

Myotis daubentonii. By Wiesław Bogdanowicz

Published 2 December 1994 by The American Society of Mammalogists

Myotis daubentonii (Kuhl, 1817)

Daubenton's Bat

- Vespertilio daubentonii* Kuhl, 1817:51. Type locality "Hanau," Hesse-Nassau, Germany.
- Vespertilio aedilis* Jenyns, 1839:73. Type locality "Auckland St. Andrew, which place is about twelve miles S.W. of Durham," England. Described from an albinistic variety.
- Vespertilio volgensis* Eversmann, 1840:24. Type locality "in den Wäldern des kasanischen und nischnigorodischen Gouvernements und im Uralgebirge," Russia.
- V[espertilio] lanatus* Crespon, 1844:15. Type locality "au sud de Nîmes," Gard, France.
- Vespertilio laniger* Peters, 1870:617. Type locality "Amoy," Fukiensien, China.
- Vespertilio capucinellus* Fitzinger, 1871:206. Type locality ? Bavaria. Based on very old specimen.
- Vespertilio minutellus* Fitzinger, 1871:206. Type locality ? Bavaria. Based on immature specimen.
- Vespertilio daubentonii albus* Fitzinger, 1871:210. Renaming of *V. aedilis* Jenyns.
- Vespertilio staufferi* Fatio, 1890:6. Type locality "Lucerne," Switzerland.
- Myotis daubentoni*: Thomas, 1898:100. First use of current name combination.
- Myotis petax* Hollister, 1912:6. Type locality "Kosh-Agatch, Chui-skaya Steppe, Altai District, Siberia; Altitude 7300 feet."
- Myotis petax loukashkini* Shamel, 1942:103. Type locality "Wutalenchieh, Third Lake, Heilungkiang Province, North Manchuria," China.
- Myotis nathalinae* Tupinier, 1977:327. Type locality "Cabezarrubias, province de Ciudad Real," Spain.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Subfamily Vespertilioninae, Genus *Myotis*, Subgenus *Leuconoe* (Corbet and Hill, 1991). The genus *Myotis* includes some 90 species (Corbet and Hill, 1991). At present, three subspecies of *M. daubentonii* are recognized (Bogdanowicz, 1990).

- M. d. daubentonii* Kuhl, 1817:51. See above (*aedilis* Jenyns, *albus* Fitzinger, *capucinellus* Fitzinger, *lanatus* Crespon, *minutellus* Fitzinger, *nathalinae* Tupinier, *petax* Hollister, *staufferi* Fatio, and *volgensis* Eversmann are synonyms).
- M. d. laniger* Peters, 1870:617. See above.
- M. d. ussuriensis* Ognev, 1927:146. Type locality "near Vladivostok," eastern Siberia (*loukashkini* Shamel, a synonym).

DIAGNOSIS. *Myotis daubentonii* is almost as small as *M. mystacinus* and *M. brandtii*, but has a larger foot that is more than half the length of the tibia, a longer calcar (about 2/3 of the margin of the uropatagium), and the plagiopatagium inserts in the middle of the metatarsus. Its penis is relatively broad but not bulbous as in *M. brandtii*. The upper molars have well developed protoconules on the anterior edge in contrast to the less developed protoconules of *M. brandtii* (Kowalski and Ruprecht, 1981). The following characters of *M. daubentonii* allow it to be distinguished from *M. dasycneme* in the field: plagiopatagium inserts on the metatarsal region; the ventral surface of uropatagium is not furred along shanks; and the forearm length < 42 mm. The plagiopatagium in *M. macrodactylus* and *M. capaccinii* inserts on the ankle or on the lower part of tibia. *Myotis daubentonii* is distinctly larger (forearm length > 33 mm) than *M. prinosus*. Other species of *Myotis* can be separated from *M. daubentonii* in the field by hind foot plus claw under 60% of tibia length (e.g., *M. frater*, *M. ikonnikovi*, *M. emarginatus*), the presence of stiff hairs at the posterior edge of

the uropatagium (*M. nattereri*), or by the appearance and dimensions of ear, tragus, and calcar (e.g., *M. nattereri*, *M. emarginatus*, and *M. bechsteini*—Corbet and Hill, 1992; Helversen, 1989a; Yoshiyuki, 1989).

GENERAL CHARACTERS. *Myotis daubentonii* is a medium-sized species of the genus *Myotis* (Fig. 1). The ears are short, rounded, and well separated, and have 4-5 transverse folds. The bluntly pointed tragus is about half the height of the pinna, and its width is about one-fifth its length. The uropatagium margin is nearly straight; the calcar is slender and lacks a keel, and extends about three-fourths of the edge of the tail membrane. The wings are reddish, dark brown, never black. The face is blunt, pinkish, usually with a bare patch around the eyes; the fur is dense and short. The dorsum is brown-gray to dark bronze, often with a reddish tinge, contrasting well with the silvery gray or almost white of the belly. The bicolored hair is darker at the base, particularly on the ventral side (Schober and Grimmberger, 1989). Albino and partial albino specimens have been reported (Červený, 1980; Schober and Grimmberger, 1989; Speakman, 1991a).

The range of measurements (in mm) for selected characters of European specimens is as follows: forearm, 33-42; head and body, 40-60; tail, 27-48; ear, 10.5-14.2; wingspan, 240-275; condylobasal length, 12.8-14.6; body mass (g), 5-15 (Bogdanowicz, 1992; Schober and Grimmberger, 1989). Measurements for 19 males and 3 females from Korea had the following ranges: forearm, 37.3-41.9; head and body, 40.0-49.7; tail, 31.7-40.1; ear, 9.1-15.7; condylobasal length, 13.2-14.7 (Yoon, 1990). Ranges of measurements for bats from Hokkaido are as follows: forearm, 34.1-38.0; head and body, 44.0-58.0; tail, 27.0-41.2; ear, 11.5-15.0; condylobasal length, 12.7-13.7 (Yoshiyuki, 1989).

Females average slightly larger than males (e.g., Speakman, 1991a; Steinborn and Vierhaus, 1984). The skulls of female Daubenton's bats from Europe were 0.6-1.4% larger than those of males in 9 of 13 characters (Bogdanowicz, 1992). No such differences were observed in specimens from Japan (Maeda, 1985).

The skull has a smooth profile (Fig. 2), and is flat and broad, with the interorbital constriction larger than the width of the rostrum across the upper canines. The postorbital process, temporal crest, and sagittal crest are weak, and the lambdoidal crest is relatively robust laterally, but is obscure medially. The palatal emargination is shallow, as long as wide, and U-shaped. The auditory bullae are



FIG. 1. Daubenton's bat, *Myotis daubentonii*, from the Nietoperek Bat Reserve, Gorzów voivodship, western Poland. Photograph by E. Grimmberger.

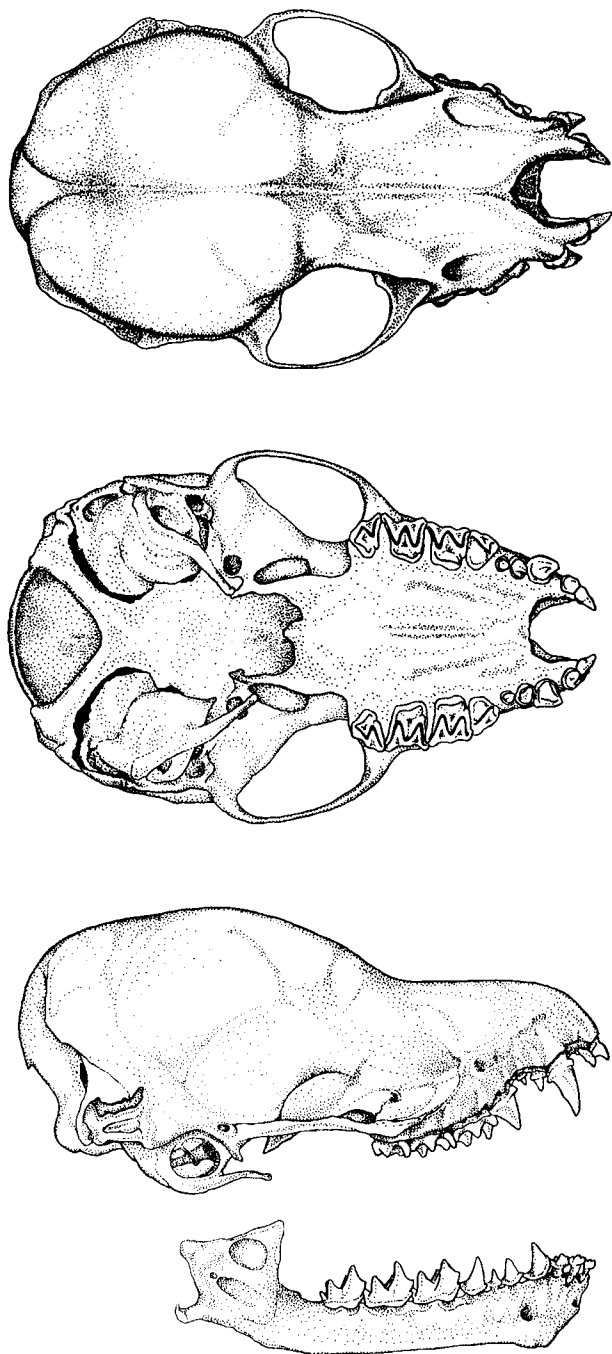


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of a male *Myotis daubentonii* from Wysoka, Gorzów voivodship, western Poland (Mammal Research Institute, Polish Academy of Sciences, Białowieża, No. 150313). Greatest length of cranium is 15.05 mm. Drawing by A. Rachwałd.

comparatively large, covering two-thirds of the cochleae (Yoshiyuki, 1989).

The dental formula is: i 2/3, c 1/1, p 3/3, m 3/3, total 38. The crown area and height of P3 is less than two-thirds that of P2; P4 is subequal to M3. M3 is slightly more than one-half the size of M2, its metacone only scarcely smaller than the paracone. All the upper molars have an evident protoconule on the anterior edge of the crown (Menu and Popelard, 1987; Yoshiyuki, 1989).

DISTRIBUTION. The geographic range of *M. daubentonii* (Fig. 3) includes a large part of the Palearctic region, from Portugal and Ireland, to eastern Siberia, Manchuria, Sakhalin, Kamchatka, the Kurile Islands, Hokkaido, Korea (e.g., Corbet and Hill, 1991;

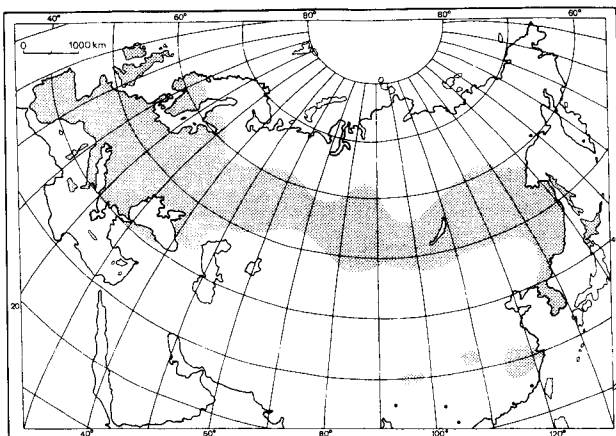


FIG. 3. Geographic distribution of *Myotis daubentonii*. Hainan (ca. 19°15'N, 109°45'E) not shown.

Krivošeev, 1984; Yoshiyuki, 1989), and eastern China (e.g., Chen et al., 1987; Zhen, 1987). In Europe it ranges from 63°N in Scandinavia (Ahlén and Gerell, 1989) to 40°N in Greece (Helsevsen and Weid, 1990). In the Near East *M. daubentonii* is probably distributed over the northern part of Anatolia, from the Uludağ to the Caucasus Mountains (Helsevsen, 1989b). It also occurs in south-western and central China (e.g., Feng et al., 1986; Wang and Zheng, 1985), Yunnan, and the island of Hainan in southern China, Hong Kong, north Vietnam, and north-east India (Corbet and Hill, 1992; J. E. Hill, in litt.). The upper altitudinal limit of this species usually is within 400–700 m a.s.l. in the summer, and 300–1,100 m a.s.l. in the winter (Húrka, 1983; see also Helsevsen et al., 1987). It rarely is found above 1,400 m (Aellen, 1962), but it has been found at 2,750 m a.s.l. in Tibet (Feng et al., 1986).

FOSSIL RECORD. *Myotis daubentonii* or *M. cf. daubentonii* were identified from the lower Pleistocene deposits of Romania (Maul, 1990), Hungary (Jánossy, 1986), and the former Czechoslovakia (Horáček, 1976, 1985); from middle and upper Pleistocene of Hungary (Jánossy, 1986; Topál, 1981) and the former Yugoslavia (Malez, 1986); from the upper Pleistocene of Bulgaria (Horáček, 1982), Germany (Brunner, 1954), Belgium (Gautier et al., 1980), and Poland (Włoszyn, 1988). Holocene remains were recorded from more than 20 sites in Europe, Siberia, and Far East of Russia (e.g., Horáček, 1976; Jánossy, 1986; Malez, 1986; Tiunov et al., 1992; Włoszyn, 1988; Yalden, 1986). The dimensions of the post-glacial specimens are close to those of extant bats (Rybář, 1980). *Myotis paradaubentonii* of the middle Pliocene of Hungary may be related to *M. daubentonii* (Topál, 1983).

FORM AND FUNCTION. The hyoid apparatus is described by Romankowowa (1963), sesamoid bones in the limbs by Romankowowa (1961) and Červený (1976), humerus by Felten et al. (1973) and Yoon and Uchida (1983), and scapula by Žalman (1971). The vertebral formula is: 7 C, 11 T, 5 L, 4 S, 11 Ca, total 38.

The adductor muscles involved in lowering the wings comprise as much as 61.9% of the total mass of the muscles of pectoral limbs. The abductors, which raise the wings, have a considerably smaller mass (16.6%). Extensors (14.4%) provide most of the power to move the wing forward, whereas antagonistic flexors (6.2%) control the backward wing movement (Kovtun, 1984).

Typical flight performance wing characteristics are: arm-wing area, 25.0–27.4 cm²; hand-wing area, 18.7–19.5 cm²; total wing area, 103.3–110.3 cm²; aspect ratio, 5.7–5.8; wing loading, 6.9–7.5 Nm⁻²; tip area ratio, 0.71–0.76; and tip shape index, 1.27–1.34 ($n = 150$; G. Jones and T. Kokurewicz, in litt.). Average aspect ratio, low wing loading, along with rather short and rounded wingtips indicate slow, efficient, and maneuverable flight (Jones and Rayner, 1991).

The surface area of the cerebral cortex ranges from 128.8 to 221.8 mm², with most of the cortex area taken up by the paleocortex (35.3%) and neocortex (33.6%). The remainder is taken up by the archicortex (14.2%), olfactory bulbs (10.1%), and interstitial cortex (6.8%—Nikitenko, 1969). Compared with the auditory center, the visual center is rather poorly developed, as indicated by a size ratio

1:0.35 (Lütgemeier, 1962). The index of encephalization of *M. daubentonii* is higher than the subfamily average (117 versus 95 — Stephan et al., 1987).

The intestinal tract is long for an insectivorous bat (3.6 times head and body length). The small intestine comprises 91.6% of the length of the intestinal tract, whereas the large intestine makes up only 8.4% (Žukova, 1989).

The morphology of the accessory glands of the male genitalia is characteristic for the genus *Myotis* (Tiunov, 1989b). The baculum is a simple, small bonelet with its lateral margins either straight or with a ridge at the central portion (Tupinier, 1977; Yoshiyuki, 1989). The arrangement and number of facial vibrissae appear to be species-specific: 1 *vibrissa superciliares*, 1 *v. angulares*, 6 *vibrissae mystaciales*, ≥ 5 *v. labii superiores*, ≥ 13 *v. submentales* (Haffner and Ziswiler, 1989).

The heart beat rate ranges from 108–120 beats/min at 8.9–10.2°C body skin temperature in torpid bats, to 450–750 beats/min (36.5–37.6°C) in bats after arousal (Eliassen, 1955). The mean blood volume is about 10% of body mass. The total blood volume in the lethargic and hibernating bats is probably unchanged, but the circulating blood volume is decreased by the slowed heart rate and blood flow. There are no differences in the red blood cell count and in hematocrit values between active and hibernating *M. daubentonii* in August, November, and April (Eliassen and Egsbaek, 1963). Sexual differences in hemograms of winter dormant adult animals included only number and volume of erythrocytes; a larger number of smaller cells found in males corresponded to the smaller number of larger cells in females; hemoglobin level and hematocrit values were identical in both sexes (Wołk and Bogdanowicz, 1987).

Myotis daubentonii is able to maintain body water and accumulate urine during hibernation. Water content in the muscles of *M. daubentonii* remained constant throughout the hibernation season at 66.1%, but this was lower than the 69.3% found in August (Eliassen and Egsbaek, 1963).

The rate of body mass loss during hibernation is higher in autumn and early winter than in late winter (Lesiński, 1986; Průcha and Hanzal, 1989; Urbańczyk, 1991a). The percentage decrease in the mean body mass per 100 days of hibernation was 20–21% (Lesiński, 1986). Energy expenditure during torpor is significantly affected by ambient temperature (Speakman et al., 1991a).

Eighteen carotenoids have been identified. Those most frequently encountered were: β -carotene, β -cryptoxanthin, zeaxanthin, astaxanthin ester, and β -apo-2'-carotenal. β -carotene in animal tissues is transformed into vitamin A. Total carotenoid contents were higher later in hibernation, suggesting *M. daubentonii* has additional sources of food during winter (Czeczuga and Ruprecht, 1982).

ONTOGENY AND REPRODUCTION.

Histological data indicate *M. daubentonii* mature sexually in their first year of life (T. Kokurewicz, in litt.; Weishaar, 1992). Mating starts when males enter nursery roosts as the young are weaned in August, and continues until April (Abelencev et al., 1956; Klawitter, 1980; Roer and Egsbaek, 1969). Mating appears to be random, unstructured, and promiscuous. Copulation occurs ventro-dorsally and is accompanied by distinctive vocalizations and body positions. Bats usually remain in copula for 15–30 min (Grimmberger et al., 1987; Roer and Egsbaek, 1969). The frequency of females that have been inseminated during hibernation was 17% in September/October, 83% in October and November, 94% in March, and 100% in late April (Strelkov, 1962). Most copulations (>80%, $n = 143$) occur in October and November (Urbańczyk, 1991a). The principal site of sperm storage is the uterotubal junction (Racey, 1975).

Ovulation and fertilization take place in the spring. Pregnancy lasts about 53–55 days (Abelencev et al., 1956; Kuzjakin, 1950), but the gestation period is variable, depending upon local conditions. There typically is one embryo (Kurskov, 1981), rarely two (Revin, 1989), and only one instance of three embryos has been recorded (Ryberg, 1947). Litter size usually is one (Kuzjakin, 1950; Schober and Grimmberger, 1989; Tiunov, 1989a), rarely two (Ryberg, 1947). During birth females reverse their normal head-down hanging posture so that the neonate is born into the uropatagium (Abelencev et al., 1956). Births usually occur in mid-June in Belarus (Kurskov, 1981) and Ukraine (Abelencev et al., 1956), in late June in Sweden (Lundberg et al., 1983), and early July in the Far East of Russia (Tiunov, 1989a). The sex ratio of newborn bats is about 1:1 (Kurskov, 1981). Lactation lasts 35–45 days (Abelencev et al., 1956; Nyholm, 1965; Tiunov, 1989a). Females possibly use olfactory and auditory cues

to recognize and nurse their own young (Swift, 1981; cited in Fenton, 1985; Tiunov, 1989a).

Energy metabolism in pregnant and lactating individuals is highly variable. This variability is greatest in late pregnancy when energy demands of females typically are higher. Endothermy usually is maintained in late pregnancy (Racey and Speakman, 1987).

The young are born blind, but with well-formed sensory hairs on the mouth. Thin, short, gray-brown hair is present on the back. The ears and wing membranes are gray-brown, and the ventral side is pinkish (Krátký, 1981). Birth mass is 1.6–2.4 g (Krátký, 1981; Tiunov, 1989a), approximately 23.1% of maternal body mass (Tiunov, 1989a). Means of measurements (in mm) of one-day-old bats are: head and body length, 32.8; tail length, 15.7; forearm length, 14.9; and condylobasal length, 10.3. Growth is rapid and allometric, with the thumbs and feet increasing little in size, whereas the wings and ears increase greatly. Hair growth proceeds from the back toward the belly. By day 21, the young attain a mass of 5.5 g, and a forearm length of 32.7 mm. The deciduous teeth (i 2/3, c 1/1, p 2/2, total 22) are almost fully erupted at birth. The permanent teeth start to erupt at approximately the 8th day. Adult dentition is complete around the 31st day. The eyes open from the 8th to the 10th day; complete hair cover is present from the 21st day, with the hair growth finished between the 31st and 35th day (Krátký, 1981). The young start to fly by week 3 (Krátký, 1981; Tiunov, 1989a), and reach adult size by 9–10 weeks (Kurskov, 1981). In summer, the young may be distinguished from the adults by their grayer and frizzy fur, rubbery membranes, and unossified metacarpal-phalangeal epiphyses. In autumn, however, these characters are less reliable. At this time young females usually can be identified by small nipples and the absence of a worn patch around them, and young males can be distinguished from adults by the condition of the testes and epididymis (Baagøe, 1977). At the latitude of Denmark, most *M. daubentonii* young can be distinguished as such up to 9 months after birth by the X-ray method (Baagøe et al., 1988). The most useful character for identifying juvenile Daubenton's in autumn and winter is the presence of a black chin spot on their lower lip, which usually is absent in individuals more than one year old (Richardson, in press).

ECOLOGY. *Myotis daubentonii* is most often associated with lakes, ponds, and streams, but also regularly hunts in deciduous and mixed forests (Ahlén, 1990). Summer shelters are usually found in hollow trees (Limpens et al., 1991), sometimes in buildings (Nyholm, 1965; Tiunov, 1989a), under bridges (Ryberg, 1947), in bird (Bäumler, 1990) and bat boxes (Gerell, 1985), and in rock crevices and nests of sand martins (Kowalski and Ruprecht, 1981).

Nursery colonies consist predominantly of adult females (e.g., Červený, 1982; Lundberg et al., 1983; Swift and Racey, 1983), and these colonies may contain more than 100 individuals (Steinborn and Vierhaus, 1984; Tiunov, 1989a). In summer, mature males form small, independent groups, or may join female colonies (Červený and Bürger, 1989; Speakman et al., 1991b; Tiunov, 1989a).

Nursery colonies start to disperse into several roosts, frequently in trees, shortly after parturition (Červený and Bürger, 1989). In late August some bats, probably adult males, begin to spend the day in relatively cold underground shelters (e.g., Klawitter, 1980; Lesiński, 1990).

Daubenton's bats hibernate in underground sites, like caves, mines, bunkers, or cellars (Bogdanowicz, 1983). The largest hibernaculum of *M. daubentonii* in Europe may be an old military fortification in the Nietoperek Bat Reserve in western Poland, with more than 17,180 individuals in February 1991 (Urbańczyk, 1991b).

This species already starts to appear in the second half of August at the Nietoperek Bat Reserve. Most settlement takes place from September to March, peaking in October and November. Some individuals may stay at the winter roost until the end of May (Bagrowska-Urbańczyk and Urbańczyk, 1983). The sex ratio varies over the hibernation period (Lesiński, 1986). Males precede females into hibernacula and depart earlier in the spring (Baagøe et al., 1988; Speakman, 1991a). The later departure of females may allow them to conserve energy until more food becomes available. Young animals make up 20–22% of the winter populations in the caves in the Netherlands and Denmark (Baagøe et al., 1988; Bezem et al., 1960).

Bats may spend the winter alone, in small groups, or in large groups up to 140 animals (Urbańczyk, 1991b), hanging free from the wall, or squeezed into crevices. They frequently form compact clusters with other species (e.g., *M. nattereri*) which have similar

thermal preferences (Bogdanowicz, 1983). Hibernaculum temperatures range from 0 to 10°C (Bogdanowicz and Urbańczyk, 1983; Hürka, 1989), temporarily down to -2°C (Mazing, 1987). Most individuals select areas at 2–6°C (Bogdanowicz and Urbańczyk, 1983), or 3–8°C (Gaisler, 1970). Hibernating *Daubenton's* bats require a minimum relative humidity of about 70%; the humidity of hibernation sites usually is over 85%, and bats are often covered with beads of moisture (Bogdanowicz and Urbańczyk, 1983). Hibernation lasts about 175–190 days in central Europe, as estimated from changes in body mass (Lesiński, 1986).

The dispersal season of *M. daubentonii* consists of many but short autumn and early spring flights between the summer and winter shelters. In Great Britain movements do not exceed 19 km (Speakman, 1991a). Longer distances were recorded on the continent of Europe, both under natural conditions (260 km; Urbańczyk, 1991b) or homing after displacements (132 km; Nyholm, 1965). A typical situation for this species was observed in eastern Germany, where 84% of all flights ($n = 37$) were 0.5 to 88.0 km (Haensel, 1978).

Both scat and stomach analyses indicate that *M. daubentonii* consumes a diversity of Diptera, Trichoptera, Ephemeroptera, Lepidoptera, and Coleoptera in western Belarus (Kurskov, 1981) and Scotland (Swift and Racey, 1983). The diet of *M. daubentonii* in Switzerland consisted mainly of Diptera (Chironomidae) and Hemiptera (Aphididae—Beck, 1987), whereas in Finland Lepidoptera and Diptera were predominate (Nyholm, 1965). In western France, predominant items in the diet of *M. daubentonii* were insects belonging to Tabanidae, crustaceans from Ostracoda and Cladocera, and particles of fresh-water fish (Brosset and Deboutteville, 1966; see Mayle, 1990). There are no other reports of *Daubenton's* bats taking fish, although they have relatively large feet possibly suitable for fishing. Parasites associated with fresh-water snails were found in dietary studies of *M. daubentonii* in England (Jones and Rayner, 1988; R. E. Stebbings, pers. comm.). In captivity this bat may consume from 7 to 10 20-mm fish per day (Brosset and Deboutteville, 1966).

A variety of predators feeds on *M. daubentonii* but none habitually preys on it. In most instances the predator appears to take advantage of opportunities associated with concentrations of bats. The mammals most usually recorded catching *Daubenton's* are domestic cats *Felis catus* (Abelencev et al., 1956; Bekker and Mostert, 1991; Richardson, 1985). Over 70 bats were killed within a few weeks by a cat sitting on a tree branch over a canal (Stebbing, 1988). Males may be more vulnerable to such predation than females because of the social calls males produce (Bekker and Mostert, 1991). A beech marten, *Martes foina*, preyed on *Daubenton's* bats hibernating in subterranean marl pits in the Netherlands (Bekker, 1988). *Myotis daubentonii* is also occasionally eaten by rodents, such as *Apodemus sylvaticus* (Bekker and Mostert, 1991), and Gliridae (Rolandez and Pont, 1986), and by shrews, such as *Sorex araneus* (Iljin, 1989). The most common avian predators of *M. daubentonii* are a few species of owls, mainly barn (*Tyto alba*), tawny (*Strix aluco*), and long-eared (*Asio otus*) owls (e.g., Bekker and Mostert, 1991; Ruprecht, 1979, 1990). *Myotis daubentonii*, however, usually makes up much less than 1.0% of all vertebrates eaten by owls (Ruprecht, 1979, 1990; Speakman, 1991b). Buzzards (*Buteo* sp.) are also known to hunt this species. Potential predators of *M. daubentonii* may also include large frogs and fish (Abelencev et al., 1956).

Survivorship of juveniles in the Netherlands during the first half of the juvenile's life was 0.50 and for adults was 0.80. There were no differences in survivorship among adults of different sex, age, or hibernacula. Mean life expectancy was 4.5 years; mean longevity, 5.0 years; and predicted life span, 20 years (Bezem et al., 1960). The annual mortality of 0.21 for *M. daubentonii* in Great Britain was lower than for other British bats (Speakman, 1991b). In western Bohemia in the Czech Republic the mean longevity was 3.5 years (Hürka, 1989). The average age of males and females hibernating in the Jizerske Mountains in northern Bohemia was slightly higher than 3.9 and 3.3 years, respectively (Nevrlý, 1987). The longevity record for *M. daubentonii* is 28 years (Červený and Bürger, 1989). The maximum age of 32 years reported by Richardson (1985) was an error (P. Richardson, in litt.).

The most common arthropod parasites collected from *M. daubentonii* are bat flies. In Poland, the Czech Republic, and Slovakia, 81–90% of the bats were infected with wingless, blood-sucking *Nycteribia kolenatii*, with an average of 3.9–4.7 flies per bat (Hürka, 1964; Nowosad, 1987). Other bat flies recorded from *M. daubentonii* include *Nycteribia schmidlii*, *N. vexata vexata*, *Pen-*

icillidia monoceros, and *Basilina nana* (e.g., Haitlinger, 1979; Hürka, 1984; Medvedev et al., 1991).

A variety of mites, ticks, and chiggers parasitize *M. daubentonii*. These include *Spinturnix daubentonii*, *S. andegavinus*, *Macronyssus ellipticus*, *M. crosbyi*, *Nycteridocoptes poppei*, and *Argas vespertilionis* (e.g., Estrada-Peña et al., 1989; Haitlinger, 1979; Medvedev et al., 1991). Fleas are frequently recorded but are not as host-specific; the most common are *Ischnopsyllus simplex* (Hürka, 1989; Skuratowicz, 1988), and in the Far East *Myodopsylla trisellii* (Medvedev et al., 1991). Bugs, such as *Cimex lectularius* (Andrejko, 1973), *C. dissimilis* (Heise, 1988), and *C. pipistrelli* (Speakman, 1991a), are rarely found on *M. daubentonii*.

Myotis daubentonii is one of the bats most heavily infested with helminths, mainly trematodes; the most common is a digenetic trematode *Plagiorchis vespertilionis* (Hürková, 1964; Matskasi, 1975; Zdzitowiecki, 1970). Nematodes parasitizing *M. daubentonii* include the genera *Molinostrongylus*, *Capillaria*, and *Litomosa* (e.g., Andrejko, 1973; Tkač and Sarpilo, 1988; Yanchev and Stoykova, 1973). The tapeworms *Hymenolepis* sp. are infrequent (Zdzitowiecki, 1970).

Among 108 *Daubenton's* bats examined in Britain, 27 contained the malaria parasite *Polychromophilus murinus*, and 57 the intraerythrocytic bacterium *Grahamella* sp. (Gardner et al., 1987). These hematozoa, however, are not considered harmful. Piroplasm, *Babesia vesperuginis*, was found in the blood of two *M. daubentonii* in the Netherlands (Goedbloed et al., 1964). *Babesia*-infected bats have significantly lowered blood hemoglobin, raised white blood cell counts, and enlarged spleens compared with uninfected bats (Gardner and Molyneux, 1987). Bacteria, *Leptospira* spp., were found in *M. daubentonii* in Denmark (Constantine, 1970). A rabies-like disease has been diagnosed in five cases: two in Denmark, and one each in Germany, Russia, and Sweden (Jüdes, 1988; Staliński, 1990); the Swedish case is most certainly erroneous (J. Rydell, in litt.). Paratuberculosis was observed in one third of adult specimens in west Germany but with no clear relation to age (Vierhaus, 1981).

In England *M. daubentonii* is contaminated with residues of organochlorine insecticides (Mitchell-Jones et al., 1989). This may contribute to population declines in some areas (Schober and Grimberger, 1989; Stebbings, 1988).

Daubenton's bat is one of the most abundant bats in Europe (Stebbing and Griffith, 1986). Populations have increased in size in many parts of its range (e.g., Helversen et al., 1987; Urbańczyk, 1989; Weinreich and Oude Voshaar, 1992). Some authors attribute this increase to favorable climatic changes (Bárta et al., 1981).

The population density of *M. daubentonii* in the Bohemian pond region in the Czech Republic was >0.01 individuals/ha (Pelikán et al., 1979), and in northeastern Scotland, near the northern limit of its distribution, was approximately 0.024 individuals/ha (Speakman et al., 1991b). A density of 27.3–45.9 individuals/ha in a small park (4.4 ha) was recorded in Bohemia (Červený and Bürger, 1989).

BEHAVIOR. In England, most bats leave their roost to forage about 30–60 min after sunset ($n = 86$ nights; Richardson, 1985); later (90–130 min after sunset, $n = 15$) in Scotland where darkness comes slower (Swift and Racey, 1983). A tendency to fly out later at times of birthing as well as during intensive feeding of young was noted by Kurskov (1981). In an old park in Bohemia in the Czech Republic, lactating females left shelters first, whereas pregnant females usually left later, often 1–2 hours after dusk (Červený and Bürger, 1989). Summer shelters are changed frequently (Červený and Bürger, 1989).

Myotis daubentonii emits only short frequency-modulated (FM) echolocation signals. The pulses emitted during the search phase go down from 70–95 kHz to 25–30 kHz with a duration of 3–4 ms, but sometimes up to near 6 ms (Ahlén, 1981; Kalko and Schnitzler, 1989; Miller and Degn, 1981). The sweep, when flying close to surface, almost always has a sinusoidal amplitude modulation with approximately 10 maxima through the pulse. As a result, the frequency spectrum shows a series of peaks with the highest sound pressure levels usually around 45 kHz (Ahlén, 1981; Benk and Schoppe, 1991). The pulse repetition rate is highly variable. Echolocation calls of *Daubenton's* bats emerging from their roosts last from 2.2 to 3.8 ms and are separated by intervals of 56 to 103 ms (Tupinier and Biraud, 1984). The interpulse intervals in straight flight are about 70–90 ms long (Ahlén, 1990). During the approach and terminal phases, pulse duration and interpulse interval are more

and more shortened. The terminal phase is reduced in frequency and typically composed of two sections; the second section is lower in frequency than the first. The bandwidth of the first harmonic at the end of the second part is sometimes only 10 kHz compared with approximately 70 kHz during search flight (Kalko and Schnitzler, 1989). The loudest pulses can be heard up to 40–50 m away when using a QMC S100 detector (Ahlén, 1981). The echolocation calls are directional, with different frequencies having different directionalities (Mogensen and Møhl, 1979).

In the Netherlands, Daubenton's bats seem to closely follow linear landscape elements on their flight paths and hesitate to cross open spaces. They also avoid light while hunting (Limpens and Kapteyn, 1991).

In Finland (60°N) during early mid-summer, this species foraged individually in woodlands, but began foraging in groups over water or pasture in August, when nights became darker. Individual territories averaged 420 m². Open feeding grounds were used by the whole colony and covered 4,580 m². Average and maximum distances between roosts and foraging area were 236 and 800 m, respectively (Nyholm, 1965). The minimum and maximum distances travelled by *M. daubentonii* from the roost centered in woodland in Scotland were 900 and 1,200 m (Swift and Racey, 1983). Distances of up to 10 km between roost and feeding sites along canals occur in central England (Richardson, 1985).

Average flight speeds of 3.4–4.1 m/s in the search flight were reported by Baagøe (1987), Jones and Rayner (1988), and Kalko and Schnitzler (1989). Bats decelerate prior to prey capture, presumably compensating for the reduced interpulse intervals in a feeding buzz (Jones and Rayner, 1988). Wingbeat rates in straight level flight are equal to 12–16 Hz. In the search phase, a single sound is produced when the wings are near the top of the stroke. With a pulse interval of 60–80 ms, a 1:1 correlation of sound emission, respiratory cycle, and wingbeat rate is likely. The estimated average reaction distance (112 cm) and detection distance (128 cm) are similar to those reported for other species (Kalko and Schnitzler, 1989).

Myotis daubentonii spends 91% of its foraging time less than 2 m above the ground or water level (Baagøe, 1987), frequently making energy savings from the ground effect (Jones and Rayner, 1991) and feeding opportunistically on swarms of insects, by slow hawking and gaffing food from the surface of water (Jones and Rayner, 1988). Small insects often are caught with the aid of the tail membrane, which is formed into a pouch, or by the wing. Immediately afterward, the prey is seized and eaten (Jones and Rayner, 1988). Daubenton's bats have a high rate of attack, with a success rate of about 50% (Kalko and Braun, 1991).

Territoriality between members of a roost occurred when strong winds restricted the foraging area available to them. When the foraging area was not restricted, group foraging was observed (Wallin, 1961).

In the temperature range of 3–5°C, hibernating bats wake up on average every 22 days, from 5 to 7°C every 14–18 days, and from 7 to 9°C every 14–16 days (Daan, 1973). The maximum duration of uninterrupted hibernation period was 79 days (Průcha and Hanzal, 1989).

GENETICS. The standard karyotype of *M. daubentonii* from Europe and Korea reveals a diploid number of 44 and a fundamental number of 52, of which the autosomes consist of 5 pairs of metacentrics and 16 pairs of acrocentrics (e.g., Hongell et al., 1989; Volleth, 1987; Yoo and Yoon, 1992; Zima and Horáček, 1985; but see Fedyk and Fedyk, 1970). *Myotis d. ussuriensis* from the Far East of Russia had $2n = 44$ and $FN = 50$ (Korablev et al., 1989), whereas *M. d. laniger* from China has $2n = 44$ and $FN = 54$ (Zhang, 1989). The X-chromosome is a medium-sized metacentric, and the Y-chromosome is a small acrocentric (Zima and Horáček, 1985). Nucleolus organizer regions occur on three pairs of autosomes (Volleth, 1987).

Two dental morphotypes of *M. daubentonii*, treated by some as separate species, are electrophoretically similar (Bogdanowicz and Wójcik, 1986). Nei's genetic distances between *M. daubentonii* and *M. myotis* and *M. blythi* were 0.387 and 0.602, respectively (Ruedi et al., 1990).

REMARKS. The generic name *Myotis* is derived from Greek *mys* mouse; *otis* genit. *ōtos* ear. The specific name *daubentonii* was used by Kuhl to honor a celebrated French naturalist L.-J.-M. Dau-

benton (1716–1800). Various authors suggest different dates for Kuhl's original book "Die deutschen Fledermäuse" (see Smeenk, 1982 for discussion). According to the opinion of the International Commission on Zoological Nomenclature (1958), the correct publication date is 1817. Leisler sometimes is quoted as an author of the original description; in fact, Leisler discovered *M. daubentonii*, but did not describe it (C. Smeenk, in litt.).

J. Gaisler, J. E. Hill, G. Jones, Z. Pucek, J. Rydell, and R. Van Den Bussche are gratefully acknowledged for critical comments on the manuscript. E. Bremond-Hoslet, Z. Frenkiel, P. Jenkins, L. Marcus, C. Smeenk, and M. Volleth helped with rare and old publications.

LITERATURE CITED

- ABELECEV, V. I., I. G. PIDOPLIČKO, AND B. M. POPOV. 1956. Fauna Ukraini. Tom 1. Ssavci. Vidavnicтво Akademii Nauk Ukrain'skoi RSR, Kiiv, 448 pp.
- AELLEN, V. 1962. Le baguement des chauves-souris au col de Bretolet (Valais). Archives des Sciences (Genève), 14(1961): 365–392.
- AHLÉN, I. 1981. Identification of Scandinavian bats by their sounds. The Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Uppsala, Report 6, 56 pp.
- . 1990. Identification of bats in flight. Swedish Society for Conservation of Nature and The Swedish Youth Association for Environmental Studies and Conservation, 50 pp.
- AHLÉN, I., AND R. GERELL. 1989. Distribution and status of bats in Sweden. Pp. 319–325, in European bat research 1987 (V. Hanák, I. Horáček, and J. Gaisler, eds.). Charles University Press, Praha, 718 pp.
- ANDREJKO, O. F. 1973. Parazity mlekopitajuščich Moldavii. Štiinca, Kišinev, 186 pp.
- BAAGØE, H. J. 1977. Age determination in bats. Videnskabelige Meddelelser Dansk Naturhistorisk Forening, 140:53–92.
- . 1987. The Scandinavian bat fauna: adaptive wing morphology and free flight in the field. Pp. 57–74, in Recent advances in the study of bats (M. B. Fenton, P. Racey, and J. M. V. Rayner, eds.). Cambridge University Press, Cambridge, 470 pp.
- BAAGØE, H. J., H. J. DEGN, AND P. NIELSEN. 1988. Departure dynamics of *Myotis daubentoni* (Chiroptera) leaving a large hibernaculum. Videnskabelige Meddelelser Dansk Naturhistorisk Forening, 147:7–24.
- BAGROWSKA-URBAŃCZYK, E., AND Z. URBAŃCZYK. 1983. Structure and dynamics of a winter colony of bats. Acta Theriologica, 28:183–196.
- BÁRTA, Z., ET AL. 1981. Výsledky zimního sčítání netopýrů v Československu: 1969–1979. Sborník Okresního muzea v Mostě, Řada přírodovedna, 3:71–116.
- BÄUMLER, W. 1990. Entwicklung einiger Nistkastenbewohner in ostbayerischen Waldgebieten. Teil II: Säuger. Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz, 63:151–155.
- BECK, A. 1987. Qualitative und quantitative Nahrungsanalysen an ausgewählten einheimischen Fledermausarten (Mammalia, Chiroptera). M.S. thesis, Zoologisches Museum der Universität, Zürich, 24 pp.
- BEKKER, J. P. 1988. Watervleermuis *Myotis daubentonii* als prooi van steenmarter *Martes foina* in ondergrondse mergelgroeven. Lutra, 31:82–85.
- BEKKER, J. P., AND K. MOSTERT. 1991. Predatie op vleermuizen in Nederland. Lutra, 34:1–26.
- BENK, A., AND R. SCHOPPE. 1991. Zur Lautvariabilität von Wasserfledermaus *Myotis daubentoni*, Kuhl 1819, und Fransenfledermaus *Myotis nattereri*, Kuhl 1818. Naturschutz und Landschaftspflege in Niedersachsen, 26:131–140.
- BEZEM, J. J., J. W. SLUTER, AND P. F. VAN HEERDT. 1960. Population statistics of five species of the bat genus *Myotis* and one of the genus *Rhinolophus*, hibernating in the caves of S. Limburg. Archives Néerlandaises de Zoologie, 13:511–539.
- BOGDANOWICZ, W. 1983. Community structure and interspecific interactions in bats hibernating in Poznań. Acta Theriologica, 28:357–370.
- . 1990. Geographic variation and taxonomy of Daubenton's bat, *Myotis daubentoni*, in Europe. Journal of Mammalogy, 71:205–218.
- . 1992. Sexual dimorphism in size of the skull in European

- Myotis daubentoni* (Mammalia: Chiroptera). Pp. 17–25, in Prague studies in mammalogy (I. Horáček and V. Vohralík, eds.). Charles University Press, Praha, 245 pp.
- BOGDANOWICZ, W., AND Z. URBAŃCZYK. 1983. Some ecological aspects of bats hibernating in the city of Poznań. *Acta Theriologica*, 24:371–385.
- BOGDANOWICZ, W., AND A. M. WÓJCİK. 1986. Morphological and electrophoretic differentiation between *Myotis daubentoni* (Kuhl, 1819) and *Myotis nathalinae* Tupinier, 1977. *Myotis*, 23–24:17–30.
- BROSSET, A., AND C. D. DEBOUTTEVILLE. 1966. Le régime alimentaire du vespertilion de Daubenton, *Myotis daubentoni*. *Mammalia*, 30:247–251.
- BRUNNER, G. 1954. Das Fuchsloch bei Siegmansbrunn (Oberf.) (Eine mediterrane RiB-Würm-Fauna). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 100:83–118.
- ČERVENÝ, J. 1976. Sezamské kosti loketního kloubu netopýrů (Microchiroptera, Dobson, 1875). *Lynx (N.S.)*, 18:27–33.
- . 1980. Abnormal coloration in bats (Chiroptera) of Czechoslovakia. *Nyctalus (N.F.)*, 1:193–202.
- . 1982. Results of investigation of bats (Chiroptera) at Loreta near Klatovy. *Lynx (N.S.)*, 21:41–65.
- ČERVENÝ, J., AND P. BÜRGER. 1989. Density and structure of the bat community occupying an old park at Žihobce (Czechoslovakia). Pp. 475–488, in *European bat research 1987* (V. Hanák, I. Horáček, and J. Gaisler, eds.). Charles University Press, Praha, 718 pp.
- CHEN, Y., W. HUANG, AND S. TANG. 1987. The chiropteran fauna of the north Jiangxi. *Acta Theriologica Sinica*, 7:13–19.
- CONSTANTINE, D. G. 1970. Bats in relation to the health, welfare, and economy of man. Pp. 319–440, in *Biology of bats* (W. A. Wimsatt, ed.). Academic Press, New York, 2:1–477.
- CORBET, G. B., AND J. E. HILL. 1991. A world list of mammalian species. Third ed. Natural History Museum Publications and Oxford University Press, London, 243 pp.
- . 1992. Mammals of the Indomalayan region: a systematic review. Natural History Museum Publications and Oxford University Press, Oxford, 488 pp.
- CRESPON, J. 1844. Faune méridionale ou description de tous les animaux vertébrés vivants et fossiles, sauvages ou domestiques qui se rencontrent toute l'année ou qui ne sont que de passage dans la plus grande partie du midi de la France. Nîmes, Vol. 1, 322 pp.
- CZECZUGA, B., AND A. L. RUPRECHT. 1982. Carotenoid contents in mammals. II. Carotenoids of some Vespertilionidae from the seasonal variation aspect. *Acta Theriologica*, 27:83–96.
- DAAN, S. 1973. Activity during natural hibernation in three species of vespertilionid bats. *Netherlands Journal of Zoology*, 23:1–71.
- ELLIASSEN, E. 1955. The temperature-rise electro-cardiogram, and electro-encephalogram of the hibernating bat during the awakening process. *Universitet I Bergen Årbok, Naturvitenskapelig rekke*, 6:2–23.
- ELIASSEN, E., AND W. ECSBAEK. 1963. Vascular changes in the hibernating bat *Myotis daubentonii* (Kuhl, 1819). *Acta Universitatis Bergensis, Series Mathematica Rerumque Naturalium*, 3:1–22.
- ESTRADA-PEÑA, A., M. A. PERIBÁÑEZ-LOPEZ, C. SANCHEZ-ACEDO, E. BALCELLS-ROCAMORA, AND J. SERRA-COBO. 1989. Distribution and faunal composition in north and northeast of Spain of some mites and ticks parasitic on Chiroptera (Spinturnicidae, Macrognathidae, Ixodidae, and Argasidae). *Acarologia*, 30:345–353.
- EVERSMANN, E. 1840. Mittheilungen ueber einige neue und einige weniger gekannte. Säugethiere Russlands. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 1:1–59.
- FATTO, V. 1890. Faune des vertébrés de la Suisse. Troisième supplément aux mammifères (Faune, Vol. I). H. Georg, Genève, 13 pp.
- FEDYK, A., AND S. FEDYK. 1970. Karyotypes of some species of vespertilionid bats from Poland. *Acta Theriologica*, 15:295–302.
- FELTEN, H., A. HELFRICHT, AND G. STORCH. 1973. Die Bestimmung der europäischen Fledermäuse nach der distalen Epiphyse des Humerus. *Senckenbergiana biologica*, 54:291–297.
- FENG, Z., G. CAI, AND C. ZHENG. 1986. The mammals of Xizang. Science Press, Beijing, 423 pp. (in Chinese with English abstract).
- FENTON, M. B. 1985. Communication in the Chiroptera. Indiana University Press, Bloomington, 161 pp.
- FITZINGER, L. J. 1871. Kritische Durchsicht der Ordnung der Flatterthiere oder Handflüger (Chiroptera). Familie der Fledermäuse (Vespertiliones). VII. Abtheilung. Sitzungsberichte der kaiserlichen Akademie der Wissenschaften. I. Abtheilung. Mathematisch-Naturwissenschaftliche Klasse, 64:203–295.
- GAISLER, J. 1970. Remarks on the thermopreferendum of Palearctic bats in their natural habitats. *Bijdragen tot de Dierkunde*, 40:33–35.
- GARDNER, R. A., AND D. H. MOLYNEUX. 1987. *Babesia vesperuginis*: natural and experimental infections in British bats (Microchiroptera). *Parasitology*, 95:461–469.
- GARDNER, R. A., D. H. MOLYNEUX, AND R. E. STEBBINGS. 1987. Studies on the prevalence of haematozoa of British bats. *Mammal Review*, 17(2/3):75–80.
- GAUTIER, A., J. DE HEINZELIN, P. BALLMANN, J. DE CONINCK, S. GEETS, AND J.-C. RAGE. 1980. La Caverne Marie-Jeanne (Hastière-Lavaux, Belgique). *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique*, 177:1–47.
- GERELL, R. 1985. Tests of bat boxes for bats. *Nyctalus (N.F.)*, 2:181–185.
- GOEDBLOED, E., L. CREMERS-HOYER, AND N. M. PERIE. 1964. Blood parasites of bats in the Netherlands. *Annals of Tropical Medicine and Parasitology*, 58:257–260.
- GRIMMBERGER, E., H. HACKETHAL, AND Z. URBAŃCZYK. 1987. Beitrag zum Paarungsverhalten der Wasserfledermaus, *Myotis daubentoni* (Kuhl, 1819), im Winterquartier. *Zeitschrift für Säugetierkunde*, 52:133–140.
- HAENSEL, J. 1978. Saisonwanderungen und Winterquartierwechsel bei Wasserfledermäusen (*Myotis daubentoni*). *Nyctalus (N.F.)*, 1:33–40.
- HAFFNER, M., AND V. ZISWILER. 1989. Tastaare als diagnostisches Merkmal bei mitteleuropäischen Vespertilionidae (Mammalia, Chiroptera). *Revue Suisse de Zoologie*, 96:663–672.
- HAILTLINGER, R. 1979. Pasożyty zewnętrzne nietoperzy Dolnego Śląska. VI. Acarina, Siphonaptera, Diptera (Nycteribiidae). *Wiadomości Parazytologiczne*, 25:119–140.
- HEISE, G. 1988. Zum Transport von Fledermauswanzen (Cimicidae) durch ihre Wirte. *Nyctalus (N.F.)*, 2:469–473.
- HELVENSEN, O. v. 1989a. Bestimmungsschlüssel für die europäischen Fledermäuse nach äußeren Merkmalen. *Myotis*, 27:41–60.
- . 1989b. New records of bats (Chiroptera) from Turkey. *Zoology in the Middle East*, 3:5–18.
- HELVENSEN, O. v., AND R. WEID. 1990. Die Verbreitung einiger Fledermausarten in Griechenland. *Bonner zoologische Beiträge*, 41:9–22.
- HELVENSEN, O. v., M. ESCHE, F. KRETZSCHMAR, AND M. BOSCHERT. 1987. Die Fledermäuse Südbadens. *Mitteilungen des Badischen Landesvereins für Naturkunde und Naturschutz (N.F.)*, 14:409–475.
- HOLLISTER, N. 1912. New mammals from the highlands of Siberia. *Smithsonian Miscellaneous Collections*, 60(14):1–6.
- HONCELL, K., N. HAGNER, J. LOKKI, AND T. STJERNBERG. 1989. Chromosome studies in Finnish bats. Pp. 101–104, in *European bat research 1987* (V. Hanák, I. Horáček, and J. Gaisler, eds.). Charles University Press, Praha, 718 pp.
- HORÁČEK, I. 1976. Přehled kvartérních netopýrů (Chiroptera) Československa. *Lynx (N.S.)*, 18:35–58.
- . 1982. K poznání glaciálních poměrů v krasu severního Bulharska. *Československý kras*, 32:95–103.
- . 1985. Survey of the fossil vertebrate localities Včeláře 1–7. *Časopis pro Mineralogii a Geologii*, 30:353–366.
- HÜRKA, K. 1964. Distribution, bionomy and ecology of the European batflies with special regard to the Czechoslovak fauna (Dip., Nycteribiidae). *Acta Universitatis Carolinae, Biologica*, 1964:167–234.
- . 1984. New taxa and new records of Palearctic Nycteribiidae and Streblidae (Diptera: Pupipara). *Věstník Československé Společnosti Zoologické*, 48:90–101.
- HÜRKA, L. 1983. Die Bewertung des Vorkommens der Fledermäuse (Mammalia: Chiroptera) in Westböhmen. *Věstník Československé Společnosti Zoologické*, 47:31–45.
- . 1989. Die Säugetiere des westlichen Teils der Tschechischen Sozialistischen Republik. II. Die Fledermäuse (Chiroptera).

- tera). Folia Museum Rerum Naturalium Bohemiae Occidentalis, Zoologica, 29:1-61.
- HŮRKOVÁ, J. 1964. Bat trematodes in Czechoslovakia. II. Parasitization of bats as hosts of trematodes. Věstník Československé Společnosti Zoologické, 28:1-13.
- ILJIN (=IL'IN), V. JU. 1989. Hibernation of bats in the forest-steppe region of the right-bank Povolzhie and their natural enemies. Pp. 495-497, in European bat research 1987 (V. Hanák, I. Horáček, and J. Gaisler, eds.). Charles University Press, Praha, 718 pp.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1958. Interpretation under the Plenary Powers of the nominal species "*Vespertilio murinus*" Linnaeus, 1758, and insertion in the "Official list of generic names in zoology" of a revised entry relating to the generic name "*Vespertilio*" Linnaeus, 1758 (Class Mammalia) ("Direction" supplementary to "Opinion" 91). Opinions and Declarations rendered by the International Commission on Zoological Nomenclature, 1, Section F, 98: 129-160.
- JÁNOSSY, D. 1986. Pleistocene vertebrate faunas of Hungary. Akadémiai Kiadó, Budapest, 208 pp.
- JENYNS, L. 1839. On a new species of bat found in the county of Durham, and preserved in the museum belonging to the Durham University. Annals and Magazine of Natural History, 3:73-76.
- JONES, G., AND J. M. V. RAYNER. 1988. Flight performance, foraging tactics and echolocation in free-living Daubenton's bats *Myotis daubentonii* (Chiroptera: Vespertilionidae). Journal of Zoology (London), 215:113-132.
- . 1991. Flight performance, foraging tactics and echolocation in the trawling insectivorous bat *Myotis adversus* (Chiroptera: Vespertilionidae). Journal of Zoology (London), 225:393-412.
- JŮDES, U. 1988. On the problem of "rabies" in bats. Macroderma, 4:11-33.
- KALKO, E., AND M. BRAUN. 1991. Foraging areas as an important factor in bat conservation: estimated capture attempts and success rate of *Myotis daubentonii* (Kuhl, 1819). Myotis, 29: 55-60.
- KALKO, E. K. V., AND H.-U. SCHNITZLER. 1989. The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentonii*. Behavioral Ecology and Sociobiology, 24:225-238.
- KLAUITTER, J. 1980. Spätsommerliche Einfüge und Überwinterungsbeginn der Wasserfledermaus (*Myotis daubentonii*) in der Spandauer Zitadelle. Nyctalus (N.F.), 1:227-234.
- KORABLEV, V. P., L. V. JAKIMENKO, AND M. P. TIUNOV. 1989. Kariotypy letučių myšej Dal'nogo Vostoka. Sovremennoje podchody k izučeniju izmenčivosti. Sbornik naučnych trudov. Dal'nevostočnoje otdelenie Akademii Nauk SSSR, Biologo-Počvennyj Institut, Vladivostok, pp. 95-98.
- KOVTUN, M. F. 1984. Stroenie i evolucija organov lokomocii rukokrylych. Naukova Dumka, Kiev, 304 pp.
- KOWALSKI, K., AND A. L. RUPRECHT. 1981. Chiroptera. Pp. 101-154, in Keys to vertebrates of Poland. Mammals (Z. Pucek, ed.). Polish Scientific Publishers, Warszawa, 367 pp.
- KRÁTĚKÝ, J. 1981. Postnatale Entwicklung der Wasserfledermaus, *Myotis daubentonii* Kuhl, 1819 und bisherge Kenntnis dieser Problematik im Rahmen der Unterordnung Microchiroptera (Mammalia: Chiroptera). Folia Musei Rerum Naturalium Bohemiae Occidentalis, Zoologica, 16:1-34.
- KRIVOŠEEV, V. G. 1984. Nazemnye mlekopitajuščie Dal'nogo Vostoka SSSR: opredelitel. Nauka, Moskva, 358 pp.
- KUHL, H. 1817. Die deutschen Fledermäuse. Privately published, Hanau, 67 pp.
- KURSKOV, A. N. 1981. Rukokrylye Belorussii. Nauka i Technika, Minsk, 136 pp.
- KUZJAKIN, A. P. 1950. Letučie myši (Sistematika, obraz žizni i pol'za dla sel'skogo i lesnogo chozjajstva). Sovetskaja Nauka, Moskva, 444 pp.
- LESIŃSKI, G. 1986. Ecology of bats hibernating underground in central Poland. Acta Theriologica, 31:507-521.
- . 1990. Changes in numbers of *Myotis daubentonii* (Kuhl, 1819) in autumn shelters and the effect of disturbance. Acta Theriologica, 35:364-368.
- LIMPENS, H. J. G. A., AND K. KAPTEYN. 1991. Bats, their behaviour and linear landscape elements. Myotis, 29:39-47.
- LIMPENS, H., W. BONGERS, AND J. KOPINGA. 1991. Het belang van oude bomen voor vleermuizen. De Levende Natuur, 4:139-144.
- LUNDBERG, K., B. ALMGREN, AND C. ODELBERG. 1983. Något om vattenfladdermusens (*Myotis daubentonii*) ekologi. Fauna och Flora, 78:237-242.
- LŮTGEMEIER, F. 1962. Histologische Besonderheiten der Gehirne von Chiropteren Körpergrösse und verschiedener Orientierungsweise. Zeitschrift für Morphologie und Ökologie der Tiere, 50:687-725.
- MAEDA, K. 1985. New records of the eastern Daubenton's bats, *Myotis daubentonii ussuriensis* Ognev, 1927, in Hokkaido and variations in external and skull dimensions. Journal of the Mammalogical Society of Japan, 10:159-164.
- MALEZ, M. 1986. Die quartären Vertebraten-Faunen in der SFR Jugoslawien. Quartärpaläontologie, 6:101-117.
- MATSKÁSI, I. 1975. Analysis of host-parasite relationship between bats and flukes in Hungary. Acta Zoologica Academiae Scientiarum Hungaricae, 21:73-86.
- MAUL, L. 1990. Überblick über die unterpleistozänen Kleinsäugerfaunen Europas. Quartärpaläontologie, 8:153-191.
- MAYLE, B. A. 1990. A biological basis for bat conservation in British woodlands—a review. Mammal Review, 20(4):159-195.
- MAZING (=MASING), M. 1987. Zimnee peredviženje rukokrylych mežu ubežiščami. Učonye Zapiski Tartuskogo Gosudarstvennogo Universiteta 769, Trudy po Zoologii, 15:41-60.
- MEDVEDEV, S. G., M. K. STANIJKOVIČ, M. P. TIUNOV, AND G. V. FARAFONOVA. 1991. Ektoparazity letučių myšej Dal'nogo Vostoka. Parazitologija, 25:27-38.
- MENU, H., AND J.-B. POPELARD. 1987. Utilisation des caractères dentaires pour la détermination des Vespertilioninés de l'ouest européen. Le Rhinolophe, 4:1-88.
- MILLER, L. A., AND H. J. DEGN. 1981. The acoustic behavior of four species of vespertilionid bats studied in the field. Journal of Comparative Physiology, Ser. A, 142:67-74.
- MITCHELL-JONES, A. J., A. S. COOKE, I. L. BOYD, AND R. E. STEBBINGS. 1989. Bats and remedial timber treatment chemicals—a review. Mammal Review, 19(3):93-110.
- MOGENSEN, F., AND B. MØHL. 1979. Sound radiation patterns in the frequency domain in cries from a vespertilionid bat. Journal of Comparative Physiology, 134:165-171.
- NEVRLÝ, M. 1987. Dvacet pět let výzkumu netopýrů na Bílé Desné v Jizerských horách. Sborník Severočeskeho muzea, Přírodní vědy, 16:231-272.
- NIKITENKO, M. F. 1969. Ekologo-morfologičeskaja charakteristika golovnogo mozga rukokrylych. Pp. 32-74, in Fauna i ekologija životnych Belorussii (M. F. Nikitenko, ed.). Nauka i Technika, Minsk, 268 pp.
- NOWOSAD, A. 1987. Materiały do znajomości Nycteribiidae (Diptera, Pupipara) Polski zachodniej i północno-zachodniej. Polskie Pismo Entomologiczne, 57:263-276.
- NYHOLM, E. S. 1965. Zur Ökologie von *Myotis mystacinus* (Leisl.) und *Myotis daubentonii* (Leisl.) (Chiroptera). Annales Zoologici Fennici, 2:77-123.
- OGNEV, S. I. 1927. A synopsis of the Russian bats. Journal of Mammalogy, 8:140-157.
- PELIKÁN, J., J. GAISLER, AND P. RÖDL. 1979. Naši savci. Československá Akademie Věd, Praha, 164 pp.
- PETERS, W. 1870. *Vespertilio laniger*. P. 617, in Catalogue of the mammals of China (south of the River Yangtze) and of the Island of Formosa (R. Swinhoe, ed.). Proceedings of the Zoological Society of London, 1870:615-653.
- PRŮCHA, M., AND V. HANZAL. 1989. Some aspects of hibernation of bats wintering in the Bohemian Karst (central Bohemia, Czechoslovakia). Acta Universitatis Carolinae, Biologica, 33: 315-333.
- RACEY, P. A. 1975. The prolonged survival of spermatozoa in bats. Biological Journal of the Linnean Society, Suppl., 1:385-416.
- RACEY, P. A., AND J. R. SPEAKMAN. 1987. The energy costs of pregnancy and lactation in heterothermic bats. Symposia of the Zoological Society of London, 57:107-127.
- REVIN, JU. V. 1989. Mlekopitajuščie Južnoj Jakutii. Nauka, Novosibirsk, 320 pp.
- RICHARDSON, P. 1985. Bats. Whittet Books, London, 128 pp.
- . In press. A new method of distinguishing Daubenton's

- bats (*Myotis daubentonii*) up to one-year old from adults. *Journal of Zoology* (London).
- ROER, H., AND W. EGSAEK. 1969. Über die Balz der Wasserfledermaus (*Myotis daubentonii*) (Chiroptera) im Winterquartier. *Lynx* (N.S.), 10:85-91.
- ROLANDEZ, J.-L., AND B. PONT. 1986. Occupation des ponts par les Chiroptères: premiers résultats de prospection. *Bièvre*, 8:17-24.
- ROMANKOWOWA, A. 1961. The sesamoid bones of the autopodia of bats. *Acta Theriologica*, 5:125-140.
- . 1963. Comparative study of the skeleton of the hyoid apparatus in some bat species. *Acta Theriologica*, 7:15-23.
- RUEDI, M., R. ARLETTAZ, AND T. MADDALENA. 1990. Distinction morphologique et biochimique de deux espèces jumelle de chauves-souris: *Myotis myotis* (Bork.) et *Myotis blythi* (Tomes) (Mammalia; Vespertilionidae). *Mammalia*, 54:415-429.
- RUPRECHT, A. L. 1979. Bats (Chiroptera) as constituents of the food of barn owls *Tyto alba* in Poland. *Ibis*, 121:489-494.
- . 1990. Nietoperze (Chiroptera) w składzie pokarmu sów z Puszczy Nadnoteckiej. *Przeгляд Zoologiczny*, 34:349-358.
- RYBÁŘ, P. 1980. Holocenní netopýři z jeskyně Záskočie v Lipovském krasu. *Československý kras*, 31(1979):19-33.
- RYBERG, O. 1947. Studies on bats and bat parasites. *Bokförlaget Svensk Natur*, Stockholm, 330 pp.
- SCHOBER, W., AND E. GRIMMBERGER. 1989. A guide to bats of Britain and Europe. The Hamlyn Publishing Group Limited, London, 224 pp.
- SHAMEL, H. H. 1942. A new *Myotis* from Manchuria. *Proceedings of the Biological Society Washington*, 55:103-104.
- SKURATOWICZ, W. 1988. Pchły (Siphonaptera: Ischnopsyllidae, Ceratophyllidae) zebrane na nietoperzach (Chiroptera) w Polsce. *Fragmenta Faunistica*, 31:429-444.
- SMEENK, C. 1982. Aantekeningen over een oude vermelding van *Nyctalus leisleri* (Kuhl, 1817) voor de provincie Groningen. *Lutra*, 25:53-59.
- SPEAKMAN, J. R. 1991a. Daubenton's bat *Myotis daubentonii*. Pp. 108-111, in *The handbook of British mammals* (G. B. Corbet and S. Harris, eds.). Third ed. Blackwell Scientific Publications, Oxford, 588 pp.
- . 1991b. The impact of predation by birds on bat populations in the British Isles. *Mammal Review*, 21(3):123-142.
- SPEAKMAN, J. R., P. I. WEBB, AND P. A. RACEY. 1991a. Effects of disturbance on the energy expenditure of hibernating bats. *Journal of Applied Ecology*, 28:1087-1104.
- SPEAKMAN, J. R., P. A. RACEY, C. M. C. CATTO, P. I. WEBB, S. M. SWIFT, AND A. M. BURNETT. 1991b. Minimum summer populations and densities of bats in N. E. Scotland, near the northern borders of their distributions. *Journal of Zoology* (London), 225:327-345.
- STALIŃSKI, J. 1990. Wściekliczna nietoperzy w Europie, 1954-1988. *Przeгляд Zoologiczny*, 34:137-152.
- STEBBINGS, R. E. 1988. The conservation of European bats. Christopher Helm, London, 246 pp.
- STEBBINGS, R. E., AND F. GRIFFITH. 1986. Distribution and status of bats in Europe. *Institute of Terrestrial Ecology, Huntingdon*, 142 pp.
- STEINBORN, G., AND H. VIERHAUS. 1984. Wasserfledermaus—*Myotis daubentonii* (Leisler in Kuhl, 1817). Pp. 101-107, in *Die Säugetiere Westfalens* (R. Schröpfer, R. Feldmann, and H. Vierhaus, eds.). *Abhandlungen aus dem Westfälischen Museum für Naturkunde*, 46(4):1-393.
- STEPHAN, H., H. D. FRAHM, AND G. BARON. 1987. Brains of vespertilionids. I. Subfamily characteristics. *Zeitschrift für zoologische Systematik und Evolutionsforschung*, 25:67-80.
- STRELKOV, P. P. 1962. The peculiarities of reproduction in bats (Vespertilionidae) near the northern border of their distribution. *Proceedings of the international symposium on methods of mammalogical investigation* (Brno, Czechoslovakia, 1960) (J. Kratochvíl and J. Pelikán, eds.). *Československá Akademie Věd, Praha*, 383 pp.
- SWIFT, S. M. 1981. Foraging, colonial and maternal behaviour of bats in north-east Scotland. Ph.D. thesis, University of Aberdeen, Aberdeen (not seen; cited in Fenton, 1985).
- SWIFT, S. M., AND P. A. RACEY. 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *Journal of Zoology* (London), 200:249-259.
- THOMAS, O. 1898. The technical names of British mammals. *The Zoologist*, 681:97-103.
- TIUNOV, M. P. 1989a. Razmnoženie, rost i razvitie vodjanoj nočnicy na juche Dal'nego Vostoka. Pp. 46-53, in *Teriologičeskie issledovanija na juche Dal'nego Vostoka*. Dal'nevostočnoe Otdelenie Akademii Nauk SSSR, Vladivostok.
- . 1989b. The taxonomic implication of different morphological systems in bats. Pp. 67-75, in *European bat research 1987* (V. Hanák, I. Horáček, and J. Gaisler, eds.). Charles University Press, Praha, 718 pp.
- TIUNOV, M. P., A. V. KOSMACH, AND E. V. ALEXEEVA. 1992. On the formation of the bat fauna in the south of the Soviet Far East. Pp.207-211, in *Prague studies in mammalogy* (I. Horáček and V. Vohralík, eds.). Charles University Press, Praha, 245 pp.
- TKAČ, V. V., AND L. D. ŠARFILO. 1988. Nematody rodu *Molionostrongylus* (Nematoda, Molineidae) ot rukokrylych fauny SSSR. *Vestnik Zoologii*, 4:3-8.
- TOPÁL, G. 1981. Bat remains from the Upper Pleistocene localities at Süttő, Hungary. *Fragmenta Mineralogica et Palaeontologica*, 10:67-70.
- . 1983. New and rare fossil mouse-eared bats from the Middle Pliocene of Hungary (Mammalia, Chiroptera). *Fragmenta Mineralogica et Palaeontologica*, 11:43-54.
- TUPINIER, Y. 1977. Description d'une chauve-souris nouvelle: *Myotis nathalinae* nov. sp. (Chiroptera—Vespertilionidae). *Mammalia*, 41:327-340.
- TUPINIER, Y., AND Y. BIRAUD. 1984. Variabilité des signaux de croisière de *Myotis daubentonii* (Kuhl, 1819) (Chiroptera: Vespertilionidae). *Myotis*, 21-22:78-81.
- URBAŃCZYK, Z. 1989. Results of the winter census of bats in Nietoperek 1985-1989. *Myotis*, 27:139-145.
- . 1991a. Hibernation of *Myotis daubentonii* and *Barbastella barbastellus* in Nietoperek Bat Reserve. *Myotis*, 29:115-120.
- . 1991b. Rezerwat Nietoperek. *Przyroda Ziemi Lubuskiej*. Lubuski Klub Przyrodników, Świebodzin, 24 pp.
- VIERHAUS, H. 1981. Zum Vorkommen parodontaler Erkrankungen bei mitteleuropäischen Fledermäusen. *Myotis*, 18-19:190-196.
- VOLLETH, M. 1987. Differences in the location of nucleolus organizer regions in European vespertilionid bats. *Cytogenetics and Cell Genetics*, 44:186-197.
- WALLIN, L. 1961. Territorialism on the hunting ground of *Myotis daubentonii*. *Säugetierkundliche Mitteilungen*, 9:156-159.
- WANG, S., AND C. ZHENG. 1985. Studies on Chinese Chiroptera with a comparison to Japanese Fauna. *Acta Theriologica Sinica*, 5:119-129 (in Chinese with English summary).
- WEINREICH, J. A., AND J. H. OUDE VOSHAAR. 1992. Population trends of bats hibernating in marl caves in the Netherlands (1943-1987). *Myotis*, 30:75-84.
- WEISHAAR, M. 1992. Zur Frage nach dem Eintritt der Geschlechtsreife bei mitteleuropäischen Fledermäusen. *Nyctalus* (N.F.), 4:312-314.
- WOŁK, E., AND W. BOGDANOWICZ. 1987. Hematology of the hibernating bat: *Myotis daubentonii*. *Comparative Biochemistry and Physiology*, A. *Comparative Physiology*, 88:637-639.
- WOŁOZYN, W. 1988. Pliocene and Pleistocene bats of Poland. *Acta Palaeontologica Polonica*, 32:207-325.
- YALDEN, D. W. 1986. Neolithic bats from Dowel Cave, Derbyshire. *Journal of Zoology* (London), 210:616-619.
- YANCHEV, YA., AND R. STOYKOVA. 1973. Study on the helminthofauna of the bats (Chiroptera) in Bulgaria. *Izvestiya na Zoologicheskaya Institut s Muzei*, 37:113-146 (in Bulgarian with English summary).
- YOO, D. H., AND M. H. YOON. 1992. A karyotypic study on six Korean vespertilionid bats. *Korean Journal of Zoology*, 35:489-496.
- YOON, M. H. 1990. Taxonomical study on four *Myotis* (Vespertilionidae) species in Korea. *Korean Journal of Systematic Zoology*, 6:173-192.
- YOON, M. H., AND T. A. UCHIDA. 1983. Identification of recent bats belonging to the Vespertilionidae by the humeral characters. *Journal of the Faculty of Agriculture, Kyushu University*, 28:31-50.

- YOSHIYUKI, M. 1989. A systematic study of the Japanese Chiroptera. National Science Museum, Tokyo, 242 pp.
- ŽALMAN, J. 1971. Diagnostische Merkmale an den Schulterblättern einiger Fledermäuse der Familie Rhinolophidae Bell, 1836 und Vespertilionidae Gray, 1821. Věstník Československé Společnosti Zoologické, 35:311-319.
- ZDZITOWIECKI, K. 1970. Helminths of bats in Poland. I. Cestodes and trematodes of the family Plagiorchiidae. Acta Parasitologica Polonica, 17:175-188.
- ZHANG, W. 1989. Study on the karyotypes of the *Myotis*. Journal of Anhui Normal University, 2:72-79 (in Chinese with English abstract).
- ZHEN, X.-Y. 1987. A survey of the bats (Chiroptera) of Fujian Province. Wuyi Science Journal, 7:237-242 (in Chinese with English summary).
- ZIMA, J., AND I. HORÁČEK. 1985. Synopsis of karyotypes of vespertilionid bats (Mammalia: Chiroptera). Acta Universitatis Carolinae, Biologica, 1985(1981):311-329.
- ŽUKOVA, N. F. 1989. Osobnosti morfologii kišečnika rukokrylych v svete problem ich filogeneza. Vestnik Zoologii, 5:67-74.

Editors of this account were J. ALDEN LACKEY and KARL F. KOOPMAN. Managing editor was JOSEPH F. MERRITT.

W. BOGDANOWICZ, MAMMAL RESEARCH INSTITUTE, POLISH ACADEMY OF SCIENCES, 17-230 BIAKOWIEŻA, POLAND.