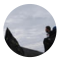
Ciechanowski, M., Zapart, A., Kokurewicz, T., Rusiński, M., M. Lazarus. 2017. Habitat selection of the pond bat Myotis dasycneme during pregnancy and lactation in Northern Poland....

Article *in* Journal of Mammalogy · February 2017

DOI: 10.1093/jmammal/gyw108



Mateusz Ciechanowski
University of Gdansk

Aneta Zapart
University of Gdansk

Tomasz Kokurewicz
Wrocław University of Environmental and Life Sciences

Marcin Rusiński
Independent Researcher

Journal of Mammalogy, 98(1):232–245, 2017
DOI:10.1093/jmammal/gyw108

Habitat selection of the pond bat (*Myotis dasycneme*) during pregnancy and lactation in northern Poland

Mateusz Ciechanowski,* Aneta Zapart, Tomasz Kokurewicz, Marcin Rusiński, and Magdalena Lazarus

Department of Vertebrate Ecology and Zoology, Faculty of Biology, University of Gdańsk, Wita Stwosza Str. 59, 80-308 Gdańsk, Poland (MC, AZ)
Wrocław University of Environmental and Life Sciences, Institute of Biology, Department of Vertebrate Ecology and Paleontology, Kożuchowska Str. 5b, 51-631 Wrocław, Poland (TK)
ANSEE Consulting, Św. Antoniego Str. 2/4, 50-073 Wrocław, Poland (MR)
Department of Plant Taxonomy and Nature Conservation, Faculty of Biology, University of Gdańsk, Wita Stwosza Str. 59, 80-308 Gdańsk, Poland (ML)

** Correspondent: matciech@kki.net.pl*

Spatial behavior and habitat use of breeding mammalian females often change after parturition, reflecting not only the sharp increase in energy demands associated with lactation, but sometimes also limitations of a central place, if they return regularly to feed their altricial young. We conducted the 1st radiotracking study of habitat preferences of the pond bat (*Myotis dasycneme*), a threatened habitat specialist, comparing movements of breeding females during pregnancy and lactation in a lakeland zone of Poland. Pond bats are known to forage almost exclusively over water bodies. We predicted that 1) females commute shorter distances during lactation than during pregnancy, as they need to return to the colony during night to feed their young, and 2) pond bats select eutrophic lakes due to greater abundance of aquatic insects. The 1st prediction was confirmed, as pregnant females covered significantly longer distances between roosts and foraging sites (median 11.4 km) than lactating females (median 2.9 km). During pregnancy, bats foraged mostly over lakes and only rarely over rivers, using both habitats as available, but carp fishponds were selected. Lactating females selected rivers and canals but avoided lakes. The 2nd prediction was confirmed only in spring. Pregnant females selected eutrophic and avoided mesotrophic lakes, whereas during lactation, mesotrophic lakes were selected and eutrophic ones were avoided. This could explain the switch from chironomids, of smaller body size and found in eutrophic waters, to larger caddisflies, found in fast-flowing rivers, observed the diet of pond bats in a previous study. Lactating females may maximize their energy gain by shifting to large insects, thus obtaining larger portions of energy by a single capture effort. This study exposes the importance of small, relatively fast-flowing rivers in an energetically crucial period of the year for a species that has been perceived as associated with larger water bodies.

Key words: breeding, Chiroptera, foraging ecology, *Myotis dasycneme*, pond bat, roosting, threatened species

Energy demands in mammals vary strongly with reproductive status. Breeding individuals expend more energy than nonbreeding ones, resulting in higher food consumption (Perez and Mooney 1986) but also higher loss of body mass, associated with faster lipid catabolism (Hildebrand et al. 2000). That brings significant ecological consequences—pregnant and lactating females may reveal stronger preference for optimal habitats (i.e., more productive or with better connectivity) than males (Safi et al. 2007; Lintott et al. 2014) or nonbreeding females (Mackie and Racey 2007; Clutton-Brock et al. 2009). Maternal care may further modify foraging ecology and behavior already shaped by energy demands. Precocial species often choose habitats or utilize resources optimal for the protection of their young from predators (Young and Isbell 1991; Miller and Litvajtis 1992; Bongi et al. 2008), while altricial species are restricted in their habitat use by distance to the nest (Morris 1984; Scheibe and O'Farrell 1995).

Energy demands also change among various stages of the reproductive cycle in breeding individuals. Pregnancy only marginally increases daily food requirements compared to nonbreeding females (Winship et al. 2002), but lactation results in the highest increase in energy intake by most mammals (Speakman 2008). Daily energy expenditure in lactating females appeared to be strongly selected (Fletcher et al. 2015) and some species reveal dietary shifts between pregnancy and lactation (Bernard and Hohn 1989). Following a general mammalian pattern, that includes insectivorous bats, production of milk during lactation significantly increases the energy demands of females in comparison to the energy required during pregnancy (Kunz 1974). That may result in: 1) changes in diet to more easily available and more energy-rich insects (Jones 1990); 2) changes in dynamics and timing of emergence patterns from roost (Swift 1980; Maier 1992; Catto et al. 1995; Speakman et al. 1995); 3) changes in spatial activity, decreasing during lactation in comparison with pregnancy (Henry et al. 2002; Lučan and Radil 2010); and 4) changes in habitat preferences (Haupt et al. 2006). The behavioral response to reproductive status might, however, be species-specific, sometimes significantly deviating from the pattern described above (e.g., Womack et al. 2013). Moreover, insect abundance reveals strong seasonal variation that results from peaks of emergence of either several species of different phenology or multiple peaks of multivoltine species (Flannagan and Lawler 1972; Crichton and Fisher 1982; Tokeshi 1995). Knowledge of space use by threatened animal species is necessary to adjust conservation measures appropriate for this species during critical phenological periods.

Habitat specialization, reflected in wing morphology, is positively correlated with extinction risk in temperate-zone bats (Safi and Kerth 2004). The pond bat (*Myotis dasycneme*) is a stenotopic, insectivorous vespertilionid species associated with some classes of riparian landscape and is considered to be of high conservation priority. Its distribution is extremely patchy across Europe, with high population densities in scattered centers of reproduction (where numerous nursery roosts occur) and vast, almost empty areas between those centers inhabited exclusively by adult males and nonreproductive females (Horáček and Hanák 1989; Limpens et al. 2000; Ciechanowski et al. 2007). It is usually classified as a water-surface forager or trawling bat (Fenton and Bogdanowicz 2002), hunting most often about 30 (10–60) cm above the surface of large lakes, ponds, rivers, and canals (of more than 2.5 m width; Boonman et al. 1995; Verboom et al. 1999; Limpens et al. 2000). Pond bats usually hawk for prey insects in flight, catching them using their wing membranes, or trawl for them on the surface of the water using their tail membranes or large feet (Britton et al. 1997). Non-biting midges (Chironomidae; both imagines and pupae), caddish-flies (Trichoptera), beetles (Coleoptera), and moths (Lepidoptera) predominate in its diet (Britton et al. 1997; Ciechanowski and Zapart 2012; Krüger et al. 2012, 2014). Because of its scattered distribution and association with threatened riparian habitats, the pond bat is classified as being near threatened in the IUCN Red List of Threatened Species (Hutson et al. 2008), is strictly protected in the European Union, included in Annex II of the EC Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC) that constitutes the legal base of the Natura 2000 ecological network, and is included in the Polish Red Data Book as endangered (Wołoszyn 2001).

In spite of its conservation status, the biology and ecology of the species is astonishingly poorly studied. Additionally, although some research on the non-hibernation biology and ecology of the pond bat has been carried out in the heavily transformed, anthropogenic (mostly agricultural) landscape of the Netherlands and Denmark (Voûte et al. 1974; Boonman et al. 1995; Britton et al. 1997; Reinhold et al. 1999; Verboom et al. 1999; Van de Sijpe et al. 2004; Van De Sijpe and Holsbeek 2007; Haarsma and Tuitert 2009), a much larger part of its geographical range covers the moderately transformed, forest-agricultural landscapes of the young, postglacial lakelands of central and eastern Europe (Horáček and Hanák 1989; Limpens et al. 2000; Ciechanowski et al. 2007).

Data about the landscape-scale habitat used by this species, collected by use of radiotracking, are very limited (Ciechanowski et al. 2007; Estók and Tamás 2008; Haarsma and Tuitert 2009), making successful protection of *M. dasycneme* difficult. Some preliminary research suggests a link between habitat use by pond bats and water quality (Van de Sijpe et al. 2004); however, this has never been properly tested.

Our 2-year investigation, using radiotracking, was aimed at revealing changes in the habitat use during pregnancy and lactation of pond bats in the young, postglacial landscape of central Europe. We predicted that 1) pond bats select eutrophic lakes due to higher nutrient content and productivity, resulting in greater abundance of aquatic insects (Forsyth 1976), and 2) lactating females commute shorter distances than pregnant females, as they need to return to the colony during the night to feed their young (Murray and Kurta 2004).

MATERIALS AND METHODS

Study area.—The study was conducted in northern Poland, in the Bory Tucholskie forests (Fig. 1) that cover almost flat, postglacial, outwash plains situated in the southern part of Pomorskie Province. Lakes comprised approximately 12% of the area, varied in size from 1 to 1,417 ha, and were classified in the following trophic classes: 1) eutrophic, usually with neutral or alkaline water (pH > 7.5), rich in nutrients, with vegetation dominated by reeds (*Phragmites communis*), bulrushes (*Typha latifolia*), hornworts (*Ceratophyllum demersum*), and pondweeds (*Potamogeton* spp.); 2) mesotrophic, with alkaline water (pH > 7.5), relatively poor in nutrients, with vegetation dominated by reeds, clubworts (*Schoenoplectus lacustris*), and stoneworts (*Chara* spp.); 3) dystrophic, usually small, with acidic water (pH < 6), extremely poor in nutrients but rich in humic acids, with vegetation consisting of *Sphagnum* peat moss, forming floating mats; and 4) oligotrophic lakes, usually small, with water of moderate acidity (pH 6.5–7.5), extremely poor in nutrients, with scarce vegetation, dominated by water lobelia (*Lobelia dortmanna*) or lake quillwort (*Isoetes lacustris*).

A few fish ponds, representing both eutrophic and oligotrophic types (for carp and trout breeding), are also present

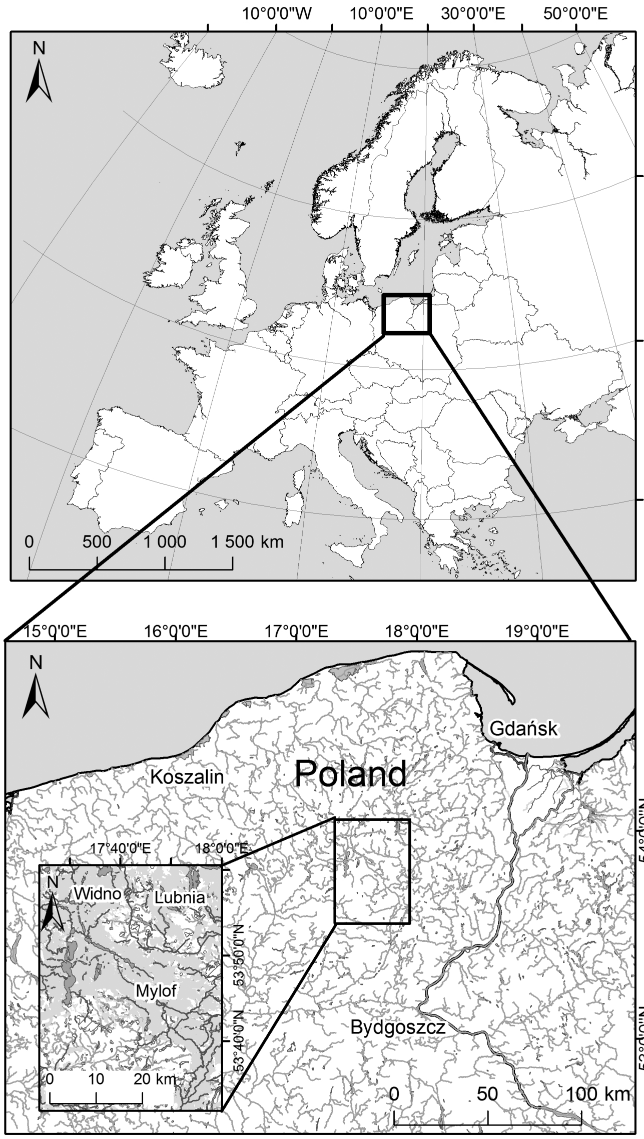


Fig. 1.—Locations of nursery roosts in Poland, where female pond bats (*Myotis dasycneme*) were radiotagged in 2012 and 2013.

in the study area. The river network is poorly developed, consisting mostly of small, fast-flowing, clean rivers, with submerged vegetation dominated by *Ranunculus fluitans*; some are connected to artificial canals, built to irrigate the meadows. Both rivers and canals do not exceed 15 m in width. Terrestrial vegetation is dominated by same-aged, intensively managed plantations of Scots pine (*Pinus sylvestris*), with small patches of beech (*Fagus sylvatica*) and oak (*Quercus robur*) on valley slopes and alder (*Alnus glutinosa*) in the lake valley bottoms. Forest glades of various sizes, composed of meadows and fields, surround villages and the city of Brusy. The southern part of the study area (studied only in 2012), belonging to Krajeńskie Lakeland, is characterized by more undulating land, exclusively eutrophic lakes (surrounded by dense reed and bulrush beds); here, the landscape is dominated by intensively farmed land dotted with numerous villages, but only small patches of deciduous forest.

Radiotracking.—In 2012, all radiotracked bats originated from a nursery roost in a forester's lodge in Lubnia (53°56.121′N, 17°48.271′E); the lodge is a brick-built, 2-story building with a wooden roof covered in tar paper, and has been known as a site of a pond bat colony since 2002 (Ciechanowski et al. 2007). It is also occupied by a nursery colony of *Pipistrellus nathusii* and *P. pygmaeus*; a single individual of *Nyctalus noctula* was also captured there. During the 1st radiotracking season, 4 individuals moved to 2 other previously unknown nursery roosts, from which all bats radiotracked in 2013 were taken. The first of these was located in a forester's lodge in Widno (53°55.950′N, 17°32.578′E); this is a 2-story building constructed of stone and wood with a metal roof and is also occupied by nursery colonies of *Eptesicus serotinus*, *P. nathusii*, and *P. pygmaeus*. Another was located in a 1-story private house in Mylof-Zapora (53°46.632′N, 17°43.045'E), built of brick with a tiled roof. Bats were mist netted at the roosts' entrances twice per year (the beginning of May and the 2nd half of June); their sex and reproductive status were examined, and body masses and right forearms were measured to an accuracy of 0.5 g and 0.1 mm, respectively. In 2012, pregnancy was recognized by gentle palpation of the abdomen, and in 2013 also by USG imaging (using a portable Mindray ultrasound scanner). Lactation was identified by the presence of bare patches of skin around enlarged nipples. Radiotransmitters weighing 0.52 g (model LB-2N; Holohil Systems, Carp, Ontario, Canada) that did not exceed 5% of the bat's body mass (Aldridge et al. 1988) were attached to the bat's back in the interscapular region by the use of bonding adhesive (Torbot, Cranston, Rhode Island).

In total, 19 pregnant females (8 in 2012 and 11 in 2013) and 19 lactating females were radiotracked. Six receivers (Australis 26k: Titley Scientific, Brendale, Australia) with Y-3 antennae and 6 cars were used during each study season to discover the locations of tagged bats in the landscape. Occasions for obtaining simultaneous bearings and locating bats by triangulation were scarce as the bats ranged over a large area, and 2 car teams hardly ever penetrated the same part of the area at the same time. Thus, we were forced to locate bats by a homing-in approach, trying to get as close as possible to a foraging individual. On every occasion when a signal from any tagged bat was received, its GPS location, azimuth, and signal strength were noted. In one case, we estimated the speed of the bat's commuting flight, based on the speed of the vehicle used to track it down. We defined "foraging" as constant flying in a single patch of habitat, with frequent changes in direction, including turning back. If such behavior was observed for up to 5 min, it was treated as a single location. If the bat foraged longer, every new 5-min interval was treated as an additional record with its azimuth and signal strength measured again. We defined "commuting" as constant bat movement with no turning back, when the signal appeared and increased its strength from one direction, then decreased, finally vanishing in another direction. Every evening, 1 team monitored presence of tagged bats in the roost and informed the other teams about the time of emergence and initial azimuth of commuting flight. Once located in the foraging site by any team, the bat was constantly monitored and—when it left the site—either followed by the same team or information about the movement (timing and direction) was given to the other teams. Bats often repeatedly used the same series of foraging sites, so, after revealing that, teams were arranged along predicted commuting paths for the 1st part of the night. At the end of each night, 1 team visited the roost, to check that all individuals arrived at the colony. When more than 1 individual foraged in the same site, we switched the receiver among frequencies every few minutes to ensure that all bats were still present there. As the bats did not forage the whole night when radiotransmitters were attached, and because most of them switched roosts after tagging, data from the 1st night for every individual were omitted from analyses to minimize the effects of disturbance. Approval for mist netting and radiotagging was granted by license of the General Directorate of Environmental Protection (DOPozgiz-4200/IV.D-2/1429/09/km), the Regional Directorate of Environmental Protection in Gdańsk (RDOŚ-Gd-PNII.6401.42.2013.EK.1), and the Local Ethical Commission (no. 25/2009). The methods used conformed to the guidelines of the American Society of Mammalogists for the use of wild animals in research (Sikes et al. 2011).

Data analysis.—Spatial analyses were conducted using ArcEditor 10.0 (Environmental Systems Research Institute Inc., Redlands, California) and Geospatial Modelling Environment software version 0.7.2.0. These programs allowed us to calculate distances of particular locations from the roost; the individual and colony minimum convex polygon (MCP); and the kernel density, as well as availability of particular habitats (inside the MCP of the colony, separately for each year and season). The proportion of recorded locations of the tagged bats over a particular class of surface waters (R) was compared with the proportion of that habitat in the total area of the colony's MCP. Selection or avoidance of habitat categories was detected by constructing individual confidence intervals for each habitat using the Z statistic with a Bonferroni adjustment. Confidence limits were set to 95% (thus, $\alpha = 0.05$) and compared with the expected proportion, based on the availability (A) of the particular habitat. If the expected value was within the confidence intervals, then we concluded that the habitat was used in proportion to its availability. If lower, then the habitat was selected; if higher, then the habitat was avoided (Byers et al. 1984).

RESULTS

Radiotracking data, daily roost types, and roost switching.—Of 38 radiotagged bats, 2 disappeared from the study area; all the data therefore were obtained from 36 individuals, that is, 17 pregnant and 19 lactating females. The last contact with a bat, usually followed by loss of the transmitter, was made after 2–12 nights (median 7.0) and the number of nights tracked varied from 1 to 9 (median 4.5), giving 3–131 (median 30.5) locations per bat (including 2–113 locations with foraging; median 20; Table 1). In total, only 19 females remained in the colonies where they were captured and radiotagged (8 during pregnancy, 11 during lactation) and 17 moved to the other roosts (10 during pregnancy, 7 during lactation). Eight females moved to other nursery colonies, that is, 2 inhabited houses and a concrete bridge in the village of Laska (1.2 km from the maternity colony in Widno), where they were roosting in crevices with another 40 pond bats. The remaining females moved to temporary daily roosts occupied by 1–2 individuals, comprising hollow black alders (*A. glutinosa*) growing in riparian forests on lake shores (3), sheds (3), barns (2), and a house (1) in the village of Lipusz, occupied by a colony of 60 Nathusius' pipistrelles *P. nathusii* (Table 1).

Home ranges, foraging distances, and nightly movements.—Over the 2 seasons, individual home ranges of radiotagged females (90% kernel) were very variable both during pregnancy (40.2–9465.9 ha, median 3783.4 ha) and lactation (31.6–5800.1 ha, median 2195.2 ha). In 2012, the communal home range of all pregnant females radiotagged in Lubnia covered 38,712 ha (by MCP) or 6,229 ha (by 90% kernel), whereas pregnant females from Widno and Mylof in 2013 used 56,028 ha (MCP) or 21,602 ha (90% kernel). In 2012, the communal home ranges of lactating females from Lubnia covered 16,670 ha (MCP) or 3,818 ha (90% kernel) whereas, in 2013, lactating females from Widno and Mylof were found in an area of 9,733 ha (MCP) or 4,981 ha (90% kernel; Figs. 2 and 3).

Pregnant females covered significantly longer distances between roosts and foraging sites (median 11379.2 m, min. 66.3 m, max. 23857.1 m, $n = 387$) than during lactation (median 2914.4 m, min. 24.4 m, max. 22057.3 m, $n = 673$; Mann–Whitney U-test: $Z = 13.18$, $P < 0.001$; Fig. 4).

The foraging pattern was also very different between pregnant and lactating individuals. During pregnancy, the bats travelled long distances every night, visiting a chain of foraging sites (usually lakes) and spending only a short time (less than 10 min) in each of them. The individual commuting path, calculated as a sum of line segments between particular locations, could cover up to 54 km, and the bat did not return to its roost until dawn (Fig. 5). In 2013, females from a maternity colony in Mylof were observed travelling up to 24 km 1-way, leaving the forest complex of Bory Tucholskie to forage on lakes located in open, fertile farmland (Fig. 2). One individual was observed returning to the same night roost (tree) 4 times during 1 night, when foraging was interrupted by light rain (resting there 9, 11, 12, and 29 min).

During lactation, most pond bats visited usually only 1 or 2 main foraging sites, foraging there approximately 2 h each time (Fig. 6) and returning to the maternity roost 1–2 times (median 1) during the night to feed pups left there. Lactating females often participated in 2 or 3 foraging bouts per night (Fig. 6). Between longer foraging bouts, bats sometimes occupied night roosts, usually trees located on lake shores, river banks, or (in 1 case) on a lake island (resting there 3–25 min, median 7 min, $n = 10$). Some individuals were observed spending a long time foraging over relatively short (less than 1 km) sections of rivers. Following a single flying bat by car on 1 occasion, we estimated its commuting speed at about 60 km/h. Tagged individuals returned to the same foraging sites more frequently during lactation than during pregnancy (Mann–Whitney U-test:

Table 1.—Biometrics, status, and tracking data of the female pond bats (*Myotis dasycneme*) studied. Explanations: pp = adult, presumably pregnant (determined visually and by palpation); p = pregnant (determined by USG); l = lactating; FA = forearm length (mm); W = weight (g); r = remained in the original colony; mc = moved to another (sub)colony; ms = moved to a solitary roost; N = unknown, bat moved out of study area; distances are given in km.

Date of tagging	Status	FA	W	Code	Colony	Number of:				Maximum distance of:		Roosting behavior
						Nights with contact	Nights until last contact	Bearings	Bearings with foraging	Nightly foraging/ commuting	Roost switch	
28 April 2012	pp	46.7	21.5	1	Lubnia	4	8	39	18	23.4	18.7	mc (Mylof)
28 April 2012	pp	49.9	21.5	8	Lubnia	3	6	11	10	9.5	17.2	mc (Widno)
28 April 2012	pp	46.9	22.5	3	Lubnia	7	8	44	21	11.3		r
28 April 2012	pp	48.3	22.0	2	Lubnia	2	4	14	11	2.7	19.8	ms (Lipusz)
28 April 2012	pp	49.0	22.5	4	Lubnia	1	2	3	3	7.6	8	ms (shed)
28 April 2012	pp	49.2	23.0	6	Lubnia	4	7	11	6	9.2	17.2	mc (Widno)
28 April 2012	pp	47.8	20.5	5	Lubnia	2	2	2	0			N
28 April 2012	pp	46.9	20.0	7	Lubnia	5	8	5	2	21.6	18.7	mc (Mylof)
17 June 2012	l	47.2	21.5	1	Lubnia	5	8	25	16	10.6	17.2	mc (Widno)
17 June 2012	l	46.7	20.5	2	Lubnia	4	7	18	15	10.8	10	ms (shed)
17 June 2012	l	46.7	19.0	3	Lubnia	7	7	59	39	8.7		r
17 June 2012	l	47.4	20.0	4	Lubnia	5	7	53	39	7.8		r
17 June 2012	l	49.2	21.5	5	Lubnia	2	3	8	4	7.2	13.4	ms (shed)
17 June 2012	l	48.2	20.0	6	Lubnia	5	7	58	56	10.8	10	ms (shed)
17 June 2012	l	46.6	19.0	7	Lubnia	4	4	19	12	7.5		r
17 June 2012	l	47.1	21.0	8	Lubnia	7	7	42	25	8		r
26 April 2013	p	46.1	16.5	2.4	Widno	4	12	17	6	5.7	1.5	ms (hollow alder)
26 April 2013	p	46.2	14	2.1	Widno	9	9	131	113	23.9	21	ms (hollow alder, barn), mc (Mylof)
26 April 2013	p	48.7	17.5	2.2	Widno	3	12	8	6	3.4	2.4	ms (hollow alder)
26 April 2013	p	49	18.5	1.1	Mylof	6	8	54	40	23.8	16	ms (hollow alder), r
26 April 2013	p	46.7	16	1.6	Mylof	4	9	97	52	24.4		r
26 April 2013	p	47.6	16	2.6	Mylof	0	0	0	0			N
26 April 2013	p	47	17	1.2	Mylof	3	8	15	7	17.6		r
26 April 2013	p	47	17	1.4	Mylof	1	9	22	20	11.8		r
26 April 2013	p	47.5	16.5	2.3	Mylof	4	8	68	32	23.2		r
26 April 2013	p	47.5	17	1.3	Mylof	2	2	6	6	16.5	16	ms (shed)
26 April 2013	p	46.5	16.5	2.5	Mylof	9	10	49	38	19.1		r
21 June 2013	l	48.3	20	1.3	Mylof	5	5	21	14	2.3		r
21 June 2013	l	49.6	20.5	1.1	Mylof	3	4	33	30	3.5		r
21 June 2013	l	47.8	20.5	1.2	Mylof	3	5	15	9	17		r
21 June 2013	l	47.2	19	1.4	Mylof	5	5	28	23	20.7		r
21 June 2013	l	47.1	19.5	1.5	Mylof	4	4	17	17	2.3		r
21 June 2013	l	48.2	19	1.6	Mylof	6	6	33	20	20.8		r
21 June 2013	l	48.2	20	2.1	Widno	9	9	97	91	4	1.2	mc (bridge in Laska)
21 June 2013	l	47.5	19.5	2.2	Widno	7	8	52	48	6.7		r
21 June 2013	l	48	20	2.3	Widno	6	9	57	55	6.7	1.2	r, mc (bridge in Laska)
21 June 2013	l	45	18.5	2.4	Widno	9	9	58	47	6.5		r
21 June 2013	l	48.2	22	2.5	Widno	7	7	111	109	4	1.2	mc (bridge in Laska)

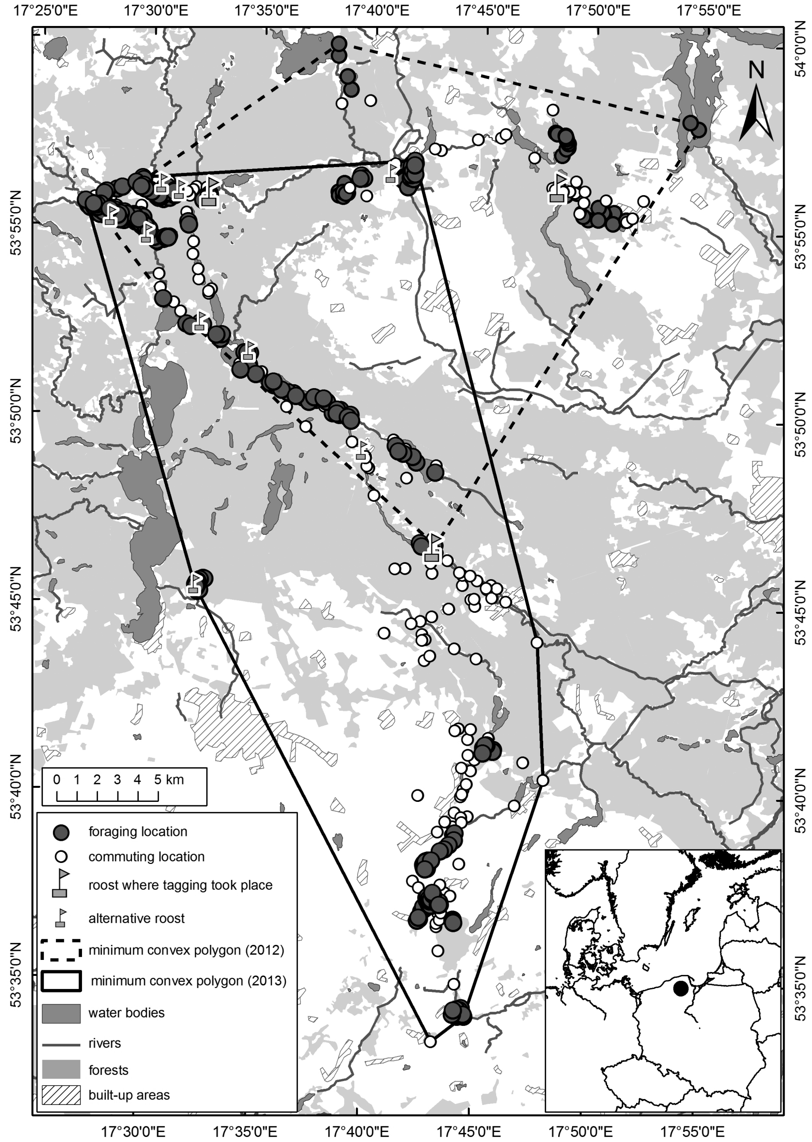


Fig. 2.—Communal home ranges and distribution of locations of radiotagged pond bats (*Myotis dasycneme*) during pregnancy at our study sites in northern Poland, 2012 and 2013.

$Z = 2.31$, $P = 0.02$), although the median number of nights/bat/site during both periods was 1 (pregnancy: *Q75%* = 2, max. 5; lactation: *Q75%* = 3, max. 9).

Both during pregnancy and lactation, some foraging sites (both river sections and lakes) were used by 2–3 tagged females at the same time.

Habitat use and habitat selection.—The main foraging sites of pond bats were lakes, rivers, canals, and fish ponds. In 2013, however, 1 pregnant female was found foraging in an open-canopy alder swamp forest between 2 lakes, while a 2nd bat foraged over a meadow. All the terrestrial locations were based on 8 and 13 bearings and were confirmed by triangulation (Table 2). Commuting flights between foraging sites were observed mainly along water courses, either natural (rivers) or artificial (canals). However, the availability of linear elements did not limit their movements; when necessary, they regularly commuted up to 3 km over open fields or pastures.

During pregnancy, bats foraged mostly over lakes and only rarely over rivers, using both habitats in proportion to their availability ($R = 0.910$, $A = 0.041$, $Z = 0.875–0.944$ and $R = 0.050$, $A = 0.056$, $Z = 0.024–0.077$), but carp fish ponds (1 site) appeared to be preferred in that period ($R = 0.040$, $A = 0.004$, $Z = 0.017–0.064$; Fig. 7).

Contrary to the behavior of pregnant bats, however, lactating females showed a strong preference for rivers and canals ($R = 0.738$, $A = 0.088$, $Z = 0.694–0.781$), while avoiding lakes ($R = 0.259$, $A = 0.907$, $Z = 0.215–0.303$; Fig. 7). Trophic classes of lakes were used unevenly. During pregnancy, bats selected eutrophic lakes ($R = 0.891$, $A = 0.727$, $Z = 0.850–0.932$) and avoided mesotrophic ones ($R = 0.095$, $A = 0.233$, $Z = 0.056–0.133$; Fig. 8) whereas, during lactation, mesotrophic lakes were selected ($R = 0.616$, $A = 0.261$, $Z = 0.517–0.715$) and eutrophic ones were avoided ($R = 0.364$, $A = 0.699$, $Z = 0.266–0.462$). Dystrophic and oligotrophic

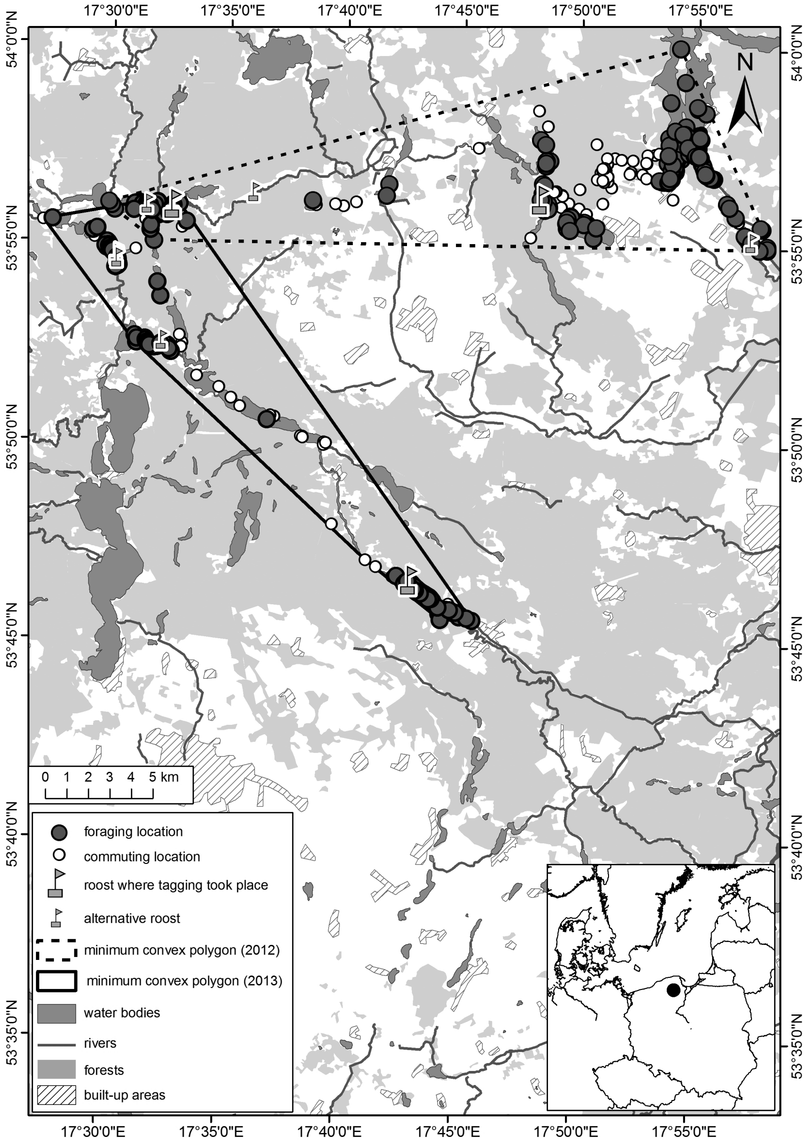


Fig. 3.—Communal home ranges and distribution of locations of radiotagged pond bats (*Myotis dasycneme*) during lactation at our study sites in northern Poland, 2012 and 2013.

lakes were used in proportion to their availability in both periods (Fig. 8).

Discussion

We confirmed fully only our 2nd prediction: that lactating females visit foraging sites located closer to the daily roost than do pregnant females. Our 1st prediction was confirmed only partially, as pond bats appear to select eutrophic lakes (i.e., water bodies with the highest productivity) only in spring, during pregnancy, whereas they shifted to mesotrophic lakes and rivers during lactation. In addition to testing predictions about the spatial behavior of pond bats, we also provide some descriptions of their roosting and foraging ecology.

Most of the nursery roosts in our study were situated in houses, which is typical for pond bat as a synanthropic species (Limpens et al. 2000; Ciechanowski et al. 2007; Haarsma and Tuitert 2009). However, the nursery colony composed of about 40 individuals occupying crevices in a concrete bridge requires more attention. This is the 2nd documented case of such roosting behavior by pond bats (Kmiecik and Kmiecik 2015), although single individuals of this species were reported to roost in similar locations in summer more frequently (Ciechanowski et al. 2007).

Our data about temporary roosts occupied by single individuals remain in accordance with earlier information (Limpens et al. 2000). These roosts include tree holes (hornbeam and Scots pine) that, even in Poland, were reported to act as mating sites or satellite roosts of larger, house-dwelling colonies used by single, lactating females with juveniles (Ciechanowski et al. 2007). Our study is apparently the first to provide direct evidence for the use of trees as night roosts by pond bats, a phenomenon already reported for other *Myotis* species (Murray and Kurta 2004) or *Vespertilio murinus* (Jaberg and Blant 2003). Night roosts may allow minimization of distances to feeding

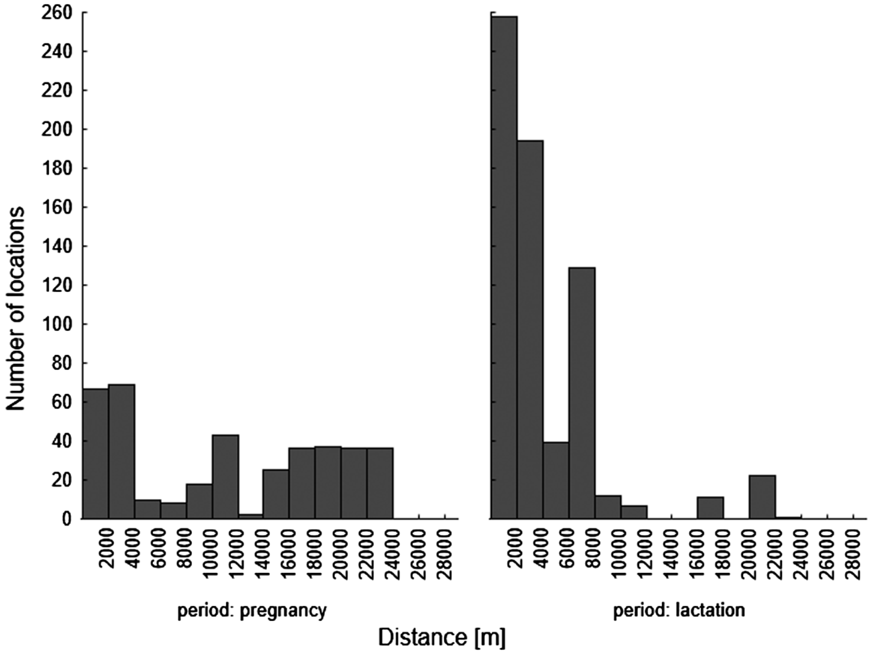


Fig. 4.—Distances between daily roost and foraging sites of radiotagged pond bats (*Myotis dasycneme*) during pregnancy and lactation at our study sites in northern Poland, 2012 and 2013.

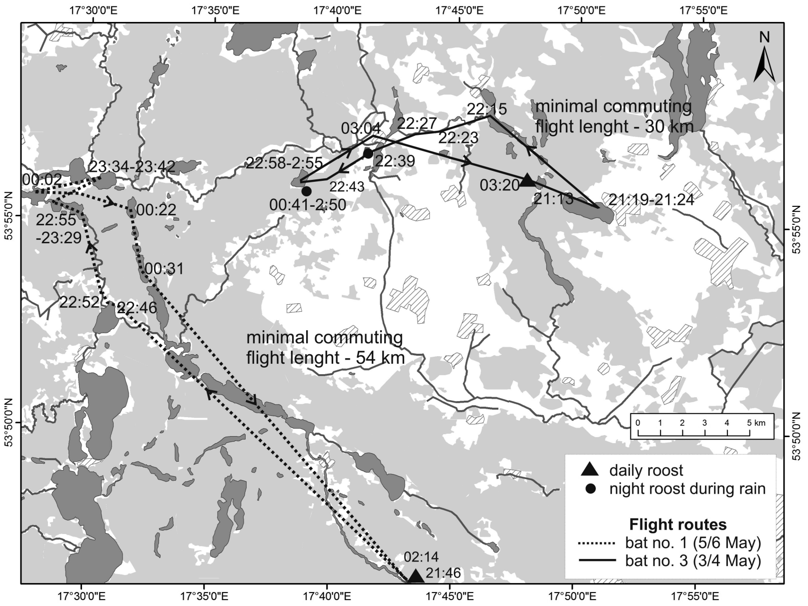


Fig. 5.—Examples of nightly flight paths by a radiotagged, pregnant pond bat (*Myotis dasycneme*) at our study site in northern Poland in 2012.

habitats and are most probably used for resting and digestion between foraging bouts (Knight and Jones 2009).

We cannot exclude the possibility that some roost switches were induced by disturbances caused by mist netting and radiotagging; however, this cannot account for all movements as some of them appeared a few days after capture. Patterns of roost switching, either in 2012 or 2013, did not resemble the typical behavior observed in a fission–fusion society that was reported in the house-dwelling *P. pygmaeus* (Bartonička et al. 2008), the tree-dwelling *Myotis bechsteinii* (Kerth et al. 2005), or *Nyctalus lasiopterus* (Popa-Lisseanu et al. 2008). After switching, most females, either pregnant or lactating, remained faithful to their new roost, at least if it was occupied by another (sub)colony (Mylof, Widno, Laska). The use by single individuals of day and night roosts situated in tree holes, sheds, barns, and houses appeared to be more flexible.

The roosting behavior of pond bats seems to be somewhere between that of attic-dwelling (originally cave-dwelling) species, revealing a strong fidelity to the same roost during the whole life span and season (e.g., *Myotis myotis*—Horacek 1981), and that represented by tree-dwelling species, living in fission–fusion societies and sometimes changing roost every few days. Among 3 European trawling *Myotis*, the obligatory house-dwelling *M. dasycneme* is an exception because *M. daubentonii* is still predominantly a tree-dweller (although it often occupies crevices in bridges) and the Mediterranean

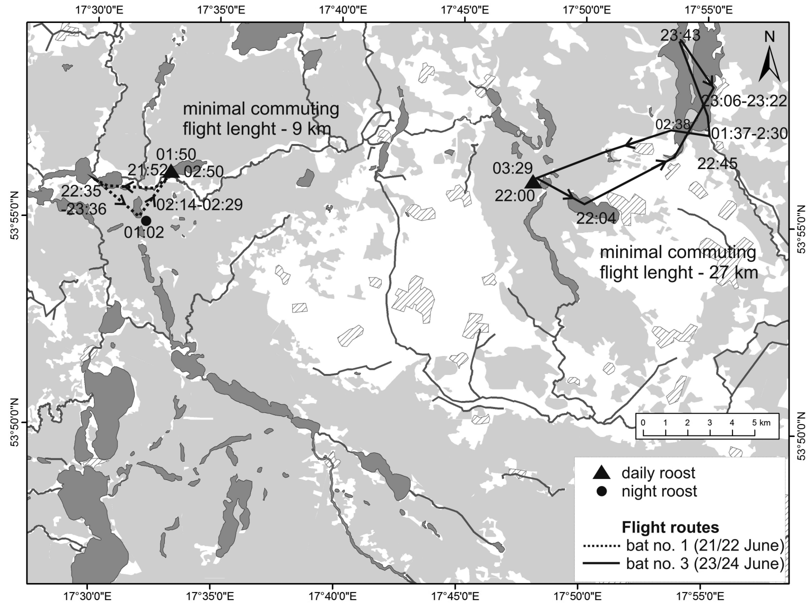


Fig. 6.—Examples of nightly flight paths by a radiotagged, lactating pond bat (*Myotis dasycneme*) at our study site in northern Poland in 2012.

Table 2.—Number of locations of foraging and commuting female pond bats (*Myotis dasycneme*) in different habitats during pregnancy and lactation in northern Poland, 2012 and 2013.

	Pregnancy		Lactation	
	Commuting	Foraging	Commuting	Foraging
Lakes	27	362	22	151
Rivers or canals	21	20	13	430
Fish ponds		16	1	2
Swamp alder forest		8		
Meadow		13		
Pine forest			3	
Edge of pine forest and field	2			
Road	1			
Other terrestrial			10	
Total	51	419	49	583

M. capaccinii roosts in caves and other underground spaces (Dietz et al. 2009).

Preliminary radiotracking of lactating females done in the 2nd Polish nursery roost in Jeleniewo (T. Kokurewicz, J. Furmankiewicz, and M. Wojciechowski, cited in Ciechanowski et al. 2007) revealed that the foraging habitats of these individuals were located 2.2–4.8 km from the roost, much closer than recorded in this study (max. 23.9 km). It is possible that during the 1st study, only foraging areas situated closest to the nursery roost were detected, so the shorter distances resulted from a more limited research effort and does not reflect real differences between populations. Estók and Tamás (2008) also recaptured a radiotagged female at a roost located 4.85 km from the capture site along a commuting path. Radiotracking surveys of pond bat roosts in the Netherlands revealed much longer flight distances, up to 18 km (Haarsma and Tuitert 2009). Distances we recorded, covered by pond bats commuting between daily roosts and their foraging sites, are among the longest in European representatives of the genus *Myotis*. Another sympatric water-surface forager, *M. daubentonii*, foraged at distances up to 6.3 km from its roost (Dietz et al. 2006). *M. capaccinii*, which much more resembles the pond bat in size, ecomorphology, and flight style, commuted up to 22.7 km to the furthest hunting sites, with an average distance of 7.5 km (Biscardi et al. 2007; Almenar et al. 2008).

Among foliage gleaners, *M. nattereri* foraged up to 5.8 km from its roost (Smith and Racey 2008), while *M. emarginatus* foraged up to 8.1 km (Zahn et al. 2009). The mouse-eared bat (*M. myotis*), a ground gleaner and the largest representative of the genus, was observed foraging from 8.9 km (Zahn et al. 2005) to 25 km from its roost (Arlettaz 1999). The long distances of foraging flights recorded during our study are unique and comparable to those observed in open-air aerial hawkers, such as *N. noctula* (Mackie and Racey 2007). The long flights are possible due to the much narrower wings of pond bat compared to another species of *Myotis*. The pond bat probably has the highest flight speed among European representatives of that genus, reaching 35 km/h during hunting (Horáček and Hanák 1989; Britton et al. 1997), but apparently much faster (60 km/h, this study) during commuting. That speed is comparable with similar values recorded in high-flying, open-space aerial hawkers with extremely long and narrow wings, e.g., *Tadarida teniotis* (50 km/h—Marques et al. 2004), a species with much higher aspect ratio and wing loading than pond bats.

Significant changes in the space use and pattern of movements between pregnancy and lactation appear to be a trade-off between response to the sharp increase in energy demands after parturition (Kunz 1974) followed by reorganization of the energy budget (Racey and Speakman 1987) and limitations of central-place foraging (Rosenberg and McKelvey 1999; Carrete and Donázar 2005), shaped by the need to return to the colony (once per night during pregnancy, at least 2 times during lactation). Lower energy demands in early pregnancy allow more energy to be spent on long-distance flights, associated with visits to several foraging sites and forced by low prey abundance in spring. Pregnant females may spend the whole night commuting and foraging, not

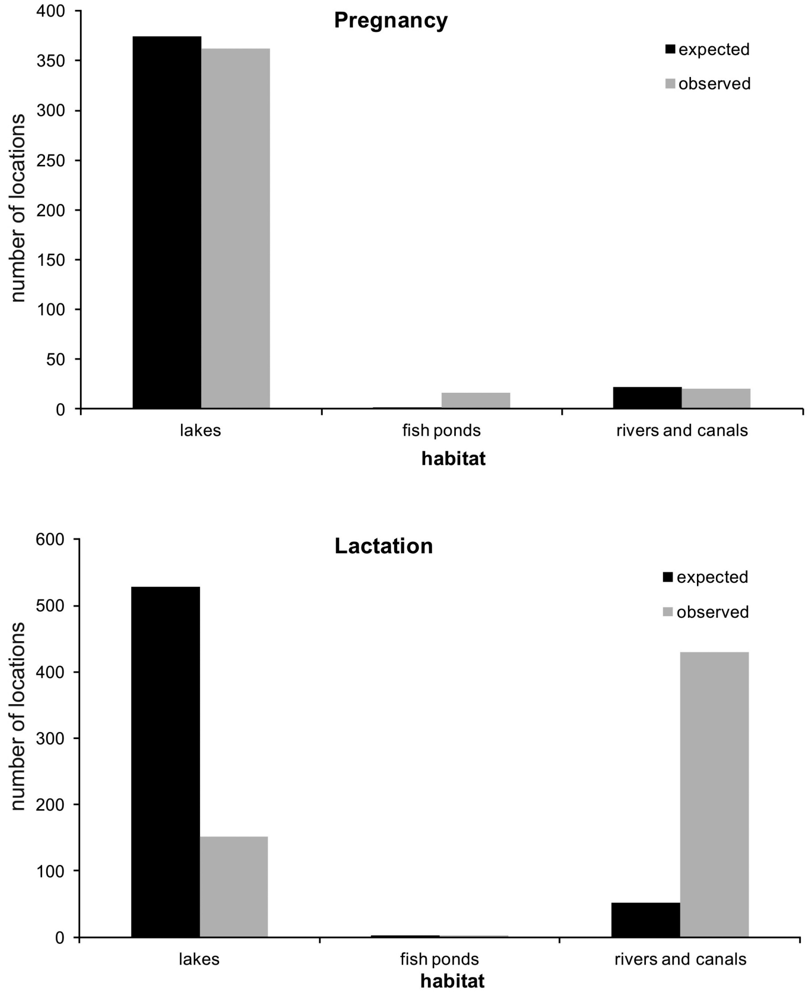


Fig. 7.—Selection of 3 types of water bodies by radiotagged pond bats (*Myotis dasycneme*) during pregnancy and lactation at our study sites in northern Poland in 2012 and 2013.

returning to the colony until dawn (Murray and Kurta 2004). Prey abundance in summer is probably much higher, however, so foraging bats may constantly exploit much smaller habitat patches with no need to travel long distances (Henry et al. 2002), saving their energy for the much higher demands of lactation (Racey and Speakman 1987). Moreover, lactating female bats exploit foraging habitats much closer to the nursery roosts because they must return to the colony to feed their pups (Henry et al. 2002; Murray and Kurta 2004; Safi et al. 2007). The observed reduction (of 74%) of flight distance in pond bats between pregnancy and lactation is much higher than that reported in another water-surface forager, the little brown bat, *Myotis lucifugus* (35%—Henry et al. 2002), presumably due to the larger body size and wing loading in *M. dasycneme* resulting in higher energy costs of flight. Some species of the genus *Myotis* do not, however, shorten their commuting distance after parturition—this is the case for both aerial-hawking *M. mystacinus* (Buckley et al. 2013) and gleaning *M. nattereri* (Lundy et al. 2012).

The observed pattern of habitat use, with a predominance of water bodies, confirms our general knowledge about the hunting tactics of the pond bat, that is, catching prey in flight in its wing membrane or trawling it from water by its tail membrane or large feet (Britton et al. 1997). Hunting over land, including peat bogs, meadows, pastures with trees, gardens, forest edges, and tree lines, is mentioned by Limpens et al. (2000); however, no details are given. Thus, our observations of radiotracked pond bats hunting in the loose alder forest and over meadows in spring are especially noteworthy and provide an example of ecological plasticity, even in the case of such a perceived habitat specialist as the pond bat that does not appear to be morphologically adapted to foliage gleaning or hawking prey in the air (Baagøe 1987; Britton et al. 1997; Fenton and Bogdanowicz 2002). Such plasticity is, however, observed in another trawling bat species, *M. daubentonii*, that is also know to hunt in forests, especially in early spring (Nyholm 1965) when weather conditions at lakes are not conducive for foraging, or prey abundance is too low.

Shifts in habitat use between pregnancy and lactation, that is, changing from hunting on lakes to more intensive hunting on rivers, and changing from eutrophic to mesotrophic lakes, appear to be adaptations to the increasing energy demands of lactating females. Rivers in the study area are mainly small, fast-flowing, and cold, which leads to a delayed emergence of aquatic insects. Pregnant females are forced to travel to the most productive patches of habitats, including either eutrophic

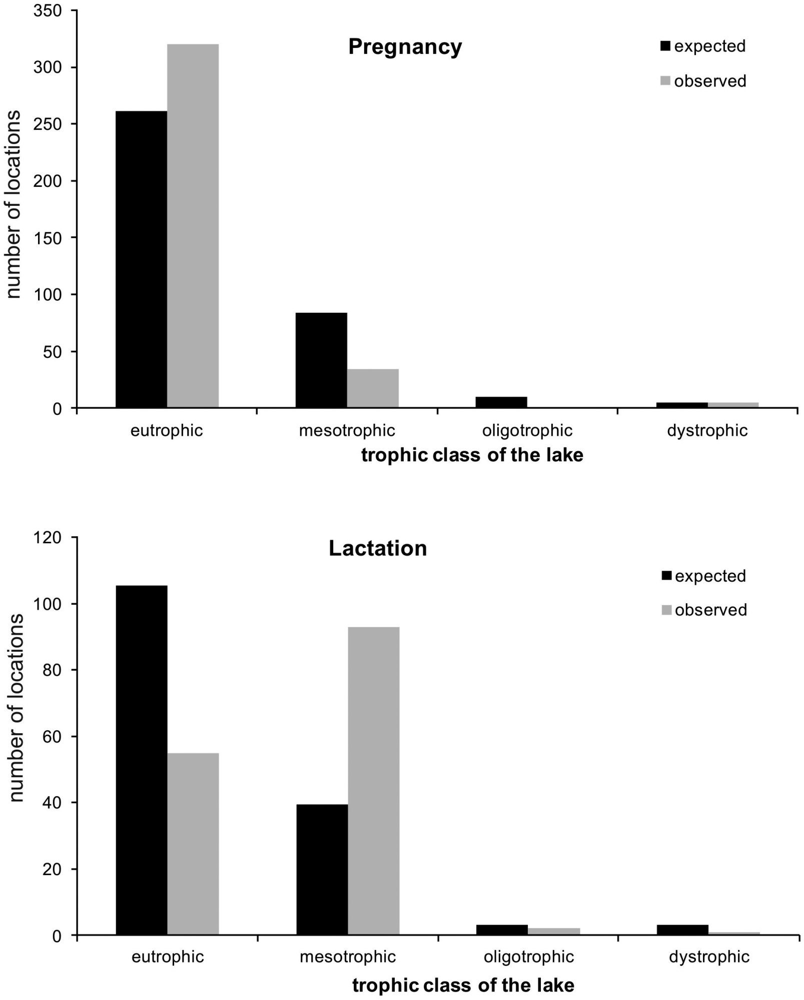


Fig. 8.—Selection of trophic classes of lakes by radiotagged pond bats (*Myotis dasycneme*) during pregnancy and lactation at our study sites in northern Poland in 2012 and 2013.

lakes or their artificial counterparts, such as fishponds, being the only selected habitat class in that period. Active seeking for waters with the highest biomass of emerging aquatic insects is probably the purpose of the distant commuting flights of pregnant females. In May 2013, they were observed leaving the Bory Tucholskie forests to forage in intensively farmed, open land where lakes receive a much higher nutrient input than lakes surrounded by intact coniferous forests with few if any human settlements. Eutrophication of lakes and rivers caused by an increased nutrient content, which produces an increased number of non-biting midges (Chironomidae), was probably the key factor responsible for the increasing population of Daubenton's bat (*M. daubentonii*) in Poland in the period 1950–1991 (Kokurewicz 1995). Selection of eutrophic, standing waters would confirm our 1st prediction; however, pond bats prefer them only in spring. Astonishingly, after parturition, they not only shift to the other habitats, but even avoid eutrophic lakes, even if they are the most productive habitats in terms of abundance of aquatic insects (Forsyth 1976).

Lactating females may maximize their energy gain by selecting large insects, consequently obtaining a larger portion of energy by a single capture effort. This could explain their switch in diet from chironomids, that are much smaller in body size and predominant in (hyper)eutrophic waters, to the much larger caddisflies, typically present not only in fast-flowing rivers but also in lakes with a lower nutrient content (that is, mesotrophic lakes buffered from eutrophication by surrounding forests) observed during our previous study on the diet of pond bats (Ciechanowski and Zapart 2012). Such a shift remained unexplained until this present study that has demonstrated the change to rivers as main foraging habitats in mid-June, corresponding to the lactation period. Furthermore, the only trichopteran family positively identified in fecal samples from Lubnia was Hydropsychidae (Ciechanowski and Zapart 2012), known as specialized rheophiles, that undergo larval development in running waters. Thus, the pond bat conforms to optimal foraging models by selecting for prey size and rejecting energetically unprofitable prey. This shift in the dominant prey component was presumably accomplished not by sensory perception of different prey classes, as in the greater horseshoe bat *Rhinolophus ferrumequinum* (Jones 1990), but by a shift among habitats of different prey composition. It was already known, that, after parturition, female bats may shift from opportunistic foraging to selective exploitation of more profitable sites, as revealed by *Eptesicus nilssonii* (Haupt et al. 2006). Our study revealed, however, that such sites are not always considered the most productive in terms of nutrient content or total biomass of insects.

This study exposes the importance of small, relatively fast-flowing rivers in an energetically crucial period of the year for a species that was generally perceived as being associated with large water bodies, either standing (lakes, artificial reservoirs, fish ponds) or slow-flowing (wide irrigation canals, dead river branches, etc.). Small rivers are recently under significant threat in Poland, not so much by pollution but rather by river engineering as a result of antiflooding policies or the increasing popularity of small hydroelectric power stations. Such modifications may lead not only to the degradation of habitats for lotic insects that comprise the main prey of pond bats during lactation, but also to the destruction of river banks with trees acting as night roosts, often a neglected habitat element of a bat home range (Knight and Jones 2009).

Acknowledgments

The authors are grateful to all who participated in the field studies: T. Bellstedt, K. Bidziński, J. Haddow, M. Halewicz, A. Haplicznik, M. Ignaczak, K. Iwińska, A. Jankowska, M. Jankowska-Jarek, M. Jaśkiewicz, A. Kiełtyka, A. Koziura, A. Królikowska, M. Krzemińska, E. Kwasiborska, K. Lis, M. Łochyński, S. Marcinkowski, T. Marszałek, A. Nalewaja, T. Narczyński, A. B. Peichert, P. Piliczewski, G. Sadowska, C. Schmidt, J. Szenborn, R. Szuflet, M. Szurlej, T. Szwarczyński, P. Tomasik, M. Więckowska, J. Wysiński, and D. Zyskowski. The study was supported by grants from Bat Conservation International (USA) and the Regional Fund for Environmental Protection and Water Management in Gdańsk WFOŚ/D/611/70/2013 received by AZ. Page charges were covered by Wrocław Centre of Biotechnology, program The Leading National Research Centre (KNOW) for years 2014–2018 (TK and MR). We are also grateful to J. Haddow (Scotland, UK) for critical remarks and English corrections.

Literature Cited

Aldridge, H. D. J. N., and R. M. Brigham. 1988. Load carrying and manoeuvrability in an insectivorous bat: a test of the 5% 'rule' of radio-telemetry. Journal of Mammalogy 69:379–382.

Almenar, D., J. Aihartza, U. Goiti, E. Salsamendi, and I. Garin. 2008. Diet and prey selection in the trawling long-fingered bat. Journal of Zoology (London) 274:340–348.

Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology 68:460–471.

Baagøe, H. J. 1987. The Scandinavian bat fauna: adaptive wing morphology, and free flight in the field. Pp. 57–74 in Recent advances in the study of bats (M. B. Fenton, P. A. Racey, and J. M. V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.

Bartonička, T., A. Bielik, and Z. Řehák. 2008. Roost switching and activity patterns in the soprano pipistrelle, *Pipistrellus pygmaeus*, during lactation. Annales Zoologici Fennici 45:503–512.

Bernard, H. J., and A. A. Hohn. 1989. Differences in feeding habits between pregnant and lactating spotted dolphins (*Stenella attenuata*). Journal of Mammalogy 70:211–215.

Biscardi, S., D. Russo, V. Casciani, D. Cesarini, M. Mei, and L. Boitani. 2007. Foraging requirements of the endangered long-fingered bat: the influence of micro-habitat structure, water quality and prey type. Journal of Zoology (London) 273:372–381.

Bongi, P., et al. 2008. Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. Journal of Zoology (London) 276:242–251.

Boonman, A. M., H. J. G. A. Limpens, and B. Verboom. 1995. The influence of landscape elements on the echolocation of the pond bat *Myotis dasycneme*. Le Rhinolophe 11:39–40.

Britton, A. R. C., G. Jones, J. M. V. Rayner, A. M. Boonman, and B. Verboom. 1997. Flight performance, echolocation and foraging behaviour in pond bats, *Myotis dasycneme* (Chiroptera: Vespertilionidae). Journal of Zoology (London) 241:503–522.

Byers, R., R. K. Steinhorst, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. Journal of Wildlife Management 48:1050–1053.

Buckley, D. J., et al. 2013. The spatial ecology of the whiskered bat (*Myotis mystacinus*) at the western extreme of its range provides evidence of regional adaptation. Mammalian Biology 78:198–204.

Carrete, M., and J. A. Donázar. 2005. Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the cinereous vulture, *Aegypius monachus*. Biological Conservation 126:582–590.

Catto, C. M. C., P. A. Racey, and P. J. Stephenson. 1995. Activity patterns of the serotine (*Eptesicus serotinus*) at a roost in southern England. Journal of Zoology (London) 235:635–644.

Ciechanowski, M., K. Sachanowicz, and T. Kokurewicz. 2007. Rare or underestimated? – The distribution and abundance of the pond bat (*Myotis dasycneme*) in Poland. Lutra 50:107–134.

Ciechanowski, M., and A. Zapart. 2012. The diet of the pond bat *Myotis dasycneme* and its seasonal variation in a forested lakeland of northern Poland. Acta Chiropterologica 14:73–80.

Clutton-Brock, T. H., G. R. Iason, S. D. Albon, and F. E. Guiness. 2009. Effects of lactation on feeding behaviour and habitat use in wild red deer hinds. Journal of Zoology (London) 198:227–236.

Crichton, M. I., and D. B. Fisher. 1982. Records of caddis flies (Trichoptera) from Rothamsted light traps at field centres. Field Studies 5:569–579.

Dietz, M., Encarnação, J. A., and E. Kalko. 2006. Small scale distribution patterns of female and male Daubenton's bats (*Myotis daubentonii*). Acta Chiropterologica 8:403–415.

Dietz, C., O. Helversen, and D. Nill. 2009. Bats of Britain, Europe and Northeastern Africa. A&C Black, London, United Kingdom.

Estók, P., and C. Tamás. 2008. Egy tavi denevér *Myotis dasycneme* (Boie, 1825) rádiós nyomkövetésének eredményei [The results of the radiotracking of a pond bat *Myotis dasycneme* (Boie, 1825)]. Denevérkutatás [Hungarian Bat Research News] 4:42–44 (in Hungarian with English summary).

Fenton, M. B., and W. Bogdanowicz. 2002. Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*. Canadian Journal of Zoology 80:1004–1013.

Flannagan, J. F., and G. H. Lawler. 1972. Emergence of caddisflies (Trichoptera) and mayflies (Ephemeroptera) from Heming Lake, Manitoba. Canadian Entomologist 104:173–183.

Fletcher, Q. E., et al. 2015. Daily energy expenditure during lactation is strongly selected in a free-living mammal. Functional Ecology 29:195–208.

Forsyth, D. J. 1976. Insects and aquatic ecosystems. The New Zealand Entomologist 6:132–137.

Haarsma, A.-J., and D. Tuitert. 2009. An overview and evaluation of methodologies for locating the summer roosts of pond bats (*Myotis dasycneme*) in the Netherlands. Lutra 52:47–64.

Haupt, M., S. Menzler, and S. Schmidt. 2006. Flexibility of habitat use in *Eptesicus nilssonii*: does the species profit from anthropogenically altered habitats? Journal of Mammalogy 87:351–361.

Henry, M., D. W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). Journal of Mammalogy 83:767–774.

Hildebrand, G. V., C. C. Schwartz, C. T. Robbins, and T. A. Hanley. 2000. Effect of hibernation and reproductive status on body mass and condition of coastal brown bears. Journal of Wildlife Management 64:178–183.

Horáček, I. 1981. Comparative notes on the population structure in several European bat species. Myotis 18–19:48–53.

Horáček, I., and V. Hanák. 1989. Distributional status of *Myotis dasycneme*. Pp. 565–590 in European bat research 1987 (V. Hanák, I. Horáček, and J. Gaisler, eds.). Charles University Press, Praha, Czechoslovakia.

Hutson, A. M., S. Aulagnier, and Z. Nagy. 2008. *Myotis dasycneme*. The IUCN Red List of Threatened Species 2008:e.T14127A4399651. http://www.iucnredlist.org/details/full/14127/0. Accessed 29 October 2015.

Jaberg, C., and J.-D. Blant 2003. Spatio-temporal utilisation of roosts by the parti-coloured bat *Vespertilio murinus* L., 1758 in Switzerland. Mammalian Biology 68:341–350.

Jones, G. 1990. Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation. Journal of Animal Ecology 59:587–602.

Kerth, G., C. Ebert, and C. Schmidtke. 2005. Group decision making in fission–fusion societies: evidence from two-field experiments in Bechstein's bats. Proceedings of the Royal Society B 7:2785–2790.

Kmiecik, A., and P. Kmiecik. 2015. Nowa kolonia rozrodcza nocka łydkowłosego *Myotis dasycneme* w moście w Wigierskim Parku Narodowym [A new nursery colony of pond bats *Myotis dasycneme* in the bridge in the Wigierski National Park]. Przegląd Przyrodniczy 26:57–60.

Knight, T., and G. Jones. 2009. Importance of night roosts for bat conservation: roosting behavior of the lesser horseshoe bat *Rhinolophus hipposideros*. Endangered Species Research 9:79–86.

Kokurewicz, T. 1995. Increased population of Daubenton's bat (*Myotis daubentonii* (Kuhl, 1819) (Chiroptera: Vespertilionidae) in Poland. Myotis 32–33:155–161.

Krüger, F., E. L. Clare, S. Greif, B. M. Siemers, W. O. Symondson, and R. S. Sommer. 2014. An integrative approach to detect subtle trophic niche differentiation in the sympatric trawling bat species *Myotis dasycneme* and *Myotis daubentonii*. Molecular Ecology 23:3657–3671.

Krüger, F., I. Harms, A. Fichtner, I. Wolz, and R. S. Sommer. 2012. High trophic similarity in the sympatric North European trawling bat species *Myotis daubentonii* and *Myotis dasycneme*. Acta Chiropterologica 14:347–356.

Kunz, T. H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). Ecology 55:693–711.

Limpens, H. J. G. A., P. H. C. Lina, and A. M. Hutson. 2000. Action plan for the conservation of the pond bat in Europe (*Myotis dasycneme*). Convention on the Conservation of European Wildlife and Natural Habitats. Nature and Environment, No. 108. Council of Europe Publishing, Strasbourg, France.

Lintott, P. R., et al. 2014. City life makes females fussy: sex differences in habitat use of temperate bats in urban areas. Royal Society Open Science 1:140200.

Lučan, R., and J. Radil. 2010. Variability of foraging and roosting activities in adult females of Daubenton's bat (*Myotis daubentonii*) in different seasons. Biologia 65:1072–1080.

Lundy, M. G., et al. 2012. Behavioural context of multi-scale species distribution models assessed by radio-tracking. Basic and Applied Ecology 13:188–195.

Mackie, I. J., and P. A. Racey. 2007. Habitat use varies with reproductive state in noctule bats (*Nyctalus noctula*): implications for conservation. Biological Conservation 140:70–77.

Maier, C. 1992. Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. Journal of Zoology (London) 228:69–80.

Marques, J. T., A. Rainho, M. Carapuço, P. Oliveira, and J. M. Palmeirim. 2004. Foraging behaviour and habitat use by the European free-tailed bat *Tadarida teniotis*. Acta Chiropterologica 6:99–100.

Miller, B. K., and J. A. Litvajtis. 1992. Habitat segregation by moose in a boreal forest ecotone. Acta Theriologica 37:41–50.

Morris, D. W. 1984. Sexual differences in habitat use by small mammals: evolutionary strategy or reproductive constraints. Oecologia 65:51–57.

Murray, S. W., and A. Kurta. 2004. Nocturnal activity of the endangered Indiana bat (*Myotis sodalis*). Journal of Zoology (London) 262:197–206.

Nyholm, E. S. 1965. Zur Ökologie von *Myotis mystacinus* (Leisl.) und *Myotis daubentoni* (Leisl.) (Chiroptera). Annales Zoologici Fennici 2:77–123.

Perez, M. A., and E. E. Mooney. 1986. Increased food and energy consumption of lactating northern fur seals *Callorhinus ursinus*. Fishery Bulletin 84:371–381.

Popa-Lisseanu, A., F. Bontadina, O. Mora, and C. Ibañez. 2008. Highly structured fission–fusion societies in an aerial-hawking, carnivorous bat. Animal Behaviour 75:471–482.

Racey, P. A., and J. R. Speakman. 1987. The energy costs of pregnancy and lactation in heterothermic bats. Symposia of the Zoological Society of London 57:107–125.

Reinhold, J. O., A. J. Hendriks, L. K. Slager, and M. Ohm. 1999. Transfer of microcontaminants from sediment to chironomids, and the risk for the pond bat *Myotis dasycneme* (Chiroptera) preying on them. Aquatic Ecology 33:363–376.

Rosenberg, D. K., and K. S. Mckelvey. 1999. Estimation of habitat selection for central-place foraging animals. Journal of Wildlife Management 63:1028–1038.

Safi, K., and G. Kerth. 2004. A comparative analysis of specialization and extinction risk in temperate-zone bats. Conservation Biology 18:1293–1303.

Safi, K., B. König, and G. Kerth. 2007. Sex differences in population genetics, home range size and habitat use of the parti-colored bat (*Vespertilio murinus*) in Switzerland and their consequences for conservation. Biological Conservation 137:28–36.

Scheibe, J.S., and M. J. O'Farrell. 1995. Habitat dynamics in *Peromyscus truei*: eclectic females, density dependence, or reproductive constraints? Journal of Mammalogy 76:368–375.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild animals in research. Journal of Mammalogy 92:235–253.

Smith, P. G., and P. A. Racey. 2008. Natterer's bats prefer foraging in broad-leaved woodlands and river corridors. Journal of Zoology (London) 275:314–322.

Speakman, J. R. 2008. The physiological costs of reproduction in small mammals. Philosophical Transactions of The Royal Society B 363:375–398.

Speakman, J. R., R. E. Stone, and J. E. Kerslake. 1995. Temporal patterns in the emergence behaviour of pipistrelle bats, *Pipistreffus pipistrellus*, from maternity colonies are consistent with an anti-predator response. Animal Behaviour 50:1147–1165.

Swift, S. M. 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. Journal of Zoology (London) 190:285–295.

Tokeshi, M. 1995. Life cycles and population dynamics. Pp. 225–268 in The Chironomidae: biology and ecology of non-biting midges (P. D. Armitage, P. S. Cranston, and L. C. V. Pinder, eds.). Chapman & Hall, London, United Kingdom.

Van De Sijpe, M., and L. Holsbeek. 2007. Hunting strategy and tympanate moth predation by the pond bat (*Myotis dasycneme*). Lutra 50:91–106.

Van De Sijpe, M., et al. 2004. Summer distribution of the pond bat *Myotis dasycneme* (Chiroptera, Vespertilionidae) in the west of Flanders (Belgium) with regard to water quality. Mammalia 68:377–386.

Verboom, B., A. M. Boonman, and H. J. G. A. Limpens. 1999. Acoustic perception of landscape elements by the pond bat (*Myotis dasycneme*). Journal of Zoology (London) 246:59–66.

Voŭte, A. M., J. W. Sluiter, M. P. Grimm. 1974. The influence of the natural light-dark cycle on the activity rhythm of pond bats (*Myotis dasycneme* Boie, 1825) during summer. Oecologia 17:221–243.

Winship, A. J., W. A. Trites, and D. A. S. Rosen. 2002. A bioenergetics model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. Marine Ecology Progress Series 229:291–312.

Wołoszyn, B. W. 2001. *Myotis dasycneme* (Boie, 1825). Pond bat. Pp. 51–52 in Polish red data book of animals. Vertebrates (Z. Głowaciński, ed.). Państwowe Wydawnictwo Rolnicze i Leśne, Warszawa, Poland (in Polish with English summary).

Womack, K. M., S. K. Amelon, and F. R. Thompson. 2013. Summer home range size of female Indiana bats (*Myotis sodalis*) in Missouri, USA. Acta Chiropterologica 15:423–429.

Young, T. P., and L. A. Isbell. 1991. Sex differences in giraffe feeding ecology: energetic and social constraints. Ethology 87:79–89.

Zahn, A., S. Bauer, E. Kriner, and J. Holzhaider. 2009. Foraging habitats of *Myotis emarginatus* in Central Europe. European Journal of Wildlife Research 56:395–400.

Zahn, A., H. Haselbach, and R. Güttinger. 2005. Foraging activity of central European *Myotis myotis* in a landscape dominated by spruce monocultures. Mammalian Biology 70:265–270.

Submitted 25 November 2015. Accepted 9 June 2016.

Associate Editor was Jorge Ortega.