the shores of water reservoirs and streams, or solitary trees in a park-like landscape. An important fact seems to be that the tree should have a high trunk below the crown and a free space in front of the entrance. In our study areas, all those conditions are best fulfilled by the oak.

As for the height of the entrance to the cavity above the ground, there are more frequent reports about the finds of *N. n.* in higher situated holes. Ryberg (1947) reports 5 to 8 m; Natuschke (1960) mostly 6 m; Stratmann (1968) 4 to 12 m; and Pan'utin (1970) 3 to 20 m the most frequent cases being 8 to 12 m. In that respect, our observations are somewhat different, since the most frequented class is 3 to 4 m. The height of the populated cavities is determined by different factors, such as the species and age of the tree, the activity of woodpeckers whose abandoned cavities are the most frequent source of tree shelters of *N. n.* (Sluiter & Heerdt 1965), anthropogenic factors, *etc.*, which in different regions can be manifested in different ways. Generally valid is probably a note by Blackmore (1963) that „the roosting hole may be at any height".

In tree hollows both individuals and all types of colonies have been found, including nurseries. Male colonies were described in detail by Löhrl (1955). Other shelters of the tree type, such as cracks behind the bark or man-made nest boxes, are populated only by individuals or small groups; numerous reports point to the fact that nest boxes are not suitable for nursery colonies of *N. n.* (*cf.*, Gaisler 1975). As for the size of colonies in tree cavities, most authors state that groups up to 50 individuals are a regular phenomenon (Ryberg 1947, Bels 1952, Abelencev & al. 1956, Stratmann 1968); exceptionally colonies of up to 400 individuals are reported (Blackmore 1963, Heerdt & Sluiter 1965). More detailed data can be found in Sluiter & Heerdt (1966) who, for 13 years of research, followed different types of summer colonies, numbering 7 to 88 individuals, the most numerous being on the one hand mixed colonies in May, and on the other hand nursery colonies recorded with the young in the latter half of July. Pan'utin (1970) does not inform about the whole sample, but states average values of the sizes of colonies of different types at different times. The largest were the colonies of pregnant females in June (40 ind. in one colony) and nursery colonies in July (51 ind. incl. the young); the average size of colonies of other types varied between 10 and 32 individuals. The values calculated from our material are somewhat lower than those of Pan'utin, but on the whole they agree with the reports of all authors, *viz.*, that *N. n.* forms mostly small colonies up to 50 individuals in the growing season.

The winter finds of *N. n.* in hollow trees are much rarer than those in summer. The colonies are usually discovered by accident, such as by felling thick trees at least 1 m in base diameter of the trunk. Most reports about such finds come from Western and Central Europe, to the north up to the southernmost tip of Sweden (Ryberg 1947, Natuschke 1960, Blackmore 1963, Heerdt & Sluiter 1965, Saint Girons 1973). Several finds in hollow trees are reported from the Ukraine and from Soviet Central Asia (Kuz'akin 1950, Abelencev & al. 1956, Strelkov 1969). The winter numbers of *N. n.* in trees seem to be higher than the summer ones; there are, however, very few reliable data: Abelencev & al. (1956) state 250; Kepka (1962) 34 and 100; Heerdt & Sluiter (1965) 100 and 152; and Gauckler & Kraus (1966) four times 20 to 30 and once 80 individuals.

Another type of shelters from which *N. n.* was reported are caves and cracks in rocks. Bianchi, Caporiacco, Massera, Valle (1949) state *N. n.* as a frequent species in one Italian cave, but Toschi & Lanza (1959) doubt the correctness of the identification of the species. Dumitrescu, Orghidan, Tanasachi (1955) found a large number of *N. n.* skeletons in the Rumanian cave Cioclovina cu Apă. The age of the find is estimated to be 2,900 years. They think it possible that *N. n.* was a cave species at that time and it changed to hollow trees only later on. Isolated finds of skeletal remains of *N. n.* in caves are known also from other publications and we ourselves found a subrecent skull of this species in the Bulgarian cave Troevratica near Karlukovo. Kuz'akin (1950) mentions a winter find of 20 males in a rock crack of Mt. Cerebeleva in the Caucasus and probable hibernation of the species in deep crevices of coastal rocks of Cape Kobuchtu in Lake Teleckoe in the Altai. The most persuasive evidence of the occurrence of *N. n.* in rock crevices was brought by Barbu & Sin (1968). The authors had followed 4 winter colonies, numbering a total of about 1,000 individuals, in vertical crevices of limestone cliffs of Cape Doloşman of Lake Razelm in Rumania. The crevices were situated 4 to 25 m above the water level on the lake and they were 1 to

2 m high, 1 to 2 m deep, and 5 to 7 cm wide. The location of these winter colonies agrees completely with our find in the rock wall near Srbsko (Pl. II, right).

On the basis of these finds we consider rock cracks and crevices to be another type of original shelters of *N. n.*, besides tree cavities. Owing to a comparatively high winter mortality rate of the species (Meise 1951, Barbu & Sin 1968) the dead animals fallen out of such cracks can later on be passively carried deeper into the caves often neighbouring with the cracks. The finds of skeletal remains of *N. n.* in caves can be explained in this way. We are not inclined to consider the changes in ecological requirements of the species during recent millenia. There remains a problem open to dispute, *viz.*, whether rock cracks are populated by this species also during the growing season; some observations from Bulgaria suggest it (Hanák, unpublished). However, an active search for, and colonial roosting in, deeper situated parts of caves is, in our opinion, improbable.

The last type of shelters are buildings. The most frequent finds – mostly in large towns – are from the period of hibernation. Winter shelters are often in various chinks in walls, in spaces under the roofs or between the ceiling and the floor, behind window frames, behind wood panelling, in ventilation shafts, *etc.* In literature there are numerous data concerning the numbers of individuals in winter colonies of *N. n.* in buildings: Löhrl (1936) caught 61 ind. from a colony in Munich; Mislin & Vischer (1942) found about 250 ind. in Basel; Meise (1951) followed a big colony in the Frauenkirche church in Dresden, numbering up to 1,200 ind., Skreb & Dulić (1955) followed a big colony of about 500 ind. in Zagreb; Abelencev & al. (1956) report a colony of 650 ind. from Užhorod and another of more than 1,000 individuals from near Mukačevo; Gauckler & Kraus (1966) found 53 ind. in Nuremberg; Braaksma & Wijngaarden (1966) in the castle of Apeldoorn in Holland, 5 ind.; and Butovskij (1974) studied a colony in Alma-Ata, numbering 1,000 to 1,500 individuals. The average number of individuals in winter colonies is thus higher than in the summer colonies. In our samples there prevail small colonies of 10 to 20 ind., which may be due, on the one hand, to incomplete samples and, on the other, to the fact that in Prague the hibernating population is divided among a large number of shelters of limited space.

This list of stations is not complete. Particularly from recent years there have been many reports of finds of *N. n.* in various parts of buildings and several times individuals or whole groups were observed to fly into buildings; also the occurrence of individual *N. n.* was ascertained in colonies of *Myotis myotis* (Haensel 1967, Roer 1977, and various contributions in the newsletter Myotis, Vols. 1969, 1974, 1975, 1976). Buildings are populated by this species not only in winter but also during spring and autumn movements and there is also evidence of the summer occurrence of *N. n.* in buildings. So far, however, nobody has proved the occurrence of nursery colonies in shelters of this type. The summer aggregations of female *N. n.* with the young seem to be strictly associated with tree cavities.

In general, we must confirm the conception of *N. n.* as a „fissure bat" (Gaisler 1966), which is not so much bound to the type of substrate of the particular shelter, but rather to microclimatic conditions which the shelter yields. This can be evidenced in the case of winter shelters for which sufficient data are available on the fact that the microclimate of the shelters in buildings

(Mislin & Vischer 1942, Butovskij 1974, and others), in rock cracks (Barbu & Sin 1968) as well as in hollow trees (Sluiter & al. 1973) is similar. The corresponding data concerning the microclimate of the summer shelters are not available so far. The choice of summer shelters is certainly influenced by the requirements for an environment offering suitable and sufficient food supply. That is why hollow trees remain the main shelters of summer colonies, particularly for nursery colonies which are the most conservative component of populations. On the whole, *N. n.* has well adapted itself to the civilization pressure and, in places, it gradually turns towards the hemisynanthropic way of life. Even if the changes in abundance of the species in time have not been reliably recorded, we can, with great probability, consider *N. n.* to be one of the least endangered bats of Europe.

Hunting activity

Already Blasius, Koch, Altum, Kolenati, and other exact observers of the 19th century found that *N. n.* flies quickly with a comparatively straight flight, mostly at the level of tree crowns or higher. The flight apparatus is fully adapted to that (Gaisler 1959). Besides general information in different monographs (Ryberg 1947, Kuz'akin 1950, Natuschke 1960, Blackmore 1963) its ways of flying and the hunting activity are described in detail by Klawitter & Vierhaus (1975). According to those authors, the activity of *N. n.* starts earlier than in most of the other European bats, as a rule several minutes to 1 hr after sunset. In spring and in autumn, the flight activity starts earlier than in high summer, and at the end of September and in October it can begin even before sunset. The flight speed varies from 30 to 54 km per hr (16 measurements). In the wood environment *N. n.* hunts at the height of about 15 m; above open terrain such as fields or lakes, 20 to 70 m; on the average, 31 m (28 observations). Under certain circumstances, such as in hunting low-flying prey or in strong wind, these bats fly lower. This corresponds with the observations by Cranbrook & Barrett (1956) who mist-netted low flying *N. n.*, taking house crickets as they flew from a municipal dump. A typical hunting ground of *N. n.* is in the wood, above all, in wood clearings and on wood edges. Owing to their great action radius, these bats can be met as far as 6 km from the nearest wood over fields, water areas, or in outskirts of villages. Inside major towns, *N. n.* does not hunt even if its shelters are situated there. Our findings fully agree with the information obtained by the above-mentioned authors.

Of all European bats, flying *N. n.* were comparatively most frequently observed during daytime. Due to the fact that sometimes it was more individuals and most cases like that were observed in late summer and in autumn, some authors considered this to be correlated with migration. Although already Löhrl (1955) was looking for a more probable explanation of this activity in hunting for food, reports on „daytime migrations" of *N. n.* have appeared even recently (Reichholf 1976). The problem was dealt with in detail by Krzanowski (1959) who listed a large number of observations but did not arrive at an unambiguous explanation. If the cause of the daytime activity were cold nights or otherwise unfavourable weather, there would be far more observations of this kind. On the other hand, it is conspicuous that a great majority of the observations were made during clear sunny days.

In our opinion, it is necessary to differentiate according to the season of the year and the behaviour of the bats flying at daytime. The daytime flight activity in winter or in mid-summer can be due to the disturbance of individuals in their shelters, or possibly due to abnormal behaviour of aberrant (*e. g.*, sick) individuals. On the other hand, flights on clear autumn or spring days, when individuals or whole groups are on the wing regularly and for a long time over a certain stretch, must be motivated by food. Such behaviour has been observed several times even with *Pipistrellus pipistrellus* and *Eptesicus serotinus* (Gaisler, unpublished). In no case do we see any reason why bats like *N. n.* should, in movements or migrations, fly at daytime when they are exposed to much greater danger from predators than at night.

The timing of the night activity has not been exactly investigated; preliminarily it seems that under normal circumstances *N. n.* hunts mainly during the first half of the night. In the aspect of the whole year, the activity lasts approximately from April to the beginning of October. There are, of course, local differences. In the central zone of the European part of the U.S.S.R., populations of this species which are migratory stay from mid-April to late September (Kuz'akin 1950, Pan'utin 1963). In the southern regions of the U.S.S.R., individuals were observed on the wing from March to late October. In southwestern Germany, according to Roer (1977), *N. n.* search for winter shelters as late as from mid-November.

Reproduction

For learning about the population ecology of the species, the most important information concerns the time of sexual maturity, litter size, and the percentage of reproducing females. Already Bels (1952) noticed that "several one-year old females are found among the pregnant ones" and some of them are "very likely pregnant". He is, however, of the opinion that "it does not yet justify the conclusion that the females reach maturity after one year". Cranbrook & Barrett (1965) found, on the basis of nettings carried out for several years, that "five certainly and six probably out of fourteen females reached sexual maturity in the year of their birth". As for the males, they judge that they do not mature during the first year. Kleiman (1969), Kleiman & Racey (1969), Racey (1970) and Racey & Kleiman (1970) published the results of their investigations on the reproduction of the species under laboratory conditions. Two out of five female *N. n.* born in captivity were observed to mate when they were about 3 months old, and both gave birth when one year old. In the males the first spermatogenesis takes place probably as late as at the age of 1 year, according to the above authors. From the papers by Pan'utin (1963, 1970), though they are in fact only abstracts of unpublished voluminous data, it is possible to judge that all yearling females take part in the reproduction process and bear young at the age of one year. The author does not give his opinion on the sexual maturation in males.

These data prove that *N. n.* females can mature during the first year of their life. Basing on our own results, we believe that in fact all yearling females do mature, but only part of them give birth to and bring up the young at the age of one year. To estimate the percentage of females giving birth to young at that time the available samples are too small. This fraction may constitute 40 to 100 %, being smaller in England than in Central and

Eastern Europe. Still greater differences appear in judging the males, as, unlike British authors, we found conclusive signs of sexual activity in most yearling males studied in this respect. In spite of this fact, young males do not participate in the reproduction and remain in juvenile colonies. For the preservation of the population their participation is not necessary, since old males mate with several females each, as will be described when discussing the population.

In one litter there are 1 to 2, rarely even 3 young (Ryberg 1947). According to Blackmore (1963) in England, litters with 1 young are the rule, whereas on the continent it is 2 young. In the material of Kleiman & Racey (1969) one parous female gives birth to an average of 1.3 young; one nulliparous female, 1.0 young. Sluiter & Heerdt (1966) published, among others, the results of their sampling nursery colonies in the latter half of July when the young already flew out of the cavities. In that sample ($n = 155$) there fall 1.2 young to 1 female. Even though the number can be reduced due to the fact that not all young flew out yet, this number obtained in Holland approaches the data from England. Pan'utin (1963, 1970) evaluated several samples: out of 15 females of unknown age, 60 % had two and 40 % one embryo; out of 9 yearling females, 22 % had two and 78 % one embryo; and 4 old females had 2 embryos each. In nurseries he found 1.8 to 1.9 young per 1 female. Our data, particularly the estimate according to the big sample from nurseries, approach most closely those of Pan'utin.

As for the average number of reproducing females, the results obtained in England also differ from the observations in the Soviet Union and Czechoslovakia. Out of 58 females – mostly of unknown age – examined by Cranbrook & Barrett (1965), only 83 % participated in the reproduction in the particular year. In the material obtained by Racey & Kleiman (1969), the percentage of females bearing the young was even lower: 44 % in parous and 25 % in nulliparous females, but the results can be distorted due to laboratory conditions. On the other hand, all females ($n = 26$) dissected by Pan'utin (1963, 1970), at the time of expected pregnancy were pregnant. Besides a small sample of females dissected in May ($n = 5$, all of them pregnant), we can use a big sample of living females examined in June, when the proof of pregnancy (according to their body mass and by the palpation method) or lactation (according to the state of their nipples) is doubtless. In this sample ($n = 172$), 90 % of females were pregnant or lactant, 10 % females without any signs of pregnancy or lactation. The females of the second group were nulliparous, and thus with greatest probability former yearlings. The first group must have also included a part of former yearling females, but their reliable distinguishing at that time is no longer possible.

From the above analysis it is evident that the reproductive rate is lowest in England and probably also in the Netherlands and highest in the central belt of the European part of the U.S.S.R. (Pan'utin's material comes mostly from the Voroněž State Reserve). The reproductive rate of the population of *N. n.* studied in Czechoslovakia lies between the two extremes, but it approaches more the situation in the U.S.S.R. On the whole, the reproductive rate is high as compared to many other bat species: quick sexual maturation, frequent births of twins, and a high percentage of reproducing females. This phenomenon is certainly in correlation with relatively high losses resulting from hibernation in little protected shelters and from great migration activity of the species.

Although no detailed work has been done on the reproduction cycle of *N. n.*, there is a lot of information concerning the partial aspects of this process, particularly in the papers quoted above. If those data are supplemented by our own results, for the time being the most complete, we can reconstruct the whole reproduction cycle of the two sexes. The resulting picture is given in Fig. 9.

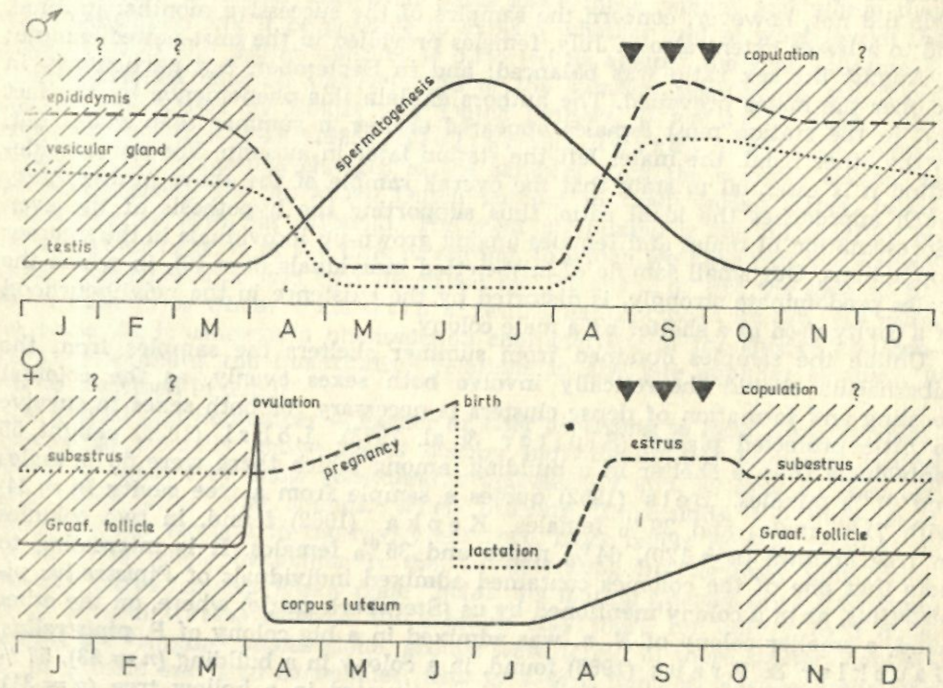


Fig. 9. A schematic representation of the reproductive cycle of sexually mature males and females of *N. noctula*. The dashed parts represent the period of hibernation.

Population

Most data published on the composition of the population concern the sex ratio. The data on the sex ratio among grown-up individuals in the summer season are biased in favour of females. More realistic are data concerning the sex ratio in the juveniles. Bels (1952) found, in a large sample ($n = 384$), 44 % of males and 56 % of females. Sluiter & Heerdt (1966) found, in a July sample ($n = 85$), 43.5 % of males and 56.5 % of females; in an August sample ($n = 94$), 49 % males and 51 % females; in September ($n = 23$), 91 % males and 9 % females. Kleiman (1969) states, among young born in captivity ($n = 19$), 47 % males and 53 % females. The hitherto greatest sample of young was obtained by Pan'utin (1970), ($n = 2,028$), of which males constituted 51 % and females 49 %. These data, together with ours, show that the sex ratio among the young is more or less balanced. The increasing number of males in the juvenile colonies in the course of summer, found out concordantly by the Dutch authors and by ourselves, will be explained below.

From the summer material of grown-up individuals, particularly the sample of Cranbrook & Barrett (1965) is worth mentioning; it was not obtained by catching the bats from their shelters, but through mist-netting. As stated by the authors themselves, there is no reason why one sex should be mist-netted more frequently than the other. In the whole sample ($n = 319$), obtained in the course of three successive growing seasons, the males constituted 48 %, the females 52 %. This more or less balanced and expected sex ratio did not, however, concern the samples of the successive months: in June, and to a lesser extent also in July, females prevailed in the mist-netted sample; in August the sex ratio was balanced; and in September, but particularly in October the males prevailed. The authors explain this phenomenon by the fact that in the station most females appeared earlier in summer than males but, on the other hand, the males left the station later in autumn. For our consideration it is essential to state that the overall sample of the above authors very much approaches the ideal ratio, thus supporting the hypothesis of the even representation of males and females among grown-up individuals in the summer populations. Our small sample of mist-netted individuals ($n = 19$), in which the males predominate strongly, is distorted by the existence in the neighbourhood of a cavity used as a shelter by a male colony.

Unlike the samples obtained from summer shelters the samples from the hibernacula should theoretically involve both sexes evenly, as the colonial roosting and formation of dense clusters is necessary for both sexes to survive in little protected places (Sluiter & al. 1973). Löhrl (1936) caught 55 individuals from a shelter in a building, among which there were 53 % males and 47 % females. Bels (1952) quotes a sample from a tree cavity ($n = 34$) with 71 % males and 29 % females. Kepka (1962) found, in two colonies in tree hollows ($n = 120$), 64 % males and 36 % females. It is interesting to note that one of the colonies contained admixed individuals of *Pipistrellus pipistrellus*, as in a colony mentioned by us (Šternberk castle) where, on the other hand, a smaller colony of *N. n.* was admixed in a big colony of *P. pipistrellus*. Gauckler & Kraus (1966) found, in a colony in a building ($n = 53$), 57 % males and 43 % females, and in a colony situated in a hollow tree ($n = 31$), 58 % males and 42 % females. Heerdt & Sluiter (1965) and Sluiter & Heerdt (1966) obtained material from four hibernating quarters in hollow trees ($n = 209$), in which the males constituted 59 % and the females 41 %. And, finally, Barbu & Sin (1968) in a sample from a rock crack ($n = 228$) found 36 % males and 64 % females.

The survey shows that males predominate in all samples from Western and Central Europe, irrespective of whether they come from trees or buildings. This opposes the possibility conjectured by us in analysing our own material, *viz.*, that the females should prefer to hibernate in trees, males in buildings. Another possiblity, *viz.*, that part of the females – or more females than males – migrate for hibernation to the south, would be supported by the sex ratio found in Rumania (Barbu & Sin 1968). In this connection it is interesting to note that the Soviet authors (Strelkov 1969, Pan'utin 1970) believe that the regions at the northern limit of the range of the species, where hibernation is not possible, are populated mainly by females, whereas most of the males stay more to the south. This would be supported by the fact that long migration flights, 300 to 1,600 km, were evidenced chiefly in females, even if it is necessary to take into consideration the possible distortion due to the majority of females in the sample of banded individuals. *Per analogiam* with

other mammals including several species of bats one should, on the other hand, assume a greater migration activity of the males. Confusions in these problems are due to insufficient knowledge of the space activity of the species. Though a considerable amount of evidence of movements is available (Roer 1971), it is impossible to conclude from them convincingly on the degree of mixing of the individual populations and their components. Further banding data are required to find out what parts of summer populations stay in various parts of Europe also in winter and what parts leave these regions and where they move. Only then will it be possible to explain whether and to what extent the composition of the winter samples is distorted as against the real situation.

More detailed data on the structure of the summer populations are found only in the papers by Soviet and Dutch authors (Pan'utin 1963, 1970; Heerdt & Sluiter 1965; Sluiter & Heerdt 1966). An overall picture of the numerical changes in the samples from the summer season, as described namely by the above Dutch authors in their second paper, tallies almost exactly with our material. The most interesting is the information on the behaviour of *N. n.* at the time of mating, to which we have referred several times. This behaviour was first described by Pan'utin, but the data of the Dutch authors to whom Pan'utin's results had not been known, are quite the same. As it concerns a phenomenon characteristic of the species and convincingly explains the quantitative relations in the late summer samples, it will be described in detail.

In August and September – earlier or later according to local climatic conditions – old sexually active males occupy individually the so-called mating roosts. In them they show considerable aggressivity and, as long as they are alone, they utter loud sounds. When uttering the sounds, the male most frequently sits straight in the cavity entrance, more rarely he flies around the shelter. The whole behaviour is that of defending his territory and luring sexually active females. Every male "holds" its mating quarter for a long time, up to several weeks, whereas the females stay there for only 1 to 2 days. Besides the "singing" males alone, groups were found in those shelters consisting of 1 male and 1 to 20 females, usually 4 to 5 females. Such aggregations are denoted as harems in recent literature (Bradbury in Wimsatt 1977). After leaving the mating roosts, the females no longer form large aggregations in the summer shelters and thus are not reliably caught in the samples.

Pan'utin writes that yearling females do not take part in the autumn mating and are inseminated only later in hibernating quarters or on their way to hibernacula. This may hold for populations living in central Russia in summer, but in Czechoslovakia we have proved that the females of the year are inseminated already at the beginning of September. This corresponds to a conspicuous decrease of juvenile females in colonial aggregations in September, found concordantly by the Dutch authors and by us. We therefore believe that in Western and Central Europe the females born in that year move to the mating quarters, probably, however, with some delay in comparison with old females.

Although the numerical predominance of females in samples of grown-up individuals from shelters for most of the growing season was established by all authors, the explanations offered by them are different. Pan'utin believes that most males do not at all move into the region he studied. Sluiter & Heerdt think that the majority of grown-up males avoid the area where they were born and disperse over a much wider area, singly or in small groups.

The females, however, return every year to the region where they were born. The total number of grown-up males and females constituting the subpopulation studied is probably the same according to the Dutch authors. There is no conclusive evidence of whether or not the members of one sex are more bound to the place of their birth than those of the other sex; again, this question remains open to dispute. The only known fact is that the two sexes often change their summer shelters.

According to P a n' u t i n (1970), 25 % of the young perish in the course of the first three weeks, and till autumn there survives approximately 1 young per 1 female. The yearly mortality rate of females is 46 %. These numbers without any specification of the initial data do not have a significant character, especially if we know how the composition of the samples can be distorted when compared to the actual population structure in the respective area. Owing to an extraordinarily low percentage of recoveries of banded individuals of *N. n.*, none of the authors has a representative sample to evaluate the age structure of the population. That is why the problem of mortality rate in the different age classes and the drawing up of life tables must be left for a later elaboration. Only then will it be possible to judge the population turnover and the production of the species.

Yet there is one important production parameter available, *viz.*, the population density. It is the more valuable, because the estimates of population density have so far been carried out in only a few species and areas concerning the European bats (*cf.*, G a i s l e r 1975). In the case of *N. n.* there exist two more data besides that of this paper (Tab. 7). P a n' u t i n (1970) gives the population density of *N. n.* in the Voronež State Reserve on an experimental plot of 3.5 km^2; in July there lived 75 to 80 individuals per km^2, or about 0.77 ind. per ha. The author notes that the species is particularly abundant in that area, the average population density in the whole reserve being lower. Details of the calculation are not given. P a n' u t i n's estimate does not differ from ours as to the order of magnitude, and therefore one can assume that in the Voronež region the species is approximately as numerous as in southern Bohemia in summer. The values between 0.3 to 0.7 ind. per ha will probably hold for optimum habitats of the species in general. Still higher a value is given by G a i s l e r (FIBRC Abstracts, Nairobi 1975) who made an estimate on an area of 40 ha near the town of Sibiu in Rumania. On the area several colonies were found which were not disturbed and the estimate was made according to the number of flying individuals with concurrent netting. The observations were facilitated by the fact that the area is a camping site illuminated at night. The resulting value of 2 ind. per ha shows that in the locality there was an extraordinary concentration of the species in late summer (observed from 28 Aug. to 2 Sept.). Irrespective of a very suitable habitat — an old oak stand — the reason for this high concentration of *N. n.* can be seen in local movements and/or the abundance of food.

In localities where *N. n.* reaches relatively high population densities it is often the most frequent bat. Bats of the genus *Pipistrellus* prevail in only some regions (L i c h a č e v 1961, P a n' u t i n 1970). Due to the fact that *N. n.* is considerably bigger than other frequent species of forest bats, it contributes a great deal to the biomass of local bat communities.

Summary

The ecology of *N. n.* was investigated in the area lying between 50°15′ to 48°40′ n. lat. and 13°10′ to 18°15′ e. long. on the basis of a sample of 1,383 individuals caught and further observations specified in the Methods. In describing the individual components of the populations the following terms are used: juveniles = young bats from the birth to the end of September; grown-ups = all individuals older than juveniles; yearlings = individuals younger than 1 year in the period from October to May; the old = all individuals older than yearlings.

The main shelters of the species studied are in hollow trees and buildings. Colonies in hollow trees were found from March to October, individuals from June to October. The largest number of members of the summer colony was 53. Five types of colonies were found, out of which nursery colonies are bound exclusively to this type of shelter. Hibernating colonies were not found in trees in the period of investigation (1955 through 1977), but they are evidenced by earlier material. The preference of different tree species is discussed on the basis of the authors' own material and that of literary data; in the region under investigation, oak was the most frequently inhabited tree species. Entrances to cavities were 1 to 16 m high, most frequently up to 5 m.

Colonies and individuals in buildings were found throughout the year with the exception of June and July. Winter colonies were always found in towns; most of the evidence is from prefabricated houses in Prague. Besides, two thanatocolonies were obtained, numbering 200 and 166 mummies or skeletons respectively. One winter colony was found in a crack of a rock wall. In the discussion it is hypothesized that besides hollow trees, rock craks are the original shelters of the species. The population of buildings and further circumstances show that *N. n.* succeeded to adapt itself to the civilization changes of the environment.

The hunting grounds of the species are lowland woods up to the elevation of 500 m, surroundings of ponds, fields among woods, parks, lanes, and vicinity of human settlements. The flight activity starts 2 to 40 min. after sunset; in five cases hunting individuals were observed at daytime (April, September, October). *N. n.* flies swiftly, as a rule 10 to 20 m high.

The course of the reproduction process is expressed in Fig. 9. The comparison with literature shows that the reproductive rate of the species in Western Europe (England, Holland) is lower than in Central and Eastern Europe. In the region under investigation, all females and most males mature as early as at the age of 3 months, thus passing from the juvenile direct to the adult stage. Although all yearling females mate, only part of them give birth to and bring up the young at the age of 1 year. Yearling males — even if sexually mature — probably do not take part in the mating. All females older than 1 year bear young from mid-June to early July. The average number of young per 1 grown-up female is 1.8 due to the fact that a prevailing number of females older than 1 year bear twins.

The composition of the population samples obtained by catching from shelters does not correspond to the actual population structure owing to different probability of ascertaining the various population components which, besides, change in the course of the year. The available information enables us, however, to explain the apparent discrepancies and to reconstruct the situation as follows: The sex ratio at birth is 1 : 1 and remains approximately balanced also among yearlings and old individuals. In summer, most of the old males live outside colonial aggregations of the females. Nursery colonies disintegrate in August and the females move to the mating quarters of old males which, at that time, show territorial behaviour. After the disintegration of nurseries the young bats form juvenile colonies in which the males predominate gradually, since even females born in that year move to mating quarters in late August and in September. The only fact that cannot be unambiguously explained is the predominance of males in all samples from hibernating quarters in Western and Central Europe; the possible causes are discussed.

Population density was estimated basing on catches from summer shelters on two plots in the optimum habitat. The average value is 0.32 ind. per ha; details are given in Tab. 7. It is possible to expect that in optimum habitats within the species' range there live 0.3 to 0.7 ind. per ha, *N. n.* being the most important bat species there from the point of view of production ecology.

Резюме

Исследование рыжей вечерницы *(N. n.)* в течение 20 лет показало, что колонии данного вида с марта по октябрь находятся в дуплах деревьев, где происходит размножение. Зимовка колоний в дуплах известна лишь по старым материалам. В зданиях этот вид отмечен круглый год, за исключением июня и июля; не установлено размножение *N. n.* в этих местах. Одна зимняя колония была найдена в трещине скалы. Собственные данные, а так же литературные, позволяют сделать вывод об отношении различных групп в популяциях к убежищам и об особенностях их поведения на охотничьих участках. В Центральной Европе все самки и большинство самцов *N. n.* достигают половой зрелости к 3 месяцам, т. е. сразу после окончания роста. У большинства самок старше года наблюдалось по 2 детеныша и среднее число детенышей на взрослую самку составило 1,8. Соотношение полов среди новорожденных 1:1, такое же соотношение полов, по нашему мнению, сохраняется и позже. Молодняк появляется на свет с половины июня до начала июля и колонии отродивших самок с молодняком распадаются в августе. Во время гона первыми переселяются самки старших возрастов в дупла старых территориальных самцов, а затем сеголетки. Сеголетки самцы в размножении участия не принимают, несмотря на половозрелость, и в ювенильных колониях самцы постепенно преобладают над самками. В октябре *N. n.* покидают летние убежища до марта или апреля. Во всех случаях зимой в Западной и Центральной Европе самцы преобладают над самками, возможные причины этого феномена дискуссионны. Средняя плотность популяции, исследованная в оптимальном биотопе, составляет 0,32 особи на га. Хотя рыжая вечерница лесной вид, он сумел приспособиться к давлению цивилизации и в некоторых случаях является полусинантропным.

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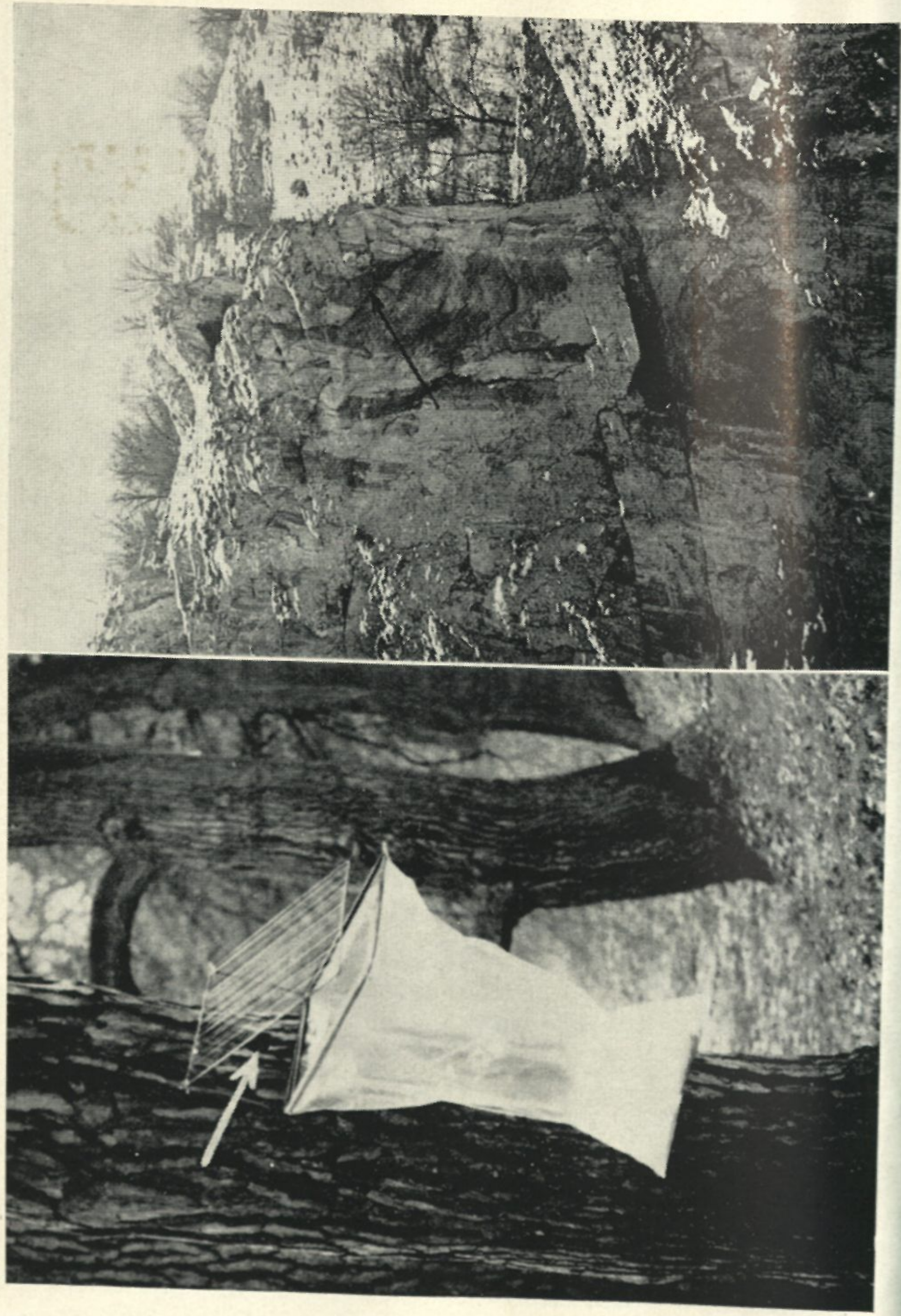
A group of dwelling houses of the Prague quarter Zahradní Město. The arrow points to one of the openings of ventillation shafts which become frequent shelters of the species, namely in winter (above). A close-up showing the location of the entrance to a winter shelter of *N. noctula* (below).



A catching device fastened in front of the entrance to a tree cavity inhabited by a summer colony (indicated by an arrow) (left).

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