

SUMMER ROOST SELECTION BY TREE-DWELLING BATS *NYCTALUS NOCTULA* AND *N. LEISLERI*: A MULTISCALE ANALYSIS

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Nyctalus noctula is one of the most common bats in the western Palearctic, whereas *N. leisleri* is relatively rare (except in Ireland, where *N. noctula* does not occur) and more limited to ancient forests. We radiotracked 26 *N. noctula* and 25 *N. leisleri* to 52 and 50 roost trees, respectively, from May to August in 1998–2002 in the Białowieża Primeval Forest in eastern Poland to test the hypothesis that *N. leisleri* has more specific tree-roosting requirements than *N. noctula*. Both species selected roosts at the microscale (cavity level), mesoscale (tree level), and megascale (plot level). *N. noctula* significantly preferred oaks, and avoided hornbeams and alders. *N. leisleri* roosted more often in oaks and ashes, and avoided hornbeams and alders. Roost trees occupied by both species were thicker and taller, with higher crowns than available trees. *N. noctula* and *N. leisleri* used oaks more frequently than ashes when average ambient temperatures were lower. Pregnant and lactating females of both species most often used oaks, whereas after the young could fly most roosts were in other tree species, mainly ashes. Reproductive status influenced the choice of roosts used by *N. noctula*, whereas both the reproductive status and ambient temperature were influential for *N. leisleri*. Both taxa preferred dying trees and avoided healthy ones, although *N. noctula* used hollows in healthy trees significantly more often than *N. leisleri*. In our opinion, more frequent use of healthy trees by *N. noctula* suggests a better ability to exploit younger, managed forests. However, differences in roost selection between these species were small.

Key words: Europe, niche segregation, *Nyctalus* species, reproductive status, roost selection, trees

Bats use a variety of daytime roosts, but more than half of the 1,100 bat species are known to roost in trees during at least part of the year (Kunz and Lumsden 2003). Therefore, understanding roost requirements of forest-dwelling bats is critical to understanding their behavior and ecology. Bats frequently select roosts rather than using trees at random (e.g., Kalcounis-Rüppell et al. 2005; Ruczyński and Bogdanowicz 2005; Russo et al. 2004; Sedgely and O'Donnell 1999), and roost selection likely depends upon roost quality (e.g., microclimate) and physical features of its surroundings (e.g., Humphrey et al. 1997; Kerth et al. 2001). Factors such as reproductive status (e.g., Speakman and Thomas 2003) and sociality (Willis and Brigham 2007) also may affect selection of roosts. Roost selection by pregnant and lactating females is consistent with minimizing energetic expenditures and maximizing the growth rate of young (Racey 1973; Racey and

Speakman 1987; Speakman and Thomas 2003). Tree-dwelling bats frequently change roosts, perhaps for physiological needs or to avoid predators. For example, *Myotis bechsteinii* selects colder bat boxes in spring and autumn but prefers warmer boxes in summer (Kerth et al. 2001). Roost switching also may represent a means of obtaining knowledge of alternative roosts (Russo et al. 2005).

Many authors have reported a correlation between animal species diversity and structural diversity of the environment. The diversity of bat communities is correlated with the presence or absence of structures used for roosting (Humphrey 1975). Habitat loss and fragmentation are probably the greatest threats to bat diversity (Hilton-Taylor 2000). However, it remains unclear if changes in forests and landscapes favor some species of tree-roosting bats over others. We propose that the relationship of roost-tree selection by bat species with different probabilities of extinction risk (International Union for the Conservation of Nature and Natural Resources 2007) can be evaluated by comparing closely related taxa (Purvis et al. 2000).

Nyctalus noctula (Schreber, 1774) and *Nyctalus leisleri* (Kuhl, 1817) are relatively closely related species (Salgueiro

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et al. 2007) that are sympatric over much of their ranges. *N. noctula* is 1 of the most common forest-dwelling species in Europe, whereas *N. leisleri* is relatively rare (Bogdanowicz 1999; Bogdanowicz and Ruprecht 2004; Shiel 1999) except in Ireland, where *N. noctula* does not occur (O'Sullivan 1994). *N. leisleri* also is more limited to ancient forests (Bogdanowicz and Ruprecht 2004). In both taxa, pregnant and lactating females usually roost in tree cavities (Gebhard and Bogdanowicz 2004; Strelkov 2000).

In the Białowieża Primeval Forest, Poland, some bird species, for example, swifts *Apus apus*, wrens *Troglodytes troglodytes* (Pugaciewicz 1997), and pied flycatchers *Ficedula hypoleuca* (Czeszczewik and Walankiewicz 2003), select nest sites in hollows that differ by type, placement, and size of tree relative to those used in managed forests. An abundance and diversity of natural cavities as well as numerous predators may influence roost-selection strategies by animals in natural, compared to managed, forests (Czeszczewik 2004; Czeszczewik and Walankiewicz 2003). Extensive human activity over at least 1,000 years in central Europe (e.g., Maruszczak 1999) makes it difficult to assess how or if changes in forests have altered "natural" roosting behavior by bats. Preserved stands in the Białowieża Primeval Forest provide an opportunity to assess such changes.

Based on the niche segregation hypothesis, we predicted that *N. noctula* and *N. leisleri*, although generally similar (Bogdanowicz and Ruprecht 2004; Gebhard and Bogdanowicz 2004), would differ in their choice of preferred roosts (Ruczyński and Bogdanowicz 2005). Differences in roost selection could contribute to niche segregation and facilitate species sympatry. To test this, we studied roost selection by both species in natural, mature stands of the Białowieża Primeval Forest by measuring roost trees used by bats relative to those potentially available, and comparing roost choice between species at the microscale (cavity level), mesoscale (tree level), and megascale (plot level).

MATERIALS AND METHODS

Study area.—The study area (about 100 km²) encompassed both mature stands in Białowieża National Park and sections that are managed but that have old-growth remnants within them (Jędrzejewska and Jędrzejewski 1998). The Białowieża Primeval Forest (= Białowieża Forest) is located on the Polish–Belarus border (approximately 52°43'N, 23°54'E) and covers 1,450 km². It is the largest remnant temperate forest in Europe. The Białowieża Forest thus constitutes a reference site for studies of woodland bat biology. The old-growth stands preserved in Białowieża National Park are formed by multistoried, unevenly aged, mixed tree species (the tallest spruces up to 57 m and several other species reaching 42–45 m); and are characterized by a large amount of dead timber and uprooted trees (Wesolowski and Tomiałojć 1995). These stands are dominated by oak *Quercus robur* (20% of the area), hornbeam *Carpinus betulus* (19%), spruce *Picea abies* (16%), alder *Alnus glutinosa* (12%), pine *Pinus sylvestris* (11%), lime *Tilia cordata* and maple *Acer platanoides* (9%), birch *Betula* spp. and poplar *Populus tremula* (7%), and ash *Fraxinus*

excelsior (6%). In the managed part of the forest, there is a reduced percentage of deciduous trees (oak [11% of the area], hornbeam [2%], and lime and maple [0%]), and a greater proportion of conifers (pine [26%] and spruce [28%])—Jędrzejewska and Jędrzejewski 1998).

The Białowieża Forest is inhabited by a variety of vertebrates that use tree holes as breeding sites including 32 species of birds (Pugaciewicz 1997), probably 11 species of bats (Kurskov 1981; Sachanowicz and Ruczyński 2001), pine martens (*Martes martes*), forest dormice (*Dryomys nitedula*), fat dormice (*Glis glis*), yellow-necked mice (*Apodemus flavicollis*), and red squirrels (*Sciurus vulgaris*)—Jędrzejewska and Jędrzejewski 1998). Tree holes also are used by invertebrates, such as bees, wasps, and beetles.

Capture of bats and location of roost trees.—We located roost sites from May to August from 1998 to 2000 and 2002 (*N. leisleri*), and in 1999–2002 (*N. noctula*). Bats were captured in mist nets (2 × 6 m and 2.5 × 4 m) set across small rivers in the forest and at a pond. Captured bats were classified by species, sex, age (juvenile or adult), and reproductive status. Roost trees were located by tracking bats with radiotransmitters (0.5 g—Biotrack, Wareham, United Kingdom, and Titley Electronics, Ballina, New South Wales, Australia; or 0.7 g—Titley Electronics, and Holohil System, Carp, Ontario, Canada) affixed to the interscapular region with rubber adhesive (Skin-Bond; Smith and Nephew, Largo, Florida). Transmitter mass represented <5% of the body mass of bats (Aldridge and Brigham 1988). Altogether, 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) were tracked using 2-element yagi antennae and receivers (Yupiteru MVT-700; Javiation, Bradford, West Yorkshire, United Kingdom; and Yaesu FT-290R; Vertex Standard, Cypress, California). We counted emerging bats at dusk to determine the number of individuals in each roost. In most cases each species roosted separately. Tagged bats were located daily for the life of transmitters. The average tracking period was 6.5 days for *N. noctula* (range 1–14 days) and 7.5 days for *N. leisleri* (range 2–13 days). Methods conformed to guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Description of roost trees and plots.—We recorded 5 features of each roost tree: tree species, diameter at breast height (DBH), tree height, height of canopy basement, and tree condition. DBH (at 1.3 m) was measured using an aluminum tree caliper. For large trees (>80 cm), DBH was calculated from circumference. Tree and canopy basement heights were measured using a clinometer (Suunto, Helsinki, Finland). Canopy basement height was measured as the height of the 1st branch off the main trunk at least 2 m long that had other branches directly above it. A single branch on a trunk was not considered the canopy basement. We classified trees into 1 of 3 condition classes: healthy—without clear defects, bark covering the whole trunk, all large branches living, and occasional small dead branches and holes present; dying—trees with clear defects, large dead branches, bark lifting from trunk, cavities or

cracks, and bracket fungi; or dead—trees with no living branches. We recorded tree species composition (stems with DBH > 25 cm) and density within a radius of 20 m of each roost tree (39 of those used by *N. noctula* and 44 by *N. leisleri*).

Additionally, to assess selection at the level of the cavity and in the immediate vicinity of the roost tree, 10 features were measured: mean distance to nearest vegetation, diameter at cavity height, height of entrance above the ground, entrance area, inside cross-section area, internal height, internal depth, cavity volume, wall thickness, and safety distance—also called marten distance (i.e., distance from the external part of entrance to the farthest recess inside the cavity) as described in detail by Ruczyński and Bogdanowicz (2005). We also measured the influence of mean daily ambient temperature on the use of roost trees by both species of *Nyctalus*. Temperature data were collected at the meteorological station in Białowieża.

Description and selection of available trees and plots.—To examine whether bats selected particular trees, we compared roost trees with potentially available trees. Available trees were classified as trees with DBH > 25 cm, a threshold based on preferences of cavity-nesting birds in the same study area (Wesolowski 1989, 1995) and because cavities were rare in smaller trees. Because bats were not recorded to use spruce, we did not consider spruce to be available.

To choose potentially available plots we randomly selected 86 points in the area where most of the roosts were found. At 46 of these points (selected using a random number generator in Microsoft Excel [Microsoft Corp., Redmond, Washington]) data also were collected on available trees. The 4 nearest available trees (1 in each quadrant) were located using the point-center method and measured in the same way as roost trees (total $n = 184$ trees). At all random points ($n = 86$) 1 potentially available plot was selected around the nearest available tree and described in the same way as roost plots. Potentially available trees were located <250 m from roost trees so that most were in the same forest stands.

Data analysis.—Characteristics of roost and available trees, as differences among bat species, were compared using either 2-sample *t*-tests when the data were normally distributed or Mann–Whitney *U*-tests when nonnormal. Differences in the occurrence of tree species and tree condition were evaluated using a *G*-test (Sokal and Rohlf 1981). Differences in the incidence of tree species on used versus available plots were assessed using a heterogeneity test (G_H —Sokal and Rohlf 1981). We used logistic regression to assess the importance of cavity parameters in tree selection by bats. The model with the highest overall percentage of correctly classified observations was determined using a stepwise (forward) procedure. In the model only significant variables, as defined by the Wald statistic and its corresponding $P < 0.05$ probability level, were retained. All statistical tests were performed using Statistica (version 6.1; Statsoft Polska Sp. z o. o., Kraków, Poland). In addition, we distinguished the most important qualities for bats from the statistically significant attributes of the trees using Akaike's information criterion model (AIC—Burnham and Anderson 2002). AIC is not a hypothesis test and does not use notions of significance. Instead, AIC focuses on the strength of

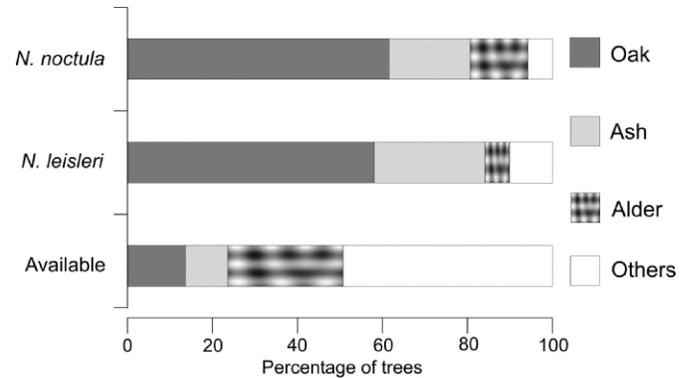


FIG. 1.—Proportion of tree species used as roosts by *Nyctalus noctula* ($n = 52$) and *N. leisleri* ($n = 50$) relative to available trees ($n = 183$ trees).

evidence and gives a measure of uncertainty for each model. The models we computed were ranked by the Akaike's weights calculated as model likelihoods scaled to sum 1. AIC calculations were made using R 2.3.0 (developed by the R Development Core Team, Vienna, Austria).

Roosting preferences of bats in trees of particular species were assessed by calculating Ivlev's electivity index (D —Jacobs 1974):

$$D = \frac{r - p}{r + p - 2pr},$$

where r is the proportion of a given tree species among the trees used by bats, and p is the proportion of a given tree species potentially available. An index value of -1 corresponds to complete avoidance, 0 to no selection, and $+1$ indicates a strong preference.

RESULTS

Characteristics of roost and random trees.—*Nyctalus noctula* most often roosted in oaks, followed by ashes and alders (Fig. 1). These bats occasionally used poplars and limes, but never spruce. Compared to available trees, preference by *N. noctula* for oaks was significant ($G = 26.9$, $df = 1$, $P < 0.001$), as was the avoidance of hornbeams ($G = 19.3$, $df = 1$, $P < 0.001$) and alders ($G = 3.9$, $df = 1$, $P < 0.05$). *N. leisleri* most frequently used oaks and ashes, less often alders, limes, maples, hornbeams, and pine, but never spruce (Fig. 1). Preferences for oaks and ashes were significant ($G = 23.1$, $df = 1$, $P < 0.001$, and $G = 5.6$, $df = 1$, $P < 0.05$, respectively), as was avoidance of alders ($G = 12.6$, $df = 1$, $P < 0.001$) and hornbeams ($G = 14.5$, $df = 1$, $P < 0.001$). Use of other trees by both bat species was not significantly different than chance. We calculated high positive values of Ivlev's index for oaks and ashes, and low values for limes, maples, pine, poplars, alders, and hornbeams (Fig. 2). There were no significant differences in selection of tree species by *N. noctula* and *N. leisleri* ($G_H = 5.6$, $df = 7$, $P = 0.59$).

In general, DBH was significantly correlated with the height of the tree ($r = 0.54$, $n = 280$, $P < 0.001$) and tree height was significantly related to height of the crown ($r = 0.48$, $n = 273$, $P < 0.001$). Roost trees occupied by both species were larger

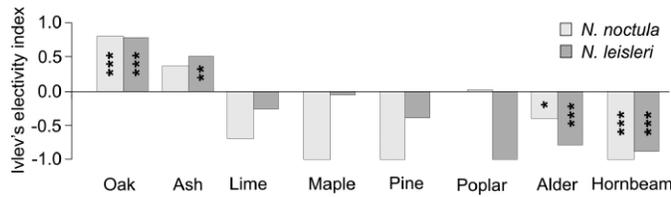


FIG. 2.—Ivlev's electivity index values for different tree species used as roosts by both *Nyctalus* species. Probability levels are: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

than available trees (Table 1). DBH was ≥ 65 cm for trees used as roosts in 96.7% of oaks used by *N. noctula* and 89.7% of those occupied by *N. leisleri*, whereas only 32.0% of oaks in the environment were that large. More than 70% of the ash trees used by *N. noctula* had a DBH ≥ 65 cm and 53.8% of those were used by *N. leisleri*. Only 16.7% of available ashes were large. The preferences for large oaks and ashes were statistically significant for both species with the exception of ashes used by *N. leisleri* (*N. noctula*— $G = 9.1, P < 0.01$ and $G = 4.8, P < 0.05$, respectively, and *N. leisleri*— $G = 11.6, P < 0.001$ and $G = 3.2, P = 0.07$, respectively; in all cases $d.f. = 1$).

Oaks used as roosts by *N. noctula* were significantly taller than random trees, whereas those used by *N. leisleri* did not differ significantly in height. Oaks used by *N. noctula* were about 4 m taller than those occupied by *N. leisleri* (Table 2). There was no difference in the height of ashes used as roosts compared to available trees for either bat species.

The basement canopy height of trees used by *N. noctula* was significantly higher than expected (Table 3). Although there was a trend for trees used by *N. leisleri* to have a higher basement canopy, the difference was not significant ($t = 1.8, d.f. = 223, P = 0.07$).

The majority of roosts were in dying trees (69% for *N. noctula* and 80% for *N. leisleri*), with fewer found in healthy and dead trees (21% and 10%, respectively, for *N. noctula*; and 6% and 14% for *N. leisleri*). Compared to available trees, both species preferred dying trees ($G = 9.0, d.f. = 1, P < 0.01$, and $G = 61.6, d.f. = 1, P < 0.001$, respectively) and avoided healthy ones ($G = 30.5, d.f. = 1, P < 0.001$, and $G = 56.5, d.f. = 1, P < 0.001$,

respectively). *N. noctula* roosted in the hollows of healthy trees more often than did *N. leisleri* ($G = 4.7, d.f. = 1, P < 0.05$). *N. noctula* did not prefer dead trees ($G = 3.0, d.f. = 1, P > 0.05$), whereas *N. leisleri* did ($G = 6.5, d.f. = 1, P < 0.01$).

Of the 5 variables used to describe each roost tree, the most important in the logistic regression modeling in both species were 3 features: tree condition, DBH, and tree height. The optimal model correctly classified 79.6% of trees used by *N. noctula* and 94.5% of the random trees ($\chi^2 = 142.1, d.f. = 3, P < 0.001$), and 73.5% of roost trees occupied by *N. leisleri* and 93.6% of the random trees ($\chi^2 = 143.0, d.f. = 3, P < 0.001$). In both species of *Nyctalus*, the same 3 variables also were chosen by AIC (Table 4).

Habitat surrounding the roost trees of bats.—In all, we recorded 12 tree species in 39 plots around roosts of *N. noctula* (861 trees), in 44 plots around roosts *N. leisleri* (886 trees), and in 86 plots around available trees (1,802 trees). Tree species that were not used, or only rarely used, by the bats as roosts (spruces, hornbeams, and alders) usually dominated in abundance, the exception being ashes. The remaining species (in decreasing order of abundance: limes, oaks, maples, poplars, birches, pines, willows, and elms) represented $< 10\%$ of stems. The composition of tree species on roost plots did not differ significantly from those on random plots (*N. noctula* and *N. leisleri*: $G_H = 6.52, d.f. = 11$, and $G_H = 8.44, d.f. = 11$, respectively; in both cases $P > 0.05$).

The average ($\pm SE$) density of trees on roost versus random plots was not significantly different (*N. noctula*: 17.6 ± 1.10 trunks/0.1 ha; *N. leisleri*: 16.0 ± 0.77 trunks/0.1 ha; and the random plots: 16.7 ± 0.62 trunks/0.1 ha). Nevertheless, densities of oaks on roost plots were significantly higher than random plots for both species (Table 5). The densities of other tree species were similar across plots. In terms of interspecific differences, however, it appears that *N. leisleri* preferred less-cluttered environments, with lower total tree densities than *N. noctula* (Table 5).

Influence of temperature and the reproductive status of bats on the use of roost trees.—*Nyctalus noctula* and *N. leisleri* roosted in oaks more frequently at lower daily ambient temperatures (17.4°C and 18.4°C , respectively) than in ashes

TABLE 1.—Diameter at breast height (cm) of trees used by *Nyctalus noctula* and *N. leisleri* and those potentially available. Probability level: NS not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (Mann–Whitney *U*-test).

Tree species	<i>N. noctula</i>			<i>N. leisleri</i>			Available			U-test		
	$\bar{X} \pm SE$	Range	<i>n</i>	$\bar{X} \pm SE$	Range	<i>n</i>	$\bar{X} \pm SE$	Range	<i>n</i>	<i>N. noctula</i> versus available	<i>N. leisleri</i> versus available	<i>N. noctula</i> versus <i>N. leisleri</i>
Oak	102.4 \pm 5.15	64–180	30	94.4 \pm 5.05	48–158	29	59.6 \pm 5.52	26–126	25	4.56***	4.06***	NS
Ash	69.5 \pm 4.48	55–112	10	69.8 \pm 6.20	38–109	13	48.3 \pm 3.79	26–87	18	3.19**	2.48*	NS
Alder	43.5 \pm 4.18	34–60	6	71.5 \pm 8.05	63–80	2	41.1 \pm 1.99	25–77	49	—	—	—
Poplar	57	52–62	2	—	—	—	36.3 \pm 2.04	31–43	7	—	—	—
Lime	120	—	1	66	50–82	2	39.9 \pm 4.48	25–99	18	—	—	—
Hornbeam	—	—	—	57	—	1	38.0 \pm 1.27	25–59	46	—	—	—
Maple	—	—	—	67	—	1	34.5 \pm 3.07	27–42	4	—	—	—
Pine	—	—	—	76	—	1	46.4 \pm 4.41	30–65	8	—	—	—
Birch	—	—	—	—	—	—	36.33 \pm 4.08	28–51	6	—	—	—
Elm	—	—	—	—	—	—	36.5	31–42	2	—	—	—
Total	87.0 \pm 4.60	34–180	49	84.1 \pm 3.86	38–158	49	43.1 \pm 1.26	25–126	183	8.72***	8.99***	NS

TABLE 2.—Heights of trees containing roosts used by *Nyctalus noctula* and *N. leisleri* and those potentially available. Probability level: NS not significant ($P > 0.05$); ** $P < 0.01$; *** $P < 0.001$ (t -test).

Tree species	<i>N. noctula</i>			<i>N. leisleri</i>			Available			<i>t</i> -test		
	$\bar{X} \pm SE$	Range	<i>n</i>	$\bar{X} \pm SE$	Range	<i>n</i>	$\bar{X} \pm SE$	Range	<i>n</i>	<i>N. noctula</i> versus available	<i>N. leisleri</i> versus available	<i>N. noctula</i> versus <i>N. leisleri</i>
Oak	34.5 ± 0.95	18–44	30	30.3 ± 1.11	15–42	29	30.6 ± 0.72	11–40	25	3.16***	NS	2.90**
Ash	32.5 ± 1.38	28–42	10	33.1 ± 1.18	26–40	13	30.7 ± 1.67	10–40	18	NS	NS	NS
Alder	27.2 ± 2.29	18.5–34.5	6	33.0 ± 3.00	30–36	2	28.2 ± 0.76	13–36	49	NS	—	—
Poplar	34.5	34–35	2	—	—	—	29.4 ± 0.61	27–32	7	—	—	—
Lime	33	—	1	30.5	23–38	2	25.3 ± 1.45	12–34	17	—	—	—
Hornbeam	—	—	—	28	—	1	22.3 ± 0.70	13–36	46	—	—	—
Maple	—	—	—	24.5	—	1	24.5 ± 2.33	20–31	4	—	—	—
Pine	—	—	—	30	—	1	30.0 ± 2.10	22–38	8	—	—	—
Birch	—	—	—	—	—	—	26.5 ± 1.91	17–29	6	—	—	—
Elm	—	—	—	—	—	—	31.5	27–36	2	—	—	—
Total	33.0 ± 0.78	18–44	49	31.0 ± 0.79	15–42	49	27.0 ± 0.44	10–40	182	6.38***	4.13***	NS

(20.3°C and 19.9°C, respectively; $t = 3.84$, $df. = 131$, $P < 0.001$ and $t = 2.49$, $df. = 147$, $P < 0.05$, respectively). *N. noctula* used oaks most frequently at 14–16°C and ashes at 22–24°C; for *N. leisleri* oaks were used most at 16–18°C and ashes at 20–22°C (Fig. 3).

Pregnant and lactating bats spent the most days in oaks, whereas other tree species were used more often after young could fly (Fig. 4). Differences in the number of days spent in oaks and ashes during the periods before (including pregnancy) and after young are able to fly were significant for both *N. noctula* ($\chi^2 = 30.58$, $df. = 1$, $P < 0.001$) and *N. leisleri* ($\chi^2 = 6.68$, $df. = 1$, $P < 0.01$).

We used a logistic regression model to assess the influence of ambient temperature and initiation of flight by young on selection of oaks and ashes as roosts. All days when the temperature reached >20°C were considered “warm” and those with lower temperatures were assigned to the “cool” category. The complete model for *N. noctula* was composed of the variables “ambient temperature” and “ability of young to fly” and correctly classified 92.7% of oaks and 47.8% of ashes ($\chi^2 = 31.9$, $df. = 2$, $P < 0.001$). The optimal model for *N. noctula* did not contain the variable “ambient temperature” and correctly classified 86.5% of oaks and 69.7% of ashes ($\chi^2 =$

28.8, $df. = 1$, $P < 0.001$). The complete model for *N. leisleri* correctly classified 89.3% of oaks and 34.8% of ashes ($\chi^2 = 15.9$, $df. = 2$, $P < 0.001$). Removal of either temperature or reproductive status significantly reduced model quality.

Microhabitat characteristics.—We used logistic analysis to assess the variables that best described the hollows used by *N. leisleri* in oaks ($n = 23$) and ashes ($n = 10$). Diameter of trunk at the level of the hollow was the most important of the 10 features measured at the cavity scale ($\chi^2 = 3.82$, $df. = 2$, $P = 0.051$). This factor correctly classified 87.0% of oaks and 33.3% of ashes as roosts. Oaks were slightly larger at the height of the hollow compared to ashes (mean ± SE, 49.3 ± 3.6 cm and 38.1 ± 5.0 cm, respectively; $Z = 2.05$, $P < 0.05$). The remaining features did not differ significantly. This analysis was not carried out for *N. noctula*, because of the small number of hollows in ashes ($n = 5$). However, average diameter of the trunk at the hollow for *N. noctula* was larger in oaks than in ashes (58.4 ± 5.7 cm versus 39.8 ± 2.6 cm).

DISCUSSION

We predicted that *N. noctula* and *N. leisleri* would differ in their choice of preferred roosts, based on the niche segregation

TABLE 3.—Canopy basement height (m) of roost trees used by both *Nyctalus* species compared with those potentially available. Probability level: NS not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (t -test).

Tree species	<i>N. noctula</i>			<i>N. leisleri</i>			Available			<i>t</i> -test		
	$\bar{X} \pm SE$	Range	<i>n</i>	$\bar{X} \pm SE$	Range	<i>n</i>	$\bar{X} \pm SE$	Range	<i>n</i>	<i>N. noctula</i> versus available	<i>N. leisleri</i> versus available	<i>N. noctula</i> versus <i>N. leisleri</i>
Oak	14.1 ± 0.68	4.5–19	30	12.7 ± 0.72	6–22	28	11.4 ± 0.62	4.5–18	24	2.81**	NS	NS
Ash	14.5 ± 0.93	9–18	10	12.2 ± 1.00	3–16	13	15.1 ± 0.92	9–23	17	NS	NS	NS
Alder	17.8 ± 2.35	10–25	6	21.0 ± 3.00	18–24	2	15.1 ± 0.62	6–25	47	NS	—	—
Poplar	12.5	4–21	2	—	—	—	18.9 ± 1.08	15–22	7	—	—	—
Lime	18	—	1	11.7	11.5–12	2	8.7 ± 1.29	1–18	18	—	—	—
Hornbeam	—	—	—	2.5	—	1	3.9 ± 0.30	1–8	46	—	—	—
Maple	—	—	—	15	—	1	9.7 ± 0.85	8–12	4	—	—	—
Pine	—	—	—	18.0	—	1	22.2 ± 3.50	7–30	6	—	—	—
Birch	—	—	—	—	—	—	13.8 ± 3.13	3–20	6	—	—	—
Elm	—	—	—	—	—	—	6.0	5–7	2	—	—	—
Total	14.6 ± 0.61	4–25	49	12.6 ± 0.63	2.5–24	48	11.2 ± 0.49	0.5–30	177	3.51***	NS	2.29*

TABLE 4.—The 3 best candidate models based on the Akaike information criterion (AIC) differentiating trees selected as roosts by *Nyctalus noctula* and *N. leisleri*, and ranked according to their ΔAIC_c value. Each candidate model was a different combination of 5 variables (tree species, diameter at breast height [DBH], tree height, tree condition, and height of canopy basement) measured for roost and random trees. AIC_c = AIC score corrected for a small sample size. ΔAIC_c = the difference in AIC_c scores between different candidate models, with the best model given a value of 0. w_i = AIC weight, which is the probability that the model is the true model given the entire set of candidate models. Evidence ratio = the ratio of w_i of the “best” model and competing models, for example, the evidence ratio of 1.7 indicates that model *i* (when $w_i > w_j$) is 1.7 times more likely than model *j* to be the best, given the entire set of candidate models and the data used.

Model (rank)	Model variables	No. parameters (K)	ΔAIC_c	w_i	Evidence ratio
<i>N. noctula</i>					
1	DBH, tree height, tree condition	4	0.00	0.462	1.0
2	DBH, tree height, tree condition, height of canopy basement	5	1.045	0.274	1.7
3	DBH, tree height, tree condition, DBH–tree height interaction	5	2.036	0.167	2.8
<i>N. leisleri</i>					
1	DBH, tree height, tree condition, DBH–tree height interaction	5	0.00	0.336	1.0
2	DBH, tree height, tree condition	4	0.11	0.319	1.1
3	DBH, tree height, tree condition, height of canopy basement, DBH–tree height interaction	6	1.50	0.159	2.1

hypothesis. However, our data illustrated striking similarities in roosts used by the 2 species, which did not support the prediction of niche theory as it applies to bats, at least at the scales we studied (cf. Ruczyński and Bogdanowicz 2005). Although there were some differences between the 2 species, the differences were small, leading to the conclusion that similar trees fulfill the roosting requirements of both *N. noctula* and *N. leisleri* in habitats rich in tree cavities.

Roost cavities used by bats and those potentially available.—Both species commonly roosted in oaks and ashes, and at a greater frequency than expected based on the availability of these tree species in the study area. Hornbeams were the most common trees (Wesołowski 1989, 1995) in the forest, but they were rarely used as roosts. In contrast, cavity-nesting birds in Białowieża frequently inhabited hornbeams (Wesołowski 1989, 1995). Both *N. noctula* and *N. leisleri* use a variety of trees as roosts throughout their range (Bogdanowicz and Ruprecht 2004; Gebhard and Bogdanowicz 2004), but they are not selected randomly.

In Białowieża, both species of *Nyctalus* occupied larger, older trees than did hollow-dwelling birds. Thicker trunks offer more insulation against extreme temperatures than do small ones (e.g., Gellman and Zielinski 1996). These trees also were taller than random trees, as has been found for roost selection by other species of bats (Bernardos et al. 2004; Kalcounis-Rüppell et al. 2005; Kunz and Lumsden 2003; Russo et al. 2004). However, the oaks used by *N. noctula* were on average 4 m taller than those occupied by *N. leisleri*. Cavities in taller trees are more likely to have entrances higher above the ground in well-insulated parts of the tree, thus enabling easy access and reducing the risk of predation (Betts 1998).

Both species of *Nyctalus* in Białowieża preferred dying trees, similar to other bats in Europe (Boonman 2000; Russo et al. 2004), North America (Kunz and Lumsden 2003; Menzel et al. 2000; Vohnhof and Barclay 1996), and Australia (Campbell et al. 2005; but see Lumsden et al. 2002). However, species- or season-specific differences in selection of roost trees exist and likely vary geographically (Kunz and Lumsden

TABLE 5.—Tree densities per 0.1 hectare on plots with roosts used by *Nyctalus noctula* (39 plots) and *N. leisleri* (44 plots) compared with the pool of those potentially available (86 plots). Probability level: NS not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$ (Mann–Whitney *U*-test).

Tree species	<i>N. noctula</i>		<i>N. leisleri</i>		Available		<i>U</i> -test		
	$\bar{X} \pm SE$	Range	$\bar{X} \pm SE$	Range	$\bar{X} \pm SE$	Range	<i>N. noctula</i> versus available	<i>N. leisleri</i> versus available	<i>N. noctula</i> versus <i>N. leisleri</i>
Oak	1.3 ± 0.20	0–5	1.3 ± 0.23	0–7	1.0 ± 0.20	0–10	2.76**	2.55*	NS
Ash	1.7 ± 0.48	0–13	2.4 ± 0.48	0–12	1.3 ± 0.22	0–10	NS	NS	NS
Alder	3.7 ± 1.07	0–29	2.4 ± 0.57	0–13	3.8 ± 0.62	0–26	NS	NS	NS
Hornbeam	3.5 ± 0.52	0–10	3.3 ± 0.49	0–14	2.6 ± 0.36	0–16	NS	NS	NS
Lime	1.8 ± 0.46	0–13	1.2 ± 0.35	0–11	1.0 ± 0.27	0–17	NS	NS	NS
Maple	0.4 ± 0.14	0–4	0.5 ± 0.12	0–3	0.3 ± 0.06	0–2	NS	NS	NS
Poplar	0.8 ± 0.38	0–10	0.1 ± 0.08	0–3	0.4 ± 0.19	0–14	NS	NS	NS
Birch	0.5 ± 0.23	0–8	0.3 ± 0.10	0–3	0.6 ± 0.22	0–13	NS	NS	NS
Willow	—	—	—	—	0.0 ± 0.01	0–1	NS	NS	NS
Elm	0.0 ± 0.02	0–1	—	—	0.1 ± 0.05	0–4	NS	NS	NS
Spruce	3.9 ± 0.40	0–10	4.5 ± 0.54	0–14	4.9 ± 0.42	0–18	NS	NS	NS
Pine	0.0 ± 0.02	0–0.8	0.1 ± 0.09	0–4	0.7 ± 0.34	0–24	NS	NS	NS
Total	17.6 ± 1.10	0–29	16.0 ± 0.77	0–14	16.7 ± 0.62	0–26	NS	NS	2.16*

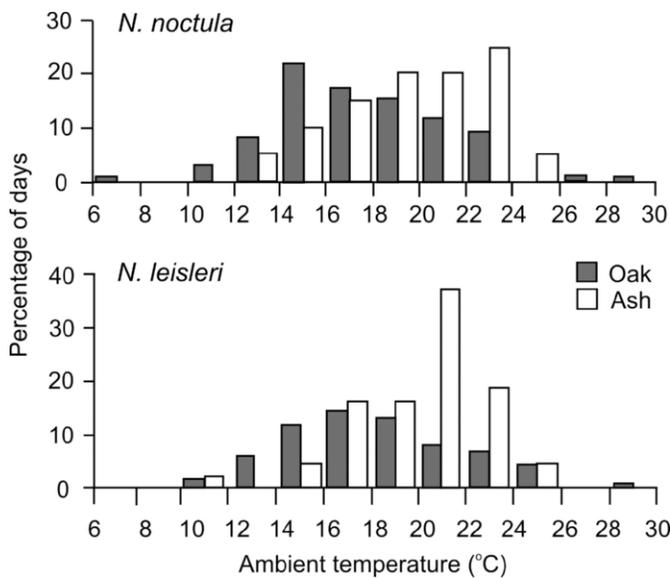


FIG. 3.—Preferences for oaks and ashes (in %) by *Nyctalus noctula* and *N. leisleri* relative to average ambient temperature on the day before the bat using the tree.

2003). For example, in Missouri, *Nycticeius humeralis* selected trees in late stages of decay during the summer, but preferred live trees in winter (Boyles and Robbins 2006). Maternity roosts of *Myotis sodalis* were typically in trees that were less cluttered and more decayed than those used by *M. septentrionalis* (Carter and Feldhamer 2005). Dead or dying trees may have more hollows suitable for bat roosts (Alatalo et al. 1988; Bennett et al. 1994; Campbell et al. 2005) although dead trees are generally less insulated than live ones because of a lack of bark and a lower water content (Maeda 1974). In Białowieża, *N. noctula* roosted in healthy trees more often than *N. leisleri*, perhaps making it less vulnerable to forestry operations directed at snags. We suggest that the more frequent use of healthy trees by *N. noctula* may enable them to exploit younger, managed forests.

Habitat surrounding the roost trees of bats.—In addition to selecting particular roost trees, bats also can select particular areas of the forest in which to roost. In general, trees used by cavity-dwelling bats tend to be located in stands with open canopy and high snag density (Kalcounis-Rüppell et al. 2005). We found that the density of oaks on occupied plots was higher than on random plots. In Arizona, forest patches immediately surrounding the roost trees of *Myotis auriculus* contained a higher density of large oaks than around randomly selected trees (Bernardos et al. 2004). High availability of potential roosts (i.e., abundant large trees and snags) in natural forests of eastern North America allows *N. humeralis* to select day-roosts with favorable landscape characteristics (i.e., closer to water and foraging sites), possibly providing benefits from reduced commuting costs (Barclay and Kurta 2007; Miles et al. 2006). Roost trees of *M. septentrionalis*, *Myotis thysanodes*, *M. volans*, and *Eptesicus fuscus* in South Dakota consistently occurred in areas with relatively high snag densities (Cryan et al. 2001). Likewise, the average density of trees on plots

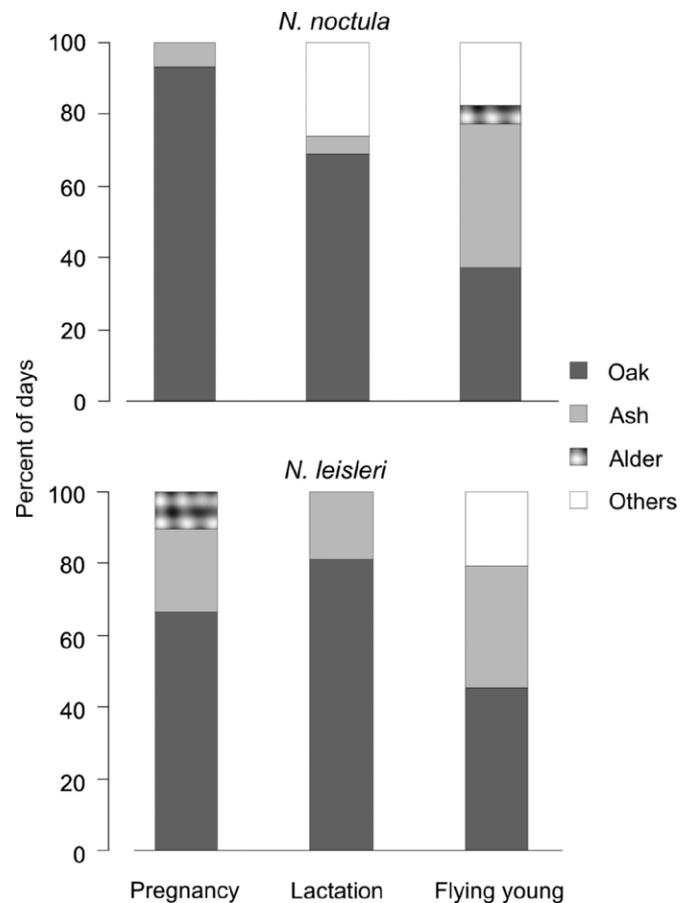


FIG. 4.—Percentage of days spent in oaks, ashes, alders, and other tree species by *Nyctalus noctula* and *N. leisleri* during pregnancy ($n = 63$ days and 54 days, respectively), lactation ($n = 64$ days and 71 days, respectively), and after the young 1st fly ($n = 36$ days and 47 days, respectively).

used by *N. noctula* was higher compared to plots used by *N. leisleri*. The significance of this is unclear. Both species may roost together (Gebhard and Bogdanowicz 2004) and it does not appear that individual *N. noctula* exclude *N. leisleri* from “better” roost sites and areas. Long-term, experimentally designed studies, including a wider diversity of forest types and management regimes, are needed to assess the importance of habitats (Miller et al. 2003).

Influence of temperature and reproductive status of bats on the use of roost trees.—Selection of trees as roosts by both species of *Nyctalus* was influenced by ambient temperature and reproductive status of the bats. Reproductive status had the most influence on the choice of tree roosts by *N. noctula*, whereas ambient temperature also was significant for *N. leisleri*. Differences between the 2 species in this respect may result from differences in hollow structure preferences (see also Ruczyński and Bogdanowicz 2005), or different thermal or physiological requirements (e.g., Baker and Lacki 2006).

The diameter of the trunk or limbs at the level of the hollow used by *Nyctalus* was greater in oaks compared to ashes. Size of a hollow ostensibly contributes to stabilization of thermal conditions in roosts (Derby and Gates 1966). Thermal

insulation of roosts could be especially important when ambient temperatures are low (Ruczyński 2006). On warmer days, bats may take advantage of the faster warming of small-diameter trunks at the height of the hollow (like those in the ashes). Lower temperatures at night would occur when bats were active, and so it would not significantly affect the energy budget of adults. Thermal stability may be important when dependent young that cannot regulate their body temperature are left in the roosts at night (McNab 1982; Sano 2000). However, after the juveniles become independent, it may be advantageous to select roost sites with different characteristics than during the period of pregnancy and lactation. We cannot exclude the possibility that independent juveniles (which were more frequently tracked than adults in that period) select hollows that are less thermally stable and use torpor and passive rewarming to save energy (Lausen and Barclay 2003; Ruczyński 2006). In fact, for *E. fuscus* occupying rock crevices, the microclimates of roosts mirrored the use of torpor during the reproductive period; roosts used during lactation were more thermally stable and remained warmer at night compared to the shallow roosts used by pregnant and postlactating females (Lausen and Barclay 2003). In Białowieża, pregnant and lactating female *Nyctalus* roosted more often in oaks than in ashes. The increase in ambient temperature and onset of flight in young coincided with more frequent use of ashes as roosts. In Bavaria, *M. bechsteinii* roosted in hollow trees in May and September, but used bat boxes during pregnancy and lactation, coinciding with higher roost temperatures (Kerth et al. 2001). On the other hand, Willis and Brigham (2007) provided evidence for the importance of sociality and social thermoregulation for forest-roosting bats. Willis and Brigham (2007) found a significant positive correlation between the number of reproductive female *E. fuscus* occupying a roost, maximum daily roost temperature, and energy savings.

Microhabitat characteristics.—The probability of a tree having a hollow is positively associated with DBH (Harper et al. 2005). Diameter at hollow height was the only 1 of 10 variables that differentiated the roosts in oaks and ashes used by *N. leisleri*. Selection of the largest available trees as roost sites is similar to behavior of bats in modified forested habitats (e.g., Sedgely and O'Donnell 2004). Vonhof and Barclay (1996) noted larger trunk diameters at the cavity level in North America, and Kaňuch (2005) reported that *N. noctula* preferred trees with a greater trunk diameter than either *Myotis nattereri* or *M. daubentonii* in Slovakia.

In summary, our study underlines the importance of particular types of roost trees at the micro-, meso-, and megascales, and is the 1st to use a multiscale approach to assess roost selection by 2 species of *Nyctalus* occurring in an area of sympatry. We found that selection of roost trees was influenced by ambient temperature and reproductive status, but despite general similarities in roost structures, the 2 species used different roosting strategies. One of the most striking differences in roost use between *N. noctula* and *N. leisleri* was tree condition (although there was still considerable overlap): both species preferred dying trees, but *N. noctula* roosted in healthy trees more often than did *N. leisleri*. Because tree roosts in

Białowieża Forest are likely selected by both species of *Nyctalus* as shelter from predation and climate (Ruczyński and Bogdanowicz 2005), the ability of *N. noctula* to exploit healthy trees may have important consequences for the ability to exploit younger forests. Such differences in the roosting behaviors of forest-dwelling bats may have important implications for species biogeography and differential risk of extinction.

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LITERATURE CITED

- ALATALO, R., A. CARLSON, AND A. LUNDBERG. 1988. Nest cavity size and clutch size of pied flycatchers *Ficedula hypoleuca* breeding in natural tree-holes. *Ornis Scandinavica* 19:317–319.
- ALDRIDGE, H. D. J. N., AND R. M. BRIGHAM. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* 69:379–382.
- BAKER, M. D., AND M. J. LACKI. 2006. Day-roosting habitat of female long-legged myotis in ponderosa pine forests. *Journal of Wildlife Management* 70:207–215.
- BARCLAY, R. M. R., AND A. KURTA. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17–59 in *Bats in forests: conservation and management* (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- BENNETT, A. F., L. F. LUMSDEN, AND A. O. NICHOLLS. 1994. Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia. *Pacific Conservation Biology* 1:222–235.
- 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.
- BETTS, B. J. 1998. Roosts used by maternity colonies of silver-haired bats in northeastern Oregon. *Journal of Mammalogy* 79:643–650.
- BOGDANOWICZ, W. 1999. *Nyctalus noctula*. Pp. 136–137 in *The 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. Fledertiere II* (J. Niethammer and F. Krapp, eds.). 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.
- BOYLES, J. G., AND L. W. ROBBINS. 2006. Characteristics of summer and winter roost trees used by evening bats (*Nycticeius humeralis*) in southwestern Missouri. *American Midland Naturalist* 155:210–220.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Springer, New York.
- CAMPBELL, S., L. F. LUMSDEN, R. KIRKWOOD, AND G. COULSON. 2005. Day roost selection by female little forest bats (*Vespadelus vulturnus*) within remnant woodland on Phillip Island, Victoria. *Wildlife Research* 32:183–191.
- CARTER, T. C., AND G. A. FELDHAMER. 2005. Roost tree use by maternity colonies of Indiana bats and northern long-eared bats in southern Illinois. *Forest Ecology and Management* 219:259–268.
- CRYAN, P. M., M. A. BOGAN, AND G. M. YANEGA. 2001. Roosting habits of four bat species in the Black Hills of South Dakota. *Acta Chiropterologica* 3:43–52.
- CZESZCZEWSKI, 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* 39:47–52.
- CZESZCZEWSKI, D., AND W. WALANKIEWICZ. 2003. Natural nest sites of the pied flycatcher in a primeval forest. *Ardea* 91:221–230.
- DERBY, R. W., AND D. M. GATES. 1966. The temperature of tree trunks—calculated and observed. *American Journal of Botany* 53:580–587.
- GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 88:809–823.
- GEHARD, J., AND W. BOGDANOWICZ. 2004. *Nyctalus noctula*—Großer Abendsegler. Pp. 607–694 in *Handbuch der Säugetiere Europas. Fledertiere II* (J. Niethammer and F. Krapp, eds.). Aula-Verlag, Wiebelsheim, Germany.
- GELLMAN, S. T., AND W. J. ZIELINSKI. 1996. Use by bats of old-growth redwood hollows on the north coast of California. *Journal of Mammalogy* 77:255–265.
- HARPER, M. J., M. A. MCCARTHY, AND R. VAN DER REE. 2005. The abundance of hollow-bearing trees in urban dry sclerophyll forest and the effect of wind on hollow development. *Biological Conservation* 122:181–192.
- HILTON-TAYLOR, C. 2000. IUCN Red list of threatened species. IUCN, Gland, Switzerland.
- HUMPHREY, S. R. 1975. Nursery roosts and community diversity of nearctic bats. *Journal of Mammalogy* 56:321–346.
- HUMPHREY, S. R., A. R. RICHTER, AND J. B. COPE. 1997. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. *Journal of Mammalogy* 58:334–346.
- INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE AND NATURAL RESOURCES. 2007. 2007 IUCN Red list of threatened species. www.iucnredlist.org. Accessed 2 December 2007.
- JACOBS, J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. *Oecologia* (Berlin) 14:413–417.
- JĘDRZEJEWSKA, B., AND W. JĘDRZEJEWSKI. 1998. Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Springer-Verlag, Berlin, Germany.
- KALCOUNIS-RÜPPELL, M. C., J. M. PSYLLAKIS, AND R. M. BRIGHAM. 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. *Wildlife Society Bulletin* 33:1123–1132.
- KAŃUCH, P. 2005. Roosting and population ecology of three syntopic tree-dwelling bat species (*Myotis nattereri*, *M. daubentonii* and *Nyctalus noctula*). *Biologia* (Bratislava) 60:579–587.
- KERTH, G., K. WEISSMANN, AND B. KÖNIG. 2001. Day roost selection in female Bechstein's bats (*Myotis bechsteini*): a field experiment to determine the influence of roost temperature. *Oecologia* 126:1–9.
- 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. 1981. *Rukokrylye Belorussii*. Nauka i Tekhnika, Minsk, Belarus.
- LAUSEN, C. L., AND R. M. R. BARCLAY. 2003. Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. *Journal of Zoology* (London) 260:235–244.
- 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.
- MAEDA, K. 1974. Éco-éthologie de la grande noctule, *Nyctalus lasiopterus*, à Sapporo, Japon. *Mammalia* 38:461–487.
- MARUSZCZAK, H. 1999. Wpływ rolniczego użytkowania ziemi na środowisko przyrodnicze w czasach historycznych. Pp. 189–202 in *Geografia Polski: środowisko przyrodnicze* (L. Starkel, ed.). PWN, Warszawa, Poland.
- MENZEL, M. A., T. C. CARTER, W. M. FORD, B. R. CHAPMAN, AND J. OZIER. 2000. Summer roost tree selection by eastern red, Seminole, and evening bats in the Upper Coastal Plain of South Carolina. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 54:304–313.
- MILES, A. C., S. B. CASTLEBERRY, D. A. MILLER, AND L. M. CONNER. 2006. Multi-scale roost-site selection by evening bats on pine-dominated landscapes in southwest Georgia. *Journal of Wildlife Management* 70:1191–1199.
- 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.
- O'SULLIVAN, P. 1994. Bats in Ireland. *Irish Naturalists' Journal* 24, supplement:1–21.
- PUGACEWICZ, E. 1997. *Ptaki lęgowe Puszczy Białowieskiej*. Północnopodlaskie Towarzystwo Ochrony Ptaków, Białowieża, Poland.
- PURVIS, A., A. PAUL-MICHAEL, J. L. GITTLEMAN, AND G. M. MACE. 2000. Nonrandom extinction and loss of evolutionary history. *Science* 288:328–330.
- RACEY, P. A. 1973. Environmental factors affecting the length of gestation in heterothermic bats. *Journal of Reproduction and Fertility*, Supplement 19:175–189.
- RACEY, P. A., AND J. R. SPEAKMAN. 1987. The energy costs of pregnancy and lactation in heterothermic bats. In *Reproductive energetics in mammals* (A. S. I. Loudon and P. A. Racey, eds.). *Symposia of the Zoological Society of London* 57:107–125.
- RUCZYŃSKI, I. 2006. Influence of temperature on maternity roost selection by noctule bats (*Nyctalus noctula*) and Leisler's bats (*N. leisleri*) in Białowieża Primeval Forest, Poland. *Canadian Journal of Zoology* 84:900–907.
- RUCZYŃSKI, I., AND W. BOGDANOWICZ. 2005. Roost cavity selection by *Nyctalus noctula* and *N. leisleri* (Vespertilionidae, Chiroptera) in

- Białowieża Primeval Forest, eastern Poland. *Journal of Mammalogy* 86:921–930.
- RUSO, D., L. CISTRONE, AND G. JONES. 2005. Spatial and temporal patterns of roost use by tree-dwelling barbastelle bats *Barbastella barbastellus*. *Ecography* 28:769–776.
- RUSO, 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.
- SACHANOWICZ, K., AND I. RUCZYŃSKI. 2001. Summer roost sites of *Myotis brandtii* (Eversmann, 1845) (Chiroptera, Vespertilionidae) in eastern Poland. *Mammalia* 65:531–535.
- SALGUEIRO, P., M. RUEDI, M. M. COEHLO, AND J. M. PALEMEIRIM. 2007. Genetic divergence and phylogeography in the genus *Nyctalus* (Mammalia: Chiroptera): implications for population history of the insular bat *Nyctalus azoreum*. *Genetica* 130:169–181.
- 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.
- SEDGELEY, J. A., AND C. F. J. O'DONNELL. 1999. Roost selection by long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and implications for the conservation of bats in managed forests. *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 *The atlas of European mammals* (A. J. Mitchell-Jones, et al., eds.). Academic Press, London, United Kingdom.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman and Co., New York.
- SPEAKMAN, J. R., AND D. W. THOMAS. 2003. Physiological ecology and energetics of bats. Pp. 430–492 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- 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.
- 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.
- 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). *Vogelwarte* 38:62–75.
- WESOŁOWSKI, T., AND L. TOMIAŁOJC. 1995. Bird studies in the Białowieża Forest—an overview. *Ornitologische Beobachtungen* 92:111–146.
- WILLIS, C. K. R., AND R. M. BRIGHAM. 2007. Social thermoregulation, not cavity microclimate, explain forest roost preferences in a cavity-dwelling bat. *Behavioral Ecology and Sociobiology* 62:97–108.

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