

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/239280408>

Roost cavity selection by *Nyctalus noctula* and *N. leisleri* (Vespertilionidae, Chiroptera) in Białowieża Primeval Forest, eastern Poland

Article in *Journal of Mammalogy* · October 2005

DOI: 10.1644/1545-1542(2005)86[921:RCSBNN]2.0.CO;2

CITATIONS

121

READS

331

2 authors:



Ireneusz Ruczyński

Polish Academy of Sciences

35 PUBLICATIONS 886 CITATIONS

[SEE PROFILE](#)



Wiesław Bogdanowicz

Polish Academy of Sciences

191 PUBLICATIONS 3,653 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



A Pan-European Species-directories Infrastructure (PESI) [View project](#)



Heritability of intraindividual variation in body temperature in fasted homeothermic rodents [View project](#)

ROOST CAVITY SELECTION BY *NYCTALUS NOCTULA* AND *N. LEISLERI* (VESPERTILIONIDAE, CHIROPTERA) IN BIAŁOWIEŻA PRIMEVAL FOREST, EASTERN POLAND

IRENEUSZ RUCZYŃSKI AND WIESŁAW BOGDANOWICZ*

Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland (IR)

Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland (WB)

The selection of roost cavities by *Nyctalus noctula* and *N. leisleri*, 2 widespread species of mainly Eurasian distribution, was examined in Białowieża Primeval Forest in eastern Poland from May to August in 1998–2002. Because *N. noctula* is one of the most common forest-dwelling bats in Europe, whereas the smaller *N. leisleri* is relatively rare across its range (except in Ireland) and more limited to ancient forests, we hypothesized that these 2 taxa may differ significantly in their tree-cavity selection. Twenty-five *N. noctula* and 26 *N. leisleri* were radiotracked to 52 and 50 roost trees, respectively. For each accessible cavity roost occupied by *N. noctula* ($n = 28$) and *N. leisleri* ($n = 39$), 16 features were measured and compared with potentially available cavities ($n = 72$). Both species were selective in roost choice, and preferred cavities located higher (averaging 19 m above the ground), in more open surroundings, with smaller entrances, and with greater safety distance (from martens) than available cavities. Nearly all roosts occupied by bats were dry inside. Both species slightly more frequently settled in cavities with entrances facing NE and SW, but the differences were not statistically significant. Compared to the pool of available cavities, *N. noctula* was statistically more frequently found in cavities with wider inside cross section and with 1 entrance, unlike *N. leisleri*, which often used cavities with more than 1 entrance (range 1–6 entrances). One of the most noticeable differences between the 2 species was roost origin. *N. leisleri* used natural cavities (90%) more often than woodpecker cavities (10%), whereas *N. noctula* showed the opposite tendency (woodpecker-made cavities accounted for just over half of roosts chosen by this species). The safety distance also was significantly larger in *N. leisleri* than in *N. noctula*. A logistic regression model for *N. noctula* incorporating 4 cavity variables (safety distance from martens, height above ground, cavity origin, and mean distance to nearest vegetation) classified roost and available cavities correctly 85% and 94% of the time, respectively. For *N. leisleri*, the use of 2 variables only (i.e., height above ground and marten distance) resulted in correct assignment of 85% of roosts and 88% of available cavities. These differences suggest that the 2 species use different antipredator strategies that may have important consequences for their different survival rates in younger forests. In general, roosts in Białowieża Primeval Forest are selected under pressures of predation and climate, and these bats tend to use safe and warm shelters.

Key words: *Nyctalus leisleri*, *Nyctalus noctula*, Poland, predation, primeval forest, radiotelemetry, roost-site selection, tree cavities

Day-roost sites used by bats in spring and summer should provide secure resting places with optimal microclimate as close as possible to areas where bats forage and drink (e.g., Kunz 1982; Kunz and Lumsden 2003). Most forest-dwelling bats of temperate regions roost in trees, although the proportion of a bat community roosting in tree cavities varies geographically (Humphrey 1975). In some areas, tree cavities

provide suitable year-round roosting habitats for bats but at higher altitudes and latitudes, these cavities may be too cold during winter, when bats must use alternative roosts or migrate (Mayle 1990). Evidently, the distribution of trees containing cavities can significantly influence the availability of bat roosts and sometimes the density of suitable trees may be more important for the presence of bats than the availability of prey (Crampton and Barclay 1998).

Cavities form in trunks and branches of living or dead trees. In general, bats most often use large, dying, or dead tree trunks as roosts (Campbell et al. 1996; Kunz and Lumsden 2003; Lacki and Baker 2003; Menzel et al. 2000, 2002; Russo et al. 2004; Sedgely and O'Donnell 1999a, 1999b, 2004; Vonhof

* Correspondent: wieslawb@miiz.waw.pl

1996; Vonhof and Barclay 1996). Knowledge of how forest-dwelling bats select roosts has increased in recent years, especially in North America (reviewed by Miller et al. 2003; see also Bernardos et al. 2004; Parsons et al. 2003; Veilleux et al. 2004; Willis et al. 2003), Australia (Lumsden et al. 2002; Tidemann and Flavel 1987), and New Zealand (Sedgeley 2003; Sedgeley and O'Donnell 1999a, 1999b, 2004). In Europe, information about roost selection at cavity level is relatively poor and rather limited to data on cavity origin, height of entrance, or entrance size (e.g., Boonman 2000; Pénicaud 2000; Russo et al. 2004; but see Rieger 1996). In general, most authors have focused on external characteristics of trees (reviewed by Kunz and Lumsden 2003; Lacki and Baker 2003), and few (e.g., Sedgeley 2001; Sedgeley and O'Donnell 1999a) have examined internal features of cavities occupied by bats.

Preferred traits of roost cavities could be species-specific and may depend on colony size, reproduction status, and climatic conditions (see Kunz and Lumsden [2003] for a review). Internal cavity dimensions strongly influence thermal characteristics (Sedgeley 2001) and security of bats (Sedgeley and O'Donnell 1999a). Temperature seems to be one of the most important factors influencing roost selection by bats, especially during breeding season. Bats, being small animals with large surface areas relative to their volumes, have unfavorable proportions of body area to body surface, and easily lose heat. Low temperatures may retard gestation and growth of young (Entwistle et al. 1997; Racey 1973; Tuttle 1976) and affect the duration of maternal care (Sano 2000). It appears that pregnant and lactating bats tend to use tree cavities with features providing the best protection of energy and maximizing the growth rate of juveniles.

During the last 1,000 years there has been dramatic deforestation in Europe (Mannion 2001; Maruszczak 1999), with most primeval forest harvested to feed the human economy. Forests have become increasingly threatened by anthropogenic factors and formerly mixed stands were either cut or transferred into monocultures. This process has caused serious changes in ecology and behavior of mammals and birds. One of the best examples is swifts (*Apus apus*), which, in some areas, moved the entire nesting process to buildings rather than holes in trees (e.g., Pugaciewicz 1997; Tomiałojć and Stawarczyk 2003).

Knowledge of roost selection by bats in natural lowland forests in Europe is limited (Kurskov 1958; Ruczyński and Ruczyńska 2000)—most studies were conducted in planted forests or in small parks located in the vicinity of towns (e.g., Boonman 2000; Červený and Bürger 1989; Heerdt and Sluiter 1965; Limpens and Bongers 1991). Additionally, several authors in their “forest” research focused on artificial shelters, such as bird- and bat-boxes (Kasprzyk and Ruczyński 2001; Kerth et al. 2001; Kowalski and Lesiński 1994; Likhachev 1961). Nevertheless, detailed interpretation of behavioral results from strongly changed habitats must be treated as uncertain. Bats in Białowieża Primeval Forest in eastern Poland—the largest remnant of original lowland forest in Europe—rarely use bird- or bat-boxes (Krzanowski 1961; D. Czeszczewik, pers. comm.; G. Lesiński, pers. comm.), possibly reflecting an

abundance of old trees with many suitable roosts (Ruczyński and Ruczyńska 2000). Unusually high numbers and diversities of cavities in this forest result from intensive rotting of wood in old or dying trees as well as the activities of 9 species of woodpeckers. Selection of tree-cavity roosts may be influenced by the presence of predators and competitors. Predation on bats may occur within the roost or during emergence (Fenton et al. 1994; Speakman 1991) and this pressure could differ in natural versus managed forests.

We studied the use of tree cavities by the noctule, *Nyctalus noctula* (Schreber, 1774), and Leisler's bat, *Nyctalus leisleri* (Kuhl, 1817)—2 widespread, mainly Eurasian, species that usually roost in trees (e.g., Bogdanowicz and Ruprecht 2004; Gebhard and Bogdanowicz 2004; Hanák and Gaisler 1983; Strelkov 2000). *N. noctula* is one of the most common forest dwelling bats in Europe, whereas the smaller *N. leisleri* is relatively rare across its range (Bogdanowicz 1999; Shiel 1999), except in Ireland, where *N. noctula* does not occur (O'Sullivan 1994; but see Bogdanowicz and Ruprecht 2004). In spring both species migrate to the Białowieża Primeval Forest, where they form breeding colonies and where young are born (Likhachev 1961; Ruczyński and Ruczyńska 2000). In autumn these bats most probably migrate to the south or southwest (Daleszczyk 2001; Kaňuch et al. 2004; see also Bogdanowicz and Ruprecht 2004; Gaisler et al. 2003).

It appears that *N. leisleri* is more connected with old-growth forest than is *N. noctula* (Červený and Bürger 1989; Heise 1982; Schmidt 1988) and we hypothesize that these 2 species differ significantly in tree-cavity selection. Greater success of *N. noctula* may be related to easier accessibility of appropriate roosts in widely distributed managed and relatively young forests.

Our research into roost-site selection at the cavity level by 2 phylogenetically related species of forest-dwelling bats during the breeding season had 3 aims: 1st, to characterize tree cavities used by bats in well-preserved stands of Białowieża Primeval Forest and determine if these cavities are representative of those available in random plots; 2nd, to perform comparisons between species; and 3rd, to provide a focus for conservation efforts.

MATERIALS AND METHODS

Study area.—Białowieża Primeval Forest is located at the Polish–Belorussian border (52°43'N, 23°54'E) and covers an area of 1,450 km². It is the largest remnant of the original temperate forest in Europe. The study area (100 km²) covered well-preserved stands of Białowieża National Park and sections that are managed forests but that have old-growth remnants (>100 years) within them. Mature stands in the area, being in the best state of preservation (i.e., in the so-called strict reserve) of Białowieża National Park, are dominated by oak (*Quercus robur*; the percentage surface area covered by tree stands dominated by this species is equal to 20%), hornbeam (*Carpinus betulus*; 19%), lime (*Tilia cordata*) and maple (*Acer platanoides*; 9% combined), spruce (*Picea abies*; 16%), pine (*Pinus sylvestris*; 11%), alder (*Alnus glutinosa*; 12%), ash (*Fraxinus excelsior*; 6%), and birch (*Betula* spp.) and aspen (*Populus tremula*; 7% combined). In the managed part of the forest, where pine (26%) and spruce (28%) dominate, the percentage of deciduous trees such as oak (11% of the area), hornbeam (2%), and lime and maple (0%) is much lower than in the strict reserve. The average age of these

managed forest stands dominated by a given species is approximately 73 years. Old-growth remnants cover approximately 20% of the managed forest (Jędrzejewski and Jędrzejewska 1995).

Białowieża Primeval Forest is situated in the temperate zone but with influences of continental climate (Olszewski 1986). The average ambient temperature observed in 1988–2002 was 14.9°C for May, 18.2°C for June, 20.1°C for July, and 18.0°C for August. The average long-term temperature for July is 17.8°C. In spring and summer, large differences (>10°C) are observed between day and night temperatures. The duration of night during the study period ranged from 7 h 15 min to 9 h 25 min.

A rich community of vertebrates uses tree holes as breeding sites in Białowieża Forest, including 32 species of birds (Pugaczewicz 1997) and probably 11 species of bats (Kurskov 1958; Ruczyński and Ruczyńska 2000; Sachanowicz and Ruczyński 2001), as well as European pine marten (*Martes martes*), forest dormouse (*Dryomys nitedula*), fat dormouse (*Glis glis*), yellow-necked field mouse (*Apodemus flavicollis*), and European red squirrel (*Sciurus vulgaris*). Tree holes are also inhabited by invertebrates, such as bees, wasps, and beetles (Ruczyński and Gutowski 2002, I. Ruczyński, pers. comm.).

Capture of bats and location of roost cavities.—We located roost sites from May to August in 1998–2000 and 2002 (*N. leisleri*) and in 1999–2002 (*N. noctula*). Bats were caught in mist nets (2 × 6 m and 2.5 × 4 m), set across small forest rivers (Łutownia, Narewka, Hwoźna, and Złota) and at a pond at the edge of the strict reserve of Białowieża National Park. Captured bats were identified to species and sex, and their age and reproductive conditions were determined. We followed guidelines of the American Society of Mammalogists (<http://www.mammalogy.org/committees/index.asp>) in all handling procedures.

Roost trees were located by radiotelemetry. We attached small transmitters (0.5 g, Biotrack, Wareham, United Kingdom, and Tittle Electronics Pty. Ltd., Ballina, New South Wales, Australia; or 0.7 g, Tittle Electronics, and Holohil System, Carp, Ontario, Canada) to the interscapular regions of bats with surgical adhesive (Skin-Bond, Smith and Nephew, Largo, Florida). The mass of applied transmitters never exceeded 5% of the bats' body mass (Aldridge and Brigham 1988). We radiotracked a total of 26 *N. noctula* (10 pregnant females, 11 lactating females, 3 juvenile females, and 2 juvenile males) and 25 *N. leisleri* (10 pregnant females, 12 lactating females, 1 juvenile female, and 2 juvenile males). We used H-shaped (handmade) antennae and receivers (Yupiteru, MVT-700, Javiation, Bradford, West Yorkshire, United Kingdom) and Yaesu (FT-290R, Vertex Standard, Cypress, California) to locate signals from tagged bats and in this way found their roost trees. By counting emerging bats at dusk we determined the numbers of individuals using the roosts we located. We located roosting bats daily over the life of the transmitters and our average tracking periods were 6.5 days (range 1–14 days) for *N. noctula* and 7.5 days (range 2–13 days) for *N. leisleri*.

We used climbing techniques to examine each roost cavity used by *Nyctalus* after the bats had left. For each roost (except for 11 roosts in dead trees, 16 not precisely located, 5 that fell to the ground or were damaged, and 7 with extremely difficult access), we measured 10 of the features applied by Sedgely and O'Donnell (1999a), including distance from roost tree to the nearest tree in which height was equal or higher than location of the respective cavity (distance was measured for 8 trees at 45° intervals); diameter of tree at cavity height (DCH); cavity height from the ground level (measured with a clinometer [Suunto, Helsinki, Finland]); entrance area (maximum horizontal size by maximum vertical size); cross-sectional area of cavity at entrance level (Fig. 1A: $i \times ii$); internal height; internal depth; capacity ((internal height of cavity + internal depth of cavity + vertical entrance size) × cross-sectional area); average wall thickness ((DCH - (i + ii)/

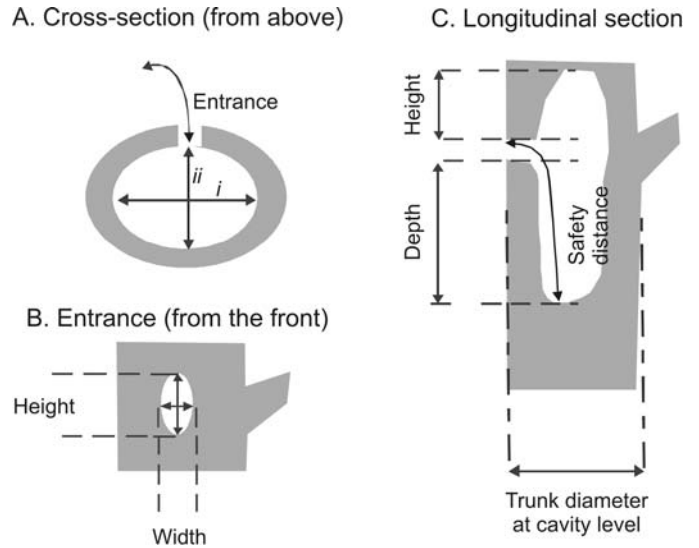


FIG. 1.—Selected measurements taken from cavities occupied by *Nyctalus noctula* and *N. leisleri* and those potentially available in Białowieża Primeval Forest. A) Cross-sectional area, width (i) × depth (ii); B) entrance as seen from in front of the tree; and C) longitudinal section of tree and cavity, as seen from the side. Other cavity features mentioned in the text are described in Sedgely and O'Donnell (1999a).

2]/2); and safety distance, also called marten distance (distance from external part of entrance to the furthest place inside cavity; however, when both dimensions of the entrance exceeded 6 cm, safety distance was estimated as 0 cm; in a typical cavity inhabited by both species of *Nyctalus*, cross-sectional area usually is larger than entrance area). We presume that large size of entrance is the main factor allowing most potential predators (such as pine martens) to penetrate the cavity, and then even a cavity 50 cm deep (or high) does not protect bats against all natural enemies. On the other hand, in several cases, the marten distance was more than 2–3 times either the internal cavity depth or height, because some cavities sometimes form complex, mazelike structures (Fig. 1).

We also measured 6 other features, including cavity location on the tree; cavity origin (made by a woodpecker or natural, i.e., formed during wood decomposition); cavity type (chamber—chambers had clearly defined space, e.g., holes made by woodpeckers; or crevices—deep but only 2–5 cm wide); cavity shape (deeper—internal cavity depth exceeded cavity height; equal—internal cavity depth and height differed by not more than 10%; higher—internal cavity height exceeded cavity depth); cavity humidity (dry; damp—with some humidity on walls or at the bottom; wet—with water inside); and compass direction of cavity entrance (NE, NW, SE, or SW—measured at 90° intervals). We also counted the number of entrances to the cavities. We measured the internal cavity with a flexible wire, which afterwards also was measured. Each cavity was illuminated and observed with the use of a small mirror mounted on a wire.

Sampling of available cavities.—To estimate which characteristics most influenced cavity selection, cavities occupied by bats were compared with those potentially available. Available cavities were sampled by using the nearest-individual method (Bullock 1996). Trees containing cavities were examined in an area of up to 250 m from roost trees, so that sampling was undertaken in similar forest stands. At each randomly selected location, the nearest trees were searched from the ground for the nearest cavity. Available cavities were located

TABLE 1.—Comparison of characteristics of cavities (“categorical” characters) occupied by *Nyctalus noctula* (N) and *N. leisleri* (L) and those potentially available (P) in trees by using Pearson’s χ^2 -test. In the 2×2 tables with frequencies < 10 , Yates’ correction applied. In 5 cases, both species occupied the same roost (ns = difference not significant).

Cavity characteristic	Cavities (n)			<i>N. noctula</i> –potential		<i>N. leisleri</i> –potential		<i>N. noctula</i> – <i>N. leisleri</i>	
	N	L	P	χ^2	P	χ^2	P	χ^2	P
Cavity origin									
Natural	13	35	56						
Made by woodpecker	15	4	16	9.26	<0.01	1.71	ns	12.99	<0.001
Cavity placement									
Trunk	24	29	65						
Branch	4	10	7	0.09	ns	3.79	ns	0.68	ns
Cavity type									
Hollow	28	30	71						
Crevice	0	9	1	0.24	ns	11.99	<0.001	5.61	<0.05
Cavity shape									
Depth > height	16	15	33						
Height > depth	10	19	28						
Height = depth ^a	2	5	10	1.33	ns	0.91	ns	2.37	ns
Cavity condition									
Dry	26	37	54						
Damp + wet	2	2	18	2.98	ns	5.48	<0.05	0.03	ns
Direction entrance faced									
NE	9	10	17						
SE	6	7	17						
SW	9	14	25						
NW	4	8	13	0.81	ns	0.51	ns	0.76	ns

^a Depth-height difference $< 10\%$.

during late autumn, winter, and early spring, with binoculars (magnification 7×50 and 10×50), in the period when trees were devoid of leaves. The number of cavities located with the help of binoculars and that we observed after climbing the tree were similar (Wilcoxon test, $Z = 1.42$, $n = 72$, $P \gg 0.05$), although 6% of cavities were not visible from the ground. Altogether, 72 trees with cavities were sampled and characterized. Every available cavity accessible by climbing was measured. If a tree had multiple cavities, only 1 (chosen randomly) was measured. Cavities were considered to be available for bats if their internal volume was greater than 50 cm^3 and horizontal and vertical dimensions of the entrance exceeded 15 mm and 25 mm, respectively. According to our experience, such cavities could be inhabited by both species of *Nyctalus*.

Data analysis.—A few variables with nonnormal distribution (as checked with Wilks–Shapiro test) were transformed by $\log(x)$ or $\log(x + 1)$ to approach normality. For statistical comparisons, t -test and F -test were used. Differences in frequency distribution were compared by χ^2 test. In the 2×2 tables with frequencies < 10 , Yates’ correction was applied. The importance of cavity parameters in roost selection of bats was checked via logistic regression. This method is distribution free and can thus include both discrete as well as continuous variables. The best logistic regression model, with the highest overall percentage of correctly classified observations, was determined by using stepwise procedure. All calculations were performed with Statistica, ver. 5.5 (StatSoft, Inc. 2000).

RESULTS

Twenty-five *N. noctula* and 26 *N. leisleri* were radiotracked to 52 and 50 roost trees, respectively. Cavities were measured for 28 roosts occupied by *N. noctula* and 39 roosts used by

N. leisleri, that is, 11 roosts in dead trees, 16 not precisely located, 5 lost, and 7 with extremely difficult access were not measured. Five roosts were inhabited by both bat species, which used them at the same time. The mean numbers of roosts located per individual were 1.92 and 2.08 for *N. leisleri* and *N. noctula*, respectively.

Characteristics of cavities selected by bats.—Woodpecker-made cavities accounted for just over half of roosts chosen by *N. noctula* (54%); the remaining 46% were of different origin (Table 1). *N. leisleri* was less frequently found in woodpecker-made cavities (10%) compared to other types of cavities (90%; Table 1). Both *N. noctula* and *N. leisleri* commonly roosted in cavities located in tree trunks (86% and 74%, respectively) rather than those in large branches (14% and 26%, respectively), but these differences were not statistically different from available cavities (Table 1). *N. noctula* used only hollow (chamber-type) cavities rather than crevices, whereas *N. leisleri* bats roosted both in hollows (77%) and crevices (23%). *N. leisleri* used crevices more frequently than would be expected based on their availability (Table 1). Cavities with depth exceeding height accounted for 62% of roosts chosen by *N. noctula* and 44% of those inhabited by *N. leisleri*. Cavities with height exceeding depth made up 39% of those inhabited by *N. noctula* and 56% of those chosen by *N. leisleri*. Nevertheless, neither *N. noctula* nor *N. leisleri* showed any significant selection for a cavity of particular shape. Nearly all roosts occupied by bats were dry. Roost cavities chosen by *N. noctula* had 1 entrance, whereas those used by *N. leisleri* often (16 of

39) had more than 1 entrance (range 1–6); in a few cases extra entrances served as emergency exits. Cavities used as roosts by both species tended to face NE or SW but observed differences were not statistically significant (Table 1). The percentages of cavities with entrances facing different compass directions occupied by *N. noctula* and *N. leisleri* relative to the available pool of cavities also were not significant (Table 1).

In studying quantitative characteristics of cavities (Table 2), we found statistically significant differences between the available pool of cavities and the 2 species in 4 variables: mean distance to nearest vegetation, height above ground, entrance area, and safety distance (the so-called marten distance; Table 3). Roosts used by *N. leisleri* also differed from available cavities in terms of internal height and depth, whereas those inhabited by *N. noctula* had statistically wider inside cross section (Table 3).

Mean distance to nearest vegetation at cavity height was greater by 4 m for cavities inhabited by the bats compared to those potentially available. Entrances to cavities occupied by *N. noctula* averaged 19.2 m above ground and those used by *N. leisleri* averaged 18.6 m. Available cavities averaged 10 m lower (Table 2). The entrance area of cavities occupied by both species was nearly half the size of available cavities. The maximum width of the used roost entrances did not exceed 8 cm in cavities occupied by *N. noctula* and up to 93% of the openings were <5 cm. *N. leisleri* also roosted in narrow cavities, with no entrance being wider than 6 cm (Table 2). A negative correlation was found between entrance dimensions in *N. noctula*; as the height increased the width decreased ($r = -0.44, n = 28, P < 0.05$).

Although the inside cross section of cavities inhabited by *N. noctula* was significantly larger than those occupied by *N. leisleri*, the cavities themselves were shallower and vertically smaller (Table 3). The respective wall thicknesses in the roosts of both taxa (as well as in the census of available cavities) were similar. Lack of difference in wall thickness reflected slightly larger trunk diameter at cavity height in roosts occupied by *N. noctula*. Both *N. noctula* and *N. leisleri* preferred cavities with a larger marten distance compared to cavities from the potentially available pool. The marten distance was significantly larger in *N. leisleri* than in *N. noctula* (Tables 2 and 3).

Characteristics influencing cavity selection by bats.—The logistic regression model we used for *N. noctula* included 6 parameters (cavity origin, mean distance to nearest vegetation, height above ground, entrance area, cavity cross section, and marten distance), which showed significant differences between roost cavities and other available cavities. The complete set of parameters correctly classified 85% of cavities occupied by *N. noctula* and 92% of potentially available cavities ($\chi^2 = 60.20, d.f. = 6, P < 0.001$). The same level of correct assignment ($\chi^2 = 60.10, d.f. = 4, P < 0.001$) also was obtained with a 4-variable model (including marten distance, height above ground, cavity origin, and mean distance to nearest vegetation at cavity height). A set of 3 variables (marten distance, cavity origin, and height above ground) allowed for the correct placement of 78% of roost cavities used by *N. noctula* and 90% available cavities ($\chi^2 = 59.47, d.f. = 3, P < 0.001$).

TABLE 2.—Cavity characteristics of roosts occupied by *Nyctalus noctula* and *N. leisleri* and those potentially available. Means and confidence limits, when necessary, were retransformed from logarithmic to linear scale by converting to antilogarithms. Sample size: *N. noctula* = 28, *N. leisleri* = 39, potential = 72, with the exception of marten distance, where *N. noctula* = 27, *N. leisleri* = 33, and potential = 51.

Cavity feature	Species	\bar{X}	Confidence limits	Range
Mean distance to nearest vegetation ^a (m)	<i>N. noctula</i>	12.37	10.5–14.6	5.9–24.5
	<i>N. leisleri</i>	11.89	10.1–13.9	3.0–50.1
	Potential	7.72	7.1–8.5	2.9–31.6
Diameter at cavity height ^a (cm)	<i>N. noctula</i>	45.69	38.7–54.0	19.0–109.0
	<i>N. leisleri</i>	41.20	36.4–46.7	18.0–90.0
	Potential	43.24	38.8–48.2	15.0–130.0
Height above ground (m)	<i>N. noctula</i>	19.25	17.1–21.4	8.0–30.0
	<i>N. leisleri</i>	18.65	17.2–20.1	9.5–26.0
	Potential	8.00	6.8–9.2	0.3–23.0
Entrance area ^a (cm ²)	<i>N. noctula</i>	20.15	17.0–23.9	7.5–77.5
	<i>N. leisleri</i>	23.31	17.1–31.7	3.8–46.8
	Potential	46.29	31.9–67.3	3.8–3,410.0
Inside cross section ^a (cm ²)	<i>N. noctula</i>	249.93	179.8–347.5	30.0–1,440.0
	<i>N. leisleri</i>	146.68	105.1–204.8	10.0–1,296.0
	Potential	145.46	106.3–199.0	6.0–2,850.0
Internal height ^b (cm)	<i>N. noctula</i>	9.54	5.1–17.6	0.0–80.0
	<i>N. leisleri</i>	21.89	13.3–36.0	0.0–130.0
	Potential	10.81	6.8–17.2	0.0–500.0
Internal depth ^b (cm)	<i>N. noctula</i>	21.74	14.9–31.8	0.0–200.0
	<i>N. leisleri</i>	23.97	15.4–37.3	0.0–180.00
	Potential	13.03	8.7–19.5	0.0–250.0
Volume ^a (dcm ³)	<i>N. noctula</i>	12.11	7.7–19.9	1.7–355.0
	<i>N. leisleri</i>	11.40	7.4–17.6	0.5–181.4
	Potential	7.72	4.5–13.3	0.1–1,026.0
Wall thickness ^a (cm)	<i>N. noctula</i>	13.33	10.3–17.2	2.5–44.5
	<i>N. leisleri</i>	12.31	9.9–15.3	1.5–43.6
	Potential	13.68	11.8–15.9	2.8–58.5
Safety distance (= marten distance) ^b (cm)	<i>N. noctula</i>	44.47	38.2–51.9	25.0–200.0
	<i>N. leisleri</i>	58.93	50.3–69.1	21.0–180.0
	Potential	13.03	8.1–21.0	0.0–200.0

^a Transformed by $\log_{10}(x)$.

^b Transformed by $\log_{10}(x + 1)$.

For *N. leisleri*, the analysis employed 8 variables (cavity type, cavity condition, mean distance to nearest vegetation, height above ground, entrance area, internal height, internal depth, and marten distance). This model correctly classified 88% of the roost cavities inhabited by *N. leisleri* as well as 92% of available cavities ($\chi^2 = 76.55, d.f. = 8, P < 0.001$). When using 2 variables only (height above ground and marten distance), we could correctly classify as many as 85% of roosts used by *N. leisleri* and 88% of available cavities ($\chi^2 = 71.99, d.f. = 2, P < 0.001$).

DISCUSSION

In Białowieża Primeval Forest, *N. noctula* did not choose more woodpecker-made cavities than other types of cavities. The ratio of woodpecker-excavated cavities to natural ones in this area is smaller than that recorded in forests in Western Europe (e.g., Boonman 2000; Kronwitter 1988; Stratmann 1978), suggesting a possible preference by bats in these regions. In Germany, these bats often settled in cavities made

TABLE 3.—Comparison of cavity characteristics of *Nyctalus noctula* and *N. leisleri* and the potentially available pool by using a *t*-test with variance evaluated separately (ns = not significant).

Cavity feature	<i>N. noctula</i> —potential			<i>N. leisleri</i> —potential			<i>N. noctula</i> — <i>N. leisleri</i>		
	<i>t</i> value	<i>df.</i>	<i>P</i> -level	<i>t</i> -value	<i>df.</i>	<i>P</i> -level	<i>t</i> value	<i>df.</i>	<i>P</i> -level
Mean distance to nearest vegetation ^a	5.27	98	<0.001	5.08	109	<0.001	0.35	65	ns
DCH ^a	0.54	98	ns	0.55	109	ns	1.03	65	ns
Height aboveground	9.44	98	<0.001	10.65	109	<0.001	0.49	65	ns
Entrance area ^a	4.05	92.3	<0.001	2.84	107.8	<0.01	0.84	56.9	ns
Inside cross section ^a	2.41	76.8	<0.05	0.04	96.1	ns	2.24	65	<0.05
Internal height ^b	0.32	60.1	ns	2.08	95.7	<0.05	2.13	65	<0.05
Internal depth ^b	1.86	84.5	ns	2.04	94.4	<0.05	0.32	65	ns
Volume ^a	1.28	91.0	ns	1.10	108.5	ns	0.19	65	ns
Wall thickness ^a	0.18	98	ns	0.83	109	ns	0.49	65	ns
Marten distance ^b	5.04	59.0	<0.001	6.13	59.9	<0.001	2.57	58.0	<0.05

^a Transformed by $\log_{10}(x)$.

^b Transformed by $\log_{10}(x + 1)$.

by the black woodpecker (*Dryocopus martius*—Kronwitter 1988; Stratmann 1978), which were not occupied by bats in Białowieża Primeval Forest, probably because of their large entrances and, in consequence, high predation pressure and poor insulation against large differences ($>10^{\circ}\text{C}$) between day and night temperatures.

Unlike *N. noctula*, *N. leisleri* more often roosted in the more frequently available natural tree cavities than woodpecker-made cavities. Natural cavities can be either hollows or crevices; the latter were preferred by *N. leisleri*. Such cavities sometimes formed complex mazelike structures that may provide better insulation from unfavorable weather conditions as well as better protection against intruders such as *A. flavicollis*, *D. nitedula*, or *G. glis*—rodents that significantly reduce breeding success rates of birds in Białowieża Primeval Forest (Walankiewicz 2002b). We saw *G. glis* in a cavity abandoned by bats the previous day and we found a dead young *N. leisleri* at the entrance, suggesting that pressure from glirids influence the bats' behavior. Complicated layout of cavities and the presence of additional entrances may increase the bats' chances to escape. The larger size of individual *N. noctula* (forearm length = 48.0–58.0 mm; reviewed by Gebhard and Bogdanowicz [2004]) may limit their access to some roosts used by *N. leisleri* (forearm length = 39.0–46.4 mm; reviewed by Bogdanowicz and Ruprecht [2004]) and make them less vulnerable to some predators.

Predation pressure on nestlings in holes made by woodpeckers is much higher than in natural tree cavities, according to D. Czeszczewik and W. Walankiewicz (in litt.). Czeszczewik and Walankiewicz suggest that woodpeckers know the holes that they made, occasionally visit such holes, and prey on nestlings if they are present. We hypothesize that *N. noctula* somehow is able to defend cavities, whereas the smaller *N. leisleri* is strongly exposed to predation. *N. leisleri* decreases risk of predation by avoiding cavities made by woodpeckers. Possibly this bat species in younger forest stands must use cavities made by woodpeckers and finally is eliminated from the landscape by predation.

In Białowieża Primeval Forest, trunk diameter at cavity height did not influence cavity selection by bats. Sedgely and

O'Donnell (1999a) obtained similar results in New Zealand, whereas Vonhof and Barclay (1996) found larger trunk diameters at the level of bat-inhabited cavities in North America. A larger trunk diameter means better insulation from the environment and more stable thermal conditions (Derby and Gates 1966).

The height of the cavity above ground was important for both species in Białowieża Primeval Forest because both species occupied cavities averaging 19 m above ground, probably representing “mean record values” for Europe (see Gebhard and Bogdanowicz 2004). In the Netherlands, roosts of *N. noctula* roosts are a few or approximately 10 m above ground (Heerdt and Sluiter 1965); in Germany, roost height in general is from 7 to 12 m (e.g., Boonman 2000; Schmidt 1988; Stratmann 1978); but in Bavaria in southern Germany Kronwitter (1988) recorded heights of 4.6–22.4 m (average 12.6 m, $n = 30$). In an old city park in the Czech Republic, bats occupied cavities at 2–8 m above ground, with *N. noctula* living “even above 10 m” (Červený and Bürger 1989). In Brittany (France) bats' cavities were found at 2–11 m (Pénicaud 2000). We believe that bats' roost choices partly reflect the heights of available trees (Faliński 1986), and higher roost entrances probably provide better protection against predators (e.g., Rydell et al. 1996; Sedgely and O'Donnell 1999a, 2004; Vonhof and Barclay 1996). In Białowieża National Park, the nest cavities of European pied flycatchers (*Ficedula hypoleuca*) located higher above ground are less often invaded than are lower ones (Czeszczewik and Walankiewicz 2003), a trend that did not apply to collared flycatchers (*Ficedula albicollis*—Walankiewicz 1991). Both *N. noctula* and *N. leisleri* roost higher in trees than sympatric cavity-nesting birds (Fig. 2), reflecting, in part, their distinct preference for oak trees (Wesołowski 1995; authors' own data). Temperature benefits arising from greater exposure of trunks to sunlight at cavity height have been identified as an important reason for bats choosing more elevated roosts (Sedgely 2001). On the other hand, all roosts of northern long-eared bats (*Myotis septentrionalis*) were located in or below the forest canopy, which suggests that solar exposure may not be as critical for selection of roost trees by maternity colonies of this species as for other tree-roosting species at more northern

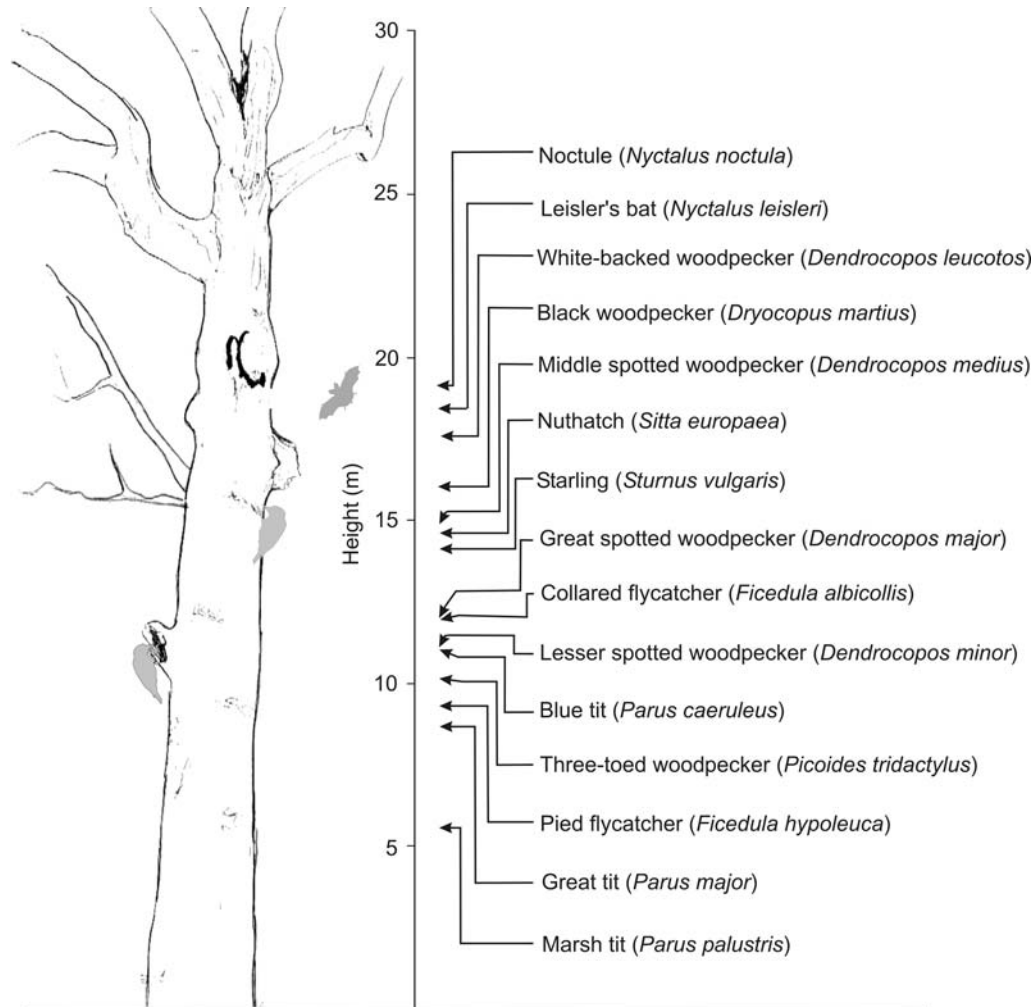


FIG. 2.—Mean cavity height of roost cavities used by bats and birds in Białowieża Primeval Forest (modified from Ruczyński 2004). Data on cavity height above ground were derived from papers documenting studies carried out in Białowieża National Park (Wesołowski 1989, 1995, 1996; Wesołowski and Tomiałojć 1986). Where bird nesting heights differed across habitats, the higher location was chosen. Drawing of tree by C. Duriez.

latitudes in North America (Menzel et al. 2002). In Białowieża Primeval Forest, we noted that temperatures on the outside of trees increased with increasing height above ground, a trend reflected by roost temperature and influencing the thermal environment of bats' roosts.

The diameter of the entrance to a cavity is related to body size of the species occupying the cavity (McComb and Noble 1981; Van Balen et al. 1982), perhaps reflecting the potential for competition with larger species. Although entrance size was similar in cavities occupied by *N. noctula* and *N. leisleri* in Białowieża Primeval Forest, the entrances greatly exceeded the minimum diameters through which bats could enter (Ruprecht 1984). A few Australian bat species choose cavities with similar entrance sizes (Tidemann and Flavel 1987). We did not find any clear evidence of competition between *N. noctula* and *N. leisleri* in Białowieża Forest (more than 10% of roosts were used by both taxa at the same time) reflecting the general situation in birds in this area (Czeszczewik 2004; Walankiewicz 1991).

Roosts with small entrances doubtless offer better protection against inclement weather conditions (e.g., Barclay et al. 1988;

Sedgeley and O'Donnell 1999a) and predators. In Białowieża Primeval Forest, bat roost cavities most often had entrances smaller than the width of a marten's head (ca. 4.5–5 cm—see Reig and Ruprecht 1989). Martens damage birds' broods with their paws and, if the entrance is big enough, they enter the cavity (Czeszczewik 2004; Walankiewicz 2002b). If the entrance is small and there is sufficient space inside the cavity (large marten distance), bats need not fear this predator. The pine marten is one of the main species contributing to brood loss in birds living in natural forest stands in Białowieża Primeval Forest (Czeszczewik 2004; Walankiewicz 1991, 2002a, 2002b; see also Wesołowski 2002). However, analysis of martens' food intake shows that they very rarely eat bats (Zalewski et al. 1995). It appears that the concentration of bats in colonies considerably reduces martens' chances of finding the "right" cavity, despite the fact that being in colonies might increase the smell coming from the roost.

Although a small entrance significantly reduces the possibility of penetration of the cavity by martens, it does not protect from smaller predators such as weasels and some rodents and

woodpeckers (e.g., Czeszczewik 2004; Wesołowski 2002). Other behavior patterns, such as the nomadic lifestyle of breeding colonies, active defense, or choosing roosts located high above the ground, may contribute to better protection of bats against these intruders.

We also believe that reduced air exchange between the cavity and its surroundings arising from small entrances and extent of the cavity (large marten distance) should limit radiation of heat from the roost and allow for protection of the bat's energy, especially when ambient temperature is low and temperature inside cavity can fall below the bat's thermoneutral zone, which is estimated to be 29°C (Speakman and Thomas 2003). Because bats can increase the temperature inside roosts by up to 5–8°C (Burnett and August 1981), temperature inside cavities without bats should exceed at least 22–24°C. The average long-term temperature for the warmest month, July, is 17.8°C (Olszewski 1986), indicating that in Białowieża Primeval Forest pregnant and lactating bats usually should use well-insulated roosts. As we discovered, the measurement of temperatures inside roost cavities and potentially available cavities shows that unused hollows were colder, especially during night. Although in some periods colder cavities can be preferred, for example, because of food limitation or high ambient temperatures, we think that such situations are much rarer, so that pregnant and lactating *N. noctula* and *N. leisleri* in Białowieża Primeval Forest follow the general pattern of temperate-climate bats and roost in the warmest available cavities (see Entwistle et al. 1997; Sedgely 2001), reflecting their thermal biology (Burnett and August 1981; Hock 1951; McNab 1982). Russo et al. (2004), although they did not measure cavity temperatures, also discovered that entrances to cavities preferred by *Barbastella barbastellus* were higher above ground and faced south more frequently than the available cavity set, suggesting selection for warm roosts by reproducing females. At the same time, roosts that are too hot were not used by the bats we studied, as observed elsewhere (Hutchinson and Lacki 2001; Kalcounis and Brigham 1998; Zahn and Henatsch 1998).

We found that *N. noctula* and *N. leisleri* select cavities because of their specific features. The most prominent impacts on cavity selection were its placement about the ground, marten distance, and cavity origin. It appears that roosts in Białowieża Primeval Forest are selected under pressure of predation and climate, and bats tend to use safe and warm roosts. Particularly noticeable differences found between the 2 species investigated concerning roost origin suggest that they use different antipredator strategies, which can have important consequences for their different survival rates in younger forests.

ACKNOWLEDGMENTS

We thank all the people who gave us their precious time during bat capture, radiotracking, location of roosts, and tree-climbing. Especially, thanks to C. Duriez, M. Pohlers, P. Zahorowicz, A. Baranowski, A. Arasim, J. Mieczkowska, S. Barthwood, J. van Beek, M. Blaice, M. Cox, A. Domen, A. Domzalska, A. Dorenda, K. Gmi-truk, J. Górniak, T. van Grup, Gryka, D. Koncewicz, K. Mazurska, A. Misiak, K. Sachanowicz, H. Zalewska, R. Szordykowski, A. Wower, K. Zajac, R. Zwolak, T. Zychowicz, and all students from the

Students' Scientific Circle from Academy of Siedlce. We are very grateful to D. Czeszczewik, W. Walankiewicz, and C. Mitrus for access to their unpublished data, and M. B. Fenton, D. Russo, B. Jedrzejewska, A. Zalewski, L. Rychlik, and 2 anonymous reviewers for critical comments and creative discussions. The project was undertaken with funding from the State Committee for Scientific Research (6POF 02118 and 3PO4F 00822) and the budget of the Mammal Research Institute PAS in Białowieża.

LITERATURE CITED

- ALDRIDGE, H. D. J. N., AND R. M. BRIGHAM. 1988. Load carrying and maneuverability in insectivorous bat: a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* 69:379–382.
- BARCLAY, R. M. R., P. A. FAURE, AND D. R. FARR. 1988. Roosting behavior and roost-selection by migrating silver-haired bats (*Lasiurus noctivagans*). *Journal of Mammalogy* 69:821–825.
- BERNARDOS, D. A., C. L. CHAMBERS, AND M. J. RABE. 2004. Selection of gambel oak roosts by southwestern myotis in ponderosa pine-dominated forests, northern Arizona. *Journal of Wildlife Management* 68:595–601.
- BOGDANOWICZ, W. 1999. *Nyctalus noctula*. Pp. 136–137 in *Atlas of European mammals* (A. J. Mitchell-Jones, et al., eds.). Academic Press, London, United Kingdom.
- BOGDANOWICZ, W., AND A. L. RUPRECHT. 2004. *Nyctalus leisleri*—Kleinabendsegler. Pp. 717–756 in *Handbuch der Säugetiere Europas* (F. Krapp, eds.). Vol. 4/II, Fledertiere II. Aula-Verlag, Wiebelsheim, Germany.
- BOONMAN, M. 2000. Roost selection by noctules (*Nyctalus noctula*) and Daubenton's bats (*Myotis daubentonii*). *Journal of Zoology* (London) 251:385–389.
- BULLOCK, J. 1996. Plants. Pp. 111–138 in *Ecological census techniques: a handbook* (W. J. Sutherland, ed.). Cambridge University Press, Cambridge, United Kingdom.
- BURNETT, C. D., AND P. V. AUGUST. 1981. Time and energy budgets for day roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). *Journal of Mammalogy* 78:1231–1239.
- CAMPBELL, L. A., J. G. HALLETT, AND M. A. O'CONNELL. 1996. Conservation of bats in managed forests: use of roosts by *Lasiurus noctivagans*. *Journal of Mammalogy* 77:976–984.
- ČERVENÝ, J., AND P. BÜRGER. 1989. Density and structure of 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, Prague, Czech Republic.
- CRAMPTON, L. H., AND M. R. BARCLAY. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* 12:1347–1358.
- CZESZCZEWIK, D. 2004. Breeding success and timing of the pied flycatcher *Ficedula hypoleuca* nesting in natural holes and nest-boxes in the Białowieża Forest, Poland. *Acta Ornithologica* 39:15–20.
- CZESZCZEWIK, D., AND W. WALANKIEWICZ. 2003. Natural nest sites of the pied flycatcher in a primeval forest. *Ardea* 91:221–230.
- DALESZCZYK, K. 2001. New data on bats (Chiroptera) hibernating in the Polish part of Białowieża Primeval Forest. *Myotis* 38 [2000]:47–50.
- DERBY, R. W., AND D. M. GATES. 1966. The temperature of tree trunks—calculated and observed. *American Journal of Botany* 53:580–587.
- ENTWISTLE, A. C., P. A. RACEY, AND J. R. SPEAKMAN. 1997. Roost selection by the brown long-eared bat *Plecotus auritus*. *Journal of Applied Ecology* 34:399–408.
- FALIŃSKI, J. B. 1986. Vegetation dynamics in temperate lowland primeval forest: ecological studies in Białowieża forest. Dr. W. Junk Publishers, Dordrecht, Netherlands.

- FENTON, M. B., I. L. RAUTENBACH, S. E. SMITH, C. M. SWANEPOEL, J. GROSELL, AND J. VAN JAARVELD. 1994. Raptors and bats: threats and opportunities. *Animal Behaviour* 48:9–18.
- GAISLER, J., V. HANÁK, V. HANZAL, AND V. JARSKÝ. 2003. Výsledky kroužkování netopýrů v České republice a na Slovensku, 1948–2000. *Vespertilio* 7:3–61.
- GEBHARD, J., AND W. BOGDANOWICZ. 2004. *Nyctalus noctula*—Großer Abendsegler. Pp. 607–694 in *Handbuch der Säugetiere Europas* (F. Krapp, ed.). Vol. 4/II, Fledertiere II. Aula-Verlag, Wiebelsheim, Germany.
- HANÁK, V., AND J. GAISLER. 1983. *Nyctalus leisleri* (Kühl, 1818), une espèce nouvelle pour le continent africain. *Mammalia* 47:585–587.
- HEERDT, P. F., AND J. W. SLUITER. 1965. Notes on the distribution and behaviour of the noctule bat (*Nyctalus noctula*) in Netherlands. *Mammalia* 29:463–477.
- HEISE, G. 1982. Nachweis des Kleinabendsegler (*Nyctalus leisleri*) im Kreis Prenzlau, Uckermark. *Nyctalus* 1:449–450.
- HOCK, R. J. 1951. The metabolic rates and body temperatures of bats. *Biological Bulletin* 101:289–299.
- HUMPHREY, S. R. 1975. Nursery roosts and community diversity of Nearctic bats. *Journal of Mammalogy* 56:321–346.
- HUTCHINSON, J. T., AND M. J. LACKI. 2001. Possible microclimate benefits of roost site selection in the red bat, *Lasiurus borealis*, in mixed mesophytic forest of Kentucky. *Canadian Field-Naturalist* 115:205–209.
- JĘDRZEJSKI, W., AND B. JĘDRZEJSKA. 1995. Projekt utworzenia Parku Narodowego Puszczy Białowieskiej. *Chrońmy Przyrodę Ojczyzn* 53:16–36.
- KALCOUNIS, M. C., AND R. M. BRIGHAM. 1998. Secondary use of aspen cavities by tree-roosting big brown bats. *Journal of Wildlife Management* 62:603–611.
- KAŃUCH, P., I. RUCZYŃSKI, AND M. CEL'UCH. 2004. Unusual change of habitat by a noctule female (*Nyctalus noctula*). *Nyctalus* 9:504–505.
- KASPRZYK, K., AND I. RUCZYŃSKI. 2001. The structure of bat communities roosting in bird nest boxes in two pine monocultures in Poland. *Folia Zoologica* 50:107–116.
- KERTH, G., K. WEISSMANN, AND B. KÖNIG. 2001. Day roost selection in female Bechstein's bats (*Myotis bechsteinii*): a field experiment to determine the influence of roost temperature. *Oecologia* 126:1–9.
- KOWALSKI, M., AND G. LESIŃSKI. 1994. Bats occupying nest boxes for birds and bats in Poland. *Nyctalus* 5:19–26.
- KRONWITTER, F. 1988. Population structure, habitat use and activity patterns of the noctule bat *Nyctalus noctula* Schreb. 1774 (Chiroptera, Vespertilionidae) revealed by radio-tracking. *Myotis* 26:23–85.
- KRZANOWSKI, A. 1961. Wyniki rozwiązania skrzynek w Białowskim Parku Narodowym. *Chrońmy Przyrodę Ojczyzn* 17:29–32.
- KUNZ, T. H. 1982. Roosting ecology of bats. Pp. 1–55 in *Ecology of bats* (T. H. Kunz, ed.). Plenum Publishing Corporation, New York.
- KUNZ, T. H., AND L. F. LUMSDEN. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–89 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- KURSKOV, A. N. 1958. Materialy k izucheniyu rukokrylykh Belovezhskoi Pushchi. *Trudy Zapovednika Okhotnichego Khozajstva Belovezhskaya Pushcha* 1:120–138.
- LACKI, B. J., AND M. D. BAKER. 2003. A prospective power analysis and review of habitat characteristics used in studies of tree-roosting bats. *Acta Chiropterologica* 5:199–208.
- LIKHACHEV, G. H. 1961. Ispolzovanie letuchimi myshami ptichikh iskusstvennykh gnezdovni. *Trudy Prioksko-Terrasnogo Gosudarstvennogo Zapovednika* 3:85–103.
- LIMPENS, G. J. G. A., AND W. BONGERS. 1991. Bats in Dutch forests. *Myotis* 29:129–136.
- LUMSDEN, L. F., A. F. BENNETT, AND J. E. SILINS. 2002. Selection of roost sites by the lesser long-eared bat (*Nyctophilus geoffroyi*) and Gould's wattled bat (*Chalinolobus gouldii*) in south-eastern Australia. *Journal of Zoology* (London) 257:207–218.
- MANNION, A. M. 2001. Zmiany środowiska Ziemi: historia środowiska przyrodniczego i kulturowego. Państwowe Wydawnictwo Naukowe, Warszawa, Poland.
- MARUSZCZAK, H. 1999. Wpływ rolniczego użytkowania ziemi na środowisko przyrodnicze w czasach historycznych. Pp. 189–202 in *Geografia Polski: środowisko przyrodnicze* (L. Starkel, ed.). Państwowe Wydawnictwo Naukowe, Warszawa, Poland.
- MAYLE, B. A. 1990. A biological basis for bat conservation in British woodlands—a review. *Mammal Review* 20:159–195.
- MCCOMB, W. C., AND R. E. NOBLE. 1981. Microclimates of nest boxes and natural cavities in bottomland hardwoods. *Journal of Wildlife Management* 45:284–289.
- MCNAB, B. K. 1982. Evolutionary alternatives in the physiological ecology of bats. Pp. 151–200 in *Ecology of bats* (T. H. Kunz, ed.). Plenum Press, New York.
- MENZEL, M. A., T. C. CARTER, W. M. FORD, B. R. CHAPMAN, AND J. OZIER. 2000. Summer roost trees selection by eastern red seminoles, and evening bats in the upper coast plain of South Carolina. *Proceedings Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 54:304–313.
- MENZEL, M. A., ET AL. 2002. Roost tree selection by northern long-eared bat (*Myotis septentrionalis*) maternity colonies in an industrial forest of the central Appalachian mountains. *Forest Ecology and Management* 155:107–114.
- MILLER, D. A., E. B. ARNETT, AND M. J. LACKI. 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. *Wildlife Society Bulletin* 31:30–44.
- OLSZEWSKI, J. L. 1986. Rola ekosystemów leśnych w modyfikacji klimatu lokalnego Puszczy Białowieskiej. Wydawnictwo PAN (Prace habilitacyjne), Ossolineum, Wrocław, Poland.
- O'SULLIVAN, P. 1994. Bats in Ireland. *Irish Naturalists' Journal* 24, supplement:1–21.
- PARSONS, S., K. J. LEWIS, AND J. M. PSYLLAKIS. 2003. Relationships between roosting habitat of bats and decay of aspen in the sub-boreal forests of British Columbia. *Forest Ecology and Management* 177:559–570.
- PÉNICAUD, P. 2000. Chauves-souris arboricoles en Bretagne (France): typologie de 60 arbres-gîtes at éléments de l'écologie des espèces observées. *Le Rhinolophe* 14:37–68.
- PUGACOWICZ, E. 1997. Ptaki legowe Puszczy Białowieskiej. Północnopodlaskie Towarzystwo Ochrony Ptaków, Białowieża, Poland.
- RACEY, P. A. 1973. Environmental factors affecting the length of gestation in heterothermic bats. *Journal of Reproduction and Fertility* 19, supplement:175–189.
- REIG, S., AND A. L. RUPRECHT. 1989. Skull variability of *Martes martes* and *Martes foina* from Poland. *Acta Theriologica* 34:595–624.
- RIEGER, V. I. 1996. Wie nutzen Wasserfledermäuse, *Myotis daubentonii* (Kuhl, 1817), ihre Tagesquartiere? *Zeitschrift für Säugetierkunde* 61:202–214.
- RUCZYŃSKI, I. 2004. Bats in trees. Pp. 121–128 in *Essays on mammals of Białowieża Forest* (B. Jędrzejewska and J. M. Wójcik, eds.). Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland.
- RUCZYŃSKI, I., AND J. M. GUTOWSKI. 2002. Czy guano nietoperzy użytkujących dziuple może być miejscem rozwoju rzadkich gatunków chrząszczy? *Przegląd Zoologiczny* 46:79–80.
- RUCZYŃSKI, I., AND I. RUCZYŃSKA. 2000. Roosting sites of Leisler's bat *Nyctalus leisleri* in Białowieża Forest—preliminary results. *Myotis* 37 [1999]:55–60.

- RUPRECHT, A. 1984. Rząd: Nietoperze—Chiroptera. Pp. 256–309 in *Klucz do oznaczania ssaków Polski* (Z. Pucek, ed.). Państwowe Wydawnictwo Naukowe, Warszawa, Poland.
- RUSSO, D., L. CISTRONE, G. JONES, AND S. MAZZOLENI. 2004. Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. *Biological Conservation* 117:73–81.
- RYDELL, J., A. ENTWISTLE, AND P. A. RACEY. 1996. Timing of foraging flights of three species of bats in relations to insect activity and predation risk. *Oikos* 76:243–252.
- SACHANOWICZ, K., AND I. RUCZYŃSKI. 2001. Summer roost sites of *Myotis brandtii* (Eversmann, 1845) (Chiroptera, Vespertilionidae) in eastern Poland. *Mammalia* 65:531–535.
- SANO, A. 2000. Postnatal growth and development of thermoregulative ability in the Japanese great horseshoe bat (*Rhinolophus ferrumequinum nippon*), related to maternal care. *Mammal Study* 25:1–15.
- SCHMIDT, A. 1988. Beobachtungen zur Lebensweise des Abendseglers, *Nyctalus noctula* (Schreber, 1774), im Süden des Bezirkes Frankfurt/O. *Nyctalus* 5:389–422.
- SEdgeLEY, J. A. 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38:425–438.
- SEdgeLEY, J. A. 2003. Roost site selection and roosting behaviour in lesser short-tailed bats (*Mystacina tuberculata*) in comparison with long-tailed bats (*Chalinolobus tuberculatus*) in Nothofagus forest, Fiordland. *New Zealand Journal of Zoology* 30:227–241.
- SEdgeLEY, J. A., AND C. F. J. O'DONNELL. 1999a. Factors influencing the selection of roost cavities by a temperate rainforest bat (Vespertilionidae: *Chalinolobus tuberculatus*) in New Zealand. *Journal of Zoology* (London) 249:437–446.
- SEdgeLEY, J. A., AND C. F. J. O'DONNELL. 1999b. Roost selection by long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and implications for the conservation of bats in managed forest. *Biological Conservation* 88:261–276.
- SEdgeLEY, J. A., AND C. F. J. O'DONNELL. 2004. Roost use by long-tailed bats in South Canterbury: examining predictions of roost-site selection in a highly fragmented landscape. *New Zealand Journal of Ecology* 28:1–18.
- SHIEL, C. 1999. *Nyctalus leisleri*. Pp. 134–135 in *Atlas of European mammals* (A. J. Mitchell-Jones et al., eds.). Academic Press, London, United Kingdom.
- SPEAKMAN, J. R. 1991. Why do insectivorous bats in Britain not fly in daylight more frequently? *Functional Ecology* 5:518–524.
- SPEAKMAN, J. R., AND D. W. THOMAS. 2003. Physiological ecology and energetics of bats. Pp. 430–490 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- STATSOFT, INC. 2000. *Statistica for Windows* [computer program manual]. StatSoft, Inc., Tulsa, Oklahoma.
- STRATMANN, B. 1978. Faunistisch-ökologische Beobachtungen an einer Population von *Nyctalus noctula* im Revier Ecktannen des StFB Waren (Müritz). *Nyctalus* 1:2–22.
- STRELKOV, P. P. 2000. Seasonal distribution of migratory bat species (Chiroptera, Vespertilionidae) in eastern Europe and adjacent territories: nursing area. *Myotis* 37[1999]:7–25.
- TIDEMANN, C. R., AND S. C. FLAVEL. 1987. Factors affecting choice of diurnal roost sites by tree-hole bats (Microchiroptera) in south-eastern Australia. *Australian Wildlife Research* 14:459–473.
- TOMIAŁOJCZAK, L., AND T. STAWARCZYK. 2003. Awifauna Polski. Rozmieszczenie, liczebność i zmiany [The avifauna of Poland. Distribution, numbers and trends]. *Pro Natura*, Wrocław, Poland.
- TUTTLE, M. D. 1976. Population ecology of the gray bat (*Myotis grisescens*): philopatry, timing and patterns of movement, weight loss during migrations, and seasonal adaptive strategies. *Occasional Papers, Museum of Natural History, University of Kansas* 54:1–38.
- VAN BALEN, J. H., C. J. H. BOOY, J. A. FRANEKER, AND E. R. OSIECK. 1982. Studies on hole-nesting birds in natural nest sites. Availability and occupation of natural nest sites. *Ardea* 70:1–24.
- VEILLEUX, J. P., J. O. WHITAKER, JR., AND S. L. VEILLEUX. 2004. Reproductive stage influences roost use by tree roosting female eastern pipistrelles, *Pipistrellus subflavus*. *Ecoscience* 11:249–256.
- VONHOF, M. J. 1996. A comparison of roost-site preferences of big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasiurus noctivagans*) in the Pend d'Oreille Valley in southern British Columbia. Pp. 62–80 in *Bats and forest symposium* (R. M. R. Barclay and R. M. Brigham, eds.). British Columbia Ministry of Forest Research Branch, Victoria, British Columbia, Canada.
- VONHOF, M. J., AND R. M. R. BARCLAY. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology* 74:1797–1805.
- WALANKIEWICZ, W. 1991. Do secondary cavity-nesting birds suffer more from competition for cavities or from predation in a primeval deciduous forest? *Natural Areas Journal* 11:203–212.
- WALANKIEWICZ, W. 2002a. Breeding losses in the collared flycatcher *Ficedula albicollis* caused by nest predators in the Białowieża National Park (Poland). *Acta Ornithologica* 37:21–26.
- WALANKIEWICZ, W. 2002b. Nest predation as a limiting factor to the breeding population size of the collared flycatcher *Ficedula albicollis* in the Białowieża National Park (NE Poland). *Acta Ornithologica* 37:91–106.
- WESOŁOWSKI, T. 1989. Nest-sites of hole-nesters in a primeval temperate forest (Białowieża National Park, Poland). *Acta Ornithologica* 25:321–351.
- WESOŁOWSKI, T. 1995. Ecology and behaviour of white woodpecker (*Dendrocopos leucotos*) in a primeval temperate forest (Białowieża National Park, Poland). *Die Vogelwarte* 38:62–75.
- WESOŁOWSKI, T. 1996. Natural nest sites of marsh tit (*Parus palustris*) in a primeval forest (Białowieża National Park, Poland). *Die Vogelwarte* 38:235–249.
- WESOŁOWSKI, T. 2002. Anti-predator adaptations in nesting marsh tits *Parus palustris*: the role of nest-site security. *Ibis* 144:593–601.
- WESOŁOWSKI, T., AND L. TOMIAŁOJCZAK. 1986. The breeding ecology of woodpeckers in a temperate primeval forest—preliminary data. *Acta Ornithologica* 22:1–21.
- WILLIS, C. K. R., K. A. KOLAR, A. L. KARST, M. C. KALCOUNIS-RUEPPELL, AND R. M. BRIGHAM. 2003. Medium- and long-term reuse of trembling aspen cavities as roosts by big brown bats (*Eptesicus fuscus*). *Acta Chiropterologica* 5:85–90.
- ZAHN, A., AND B. HENATSCH. 1998. Bevorzugt *Myotis emarginatus* kühlere Wochenstubenquartiere als *Myotis myotis*? *Zeitschrift für Säugetierkunde* 63:26–31.
- ZALEWSKI, A., W. JĘDRZEJEWSKI, AND B. JĘDRZEJEWSKA. 1995. Pine marten home ranges, numbers and predation on vertebrates in a deciduous forest (Białowieża National Park, Poland). *Annales Zoologici Fennici* 32:131–144.

Submitted 28 December 2004. Accepted 23 March 2005.

Associate Editor was William L. Gannon.