



Pond Bat *Myotis dasycneme* (Boie, 1825)

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Common Names

English	Pond bat
German	Teichfledermaus
French	Murin des marais
Spanish	Murciélago lagunero
Italian	Vespertilio dasycneme
Russian (in Cyrillic)	Ночница прудовая

Taxonomy, Systematics and Paleontology

Myotis dasycneme (Fig. 1) is one of more than 100 currently known *Myotis* species (Burgin et al. 2018). *Myotis* has evolved by means of three main foraging strategies and morphological types (i.e., ecomorphs; Findley 1972). The phenotypic characteristics of each ecomorph appear to have evolved independently (Ruedi and Mayer 2001;



Fig. 1 Typical free-hanging posture during hibernation (Photograph Yves Adams)

Ghazali et al. 2017). The pond bat belongs to the ecomorph Leuconoe (near-water hunters).

In the winter of 1822, Boie received several bats captured in the caves of Dagbjerg, located in present-day Jutland, Denmark. They were originally identified as *Vespertilio mystacinus*. Due to the abnormal size of the female bat in the sample, the bats were described by Boie as a new species in 1825, *Vespertilio dasycneme* (Tupinier 2001). After reassigning a number of species in the genus *Vespertilio* to *Myotis*, this species is now named *Myotis dasycneme* (Boie, 1825).

The first fossil records similar to the modern pond bat are three million years old (Kowalski 1956) and were found in late Pliocene fossil layers in caves in Poland (MN14-17 in Fig. 2). These fossil remains are morphologically similar to recent pond bat bones (Ciechanowski et al. 2007), suggesting that little change has occurred over time. The date of the first appearance of *Myotis dasycneme* and its location of origin are still unknown.

Few articles have been published on the pond bat distribution during the Pliocene and Pleistocene (e.g., Topál 1963; Jánossy 1964; Mein 1975; Horáček 1976; Jánossy and Kordos 1977; Rabeder 1977; Postawa 2004; Argenti et al. 2008; Popov and Lakovski 2019, Fig. 2). According to these studies, the pond bat occurred within the present-day borders of Austria, Czechia, France, Germany, Hungary, Italy, Poland, and Slovakia. The different distribution of waterbodies during the Pliocene and Pleistocene (Fortelius et al. 2002) can explain the findings of pond bat fossils in sites that would otherwise be unsuitable in today's landscapes. With decreasing temperatures, the ice coverage

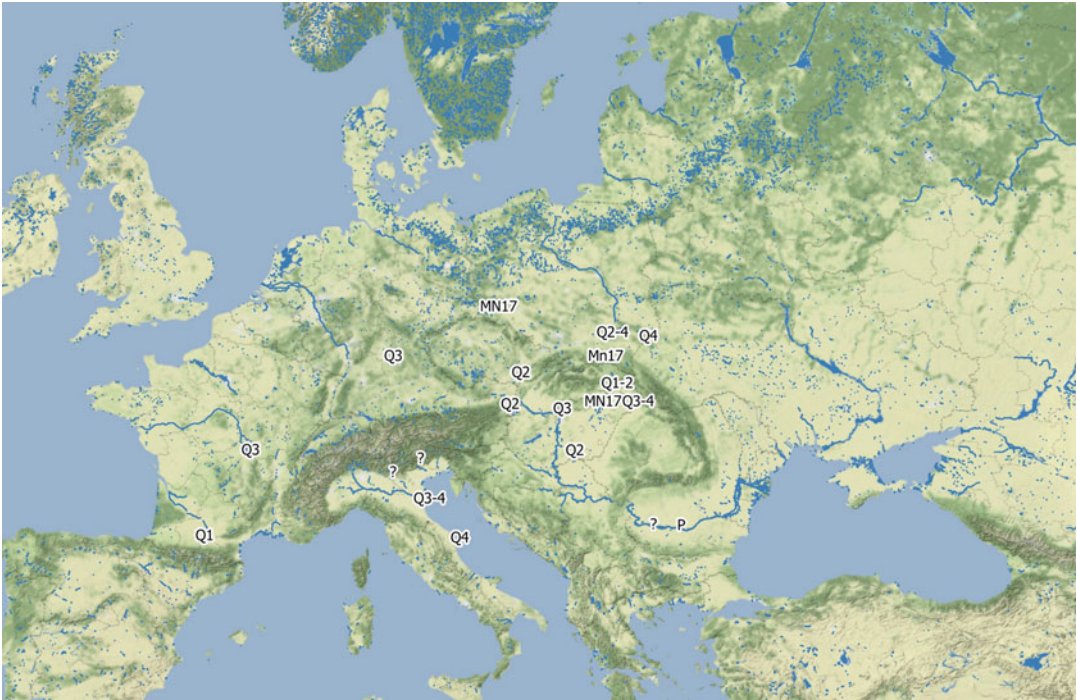


Fig. 2 Fossil records of the pond bat, *Myotis dasycneme* (sl.), in Europe. Main waterbodies and waterways are indicated in blue; areas relief are indicated in darker shades of green. Observations are clustered in the following periods: MN zonation (“Mammal Neogene”) correlates

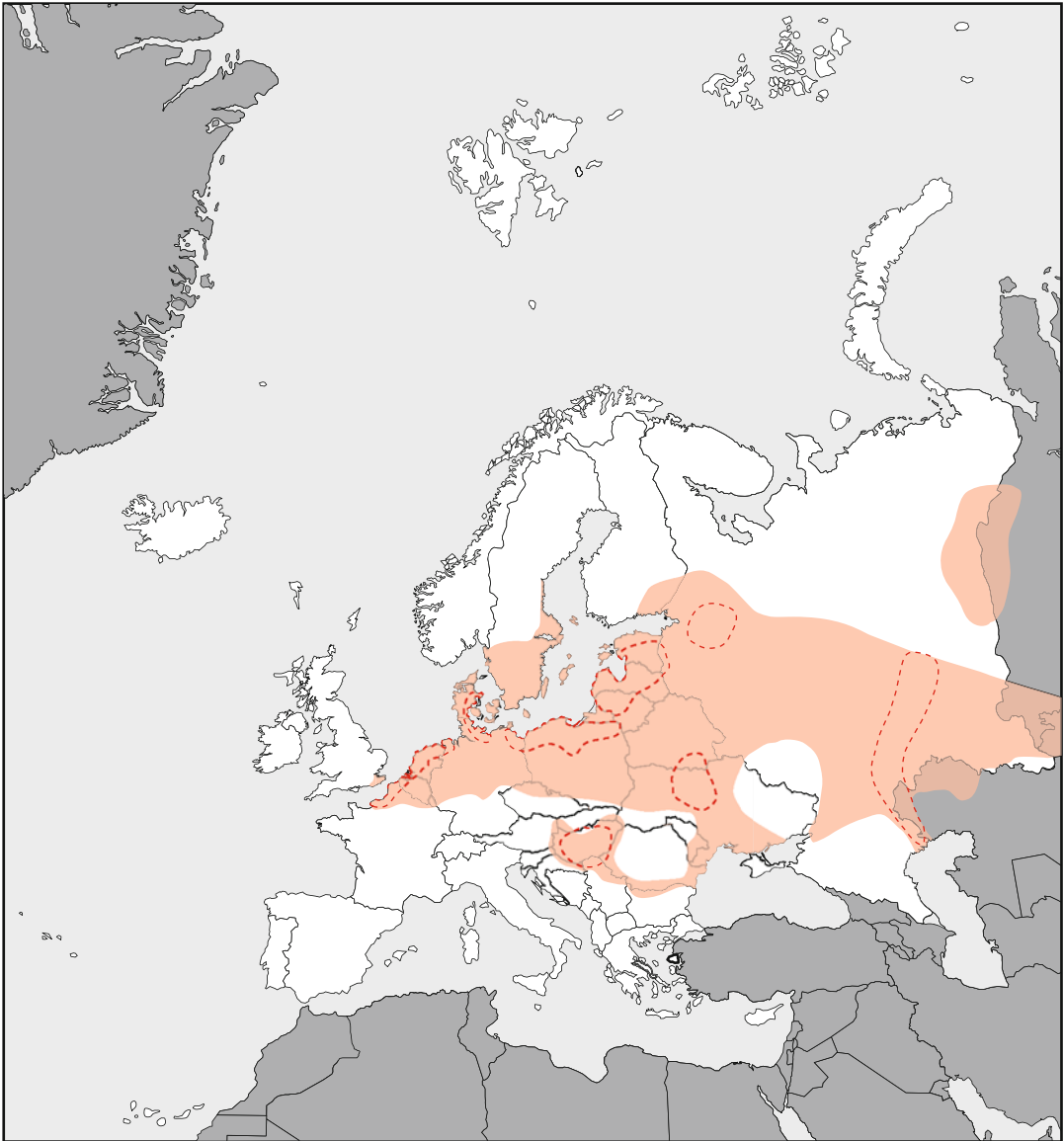
mammal-bearing fossil localities in the Miocene (Zones MN1–MN13) and Pliocene (MN14–MN17) epochs of Europe; Quaternary epoch (Early Pleistocene Q1, Middle Pleistocene Q2, Late Pleistocene Q3, and Holocene Q4); and Postglacial (P)

in northern regions expanded, lowering the sea level in the process. The temperature changes altered the vegetation and associated insect diversity. Grasslands began to predominate in lowland areas and created unsuitable conditions for the pond bat. Peat formation began from the late Boreal period (10.640–9.220 years ago) onwards. In this period, tree cavities were most likely used as roosts all year round (Sluiter et al. 1971). In contrast to the Daubenton’s bat (*Myotis daubentonii*), the pond bat did not cross the North Sea, which only filled up 9000 years ago, suggesting the distribution of the pond bat did not reach as far west or north as it does today.

Current Distribution

The pond bat is distributed from France eastward to the Ural/Chelyabinsk region (Snit’ko and Snit’ko 2017) and the Yenisey region in central

Russia. It occurs in lowlands of the Palearctic (between latitude 49 and 61) (Fig. 3). Throughout its range, pond bats tend to show a semi-continuous distribution pattern (Horáček and Hanák 1989; Horáček 1999), with few areas of high pond bat density, where most if not all maternity roosts are located, within larger areas of low to very low pond bat densities, with most observations referred to overwintering individuals or, in summer, winter nonbreeding bats. Large breeding populations are found in the Netherlands, the Baltic States, and Russia. Dunkirk and Looberghe (France) are considered the westernmost breeding locations in Europe, and Estonia the northernmost (59 °N). The relatively northern distribution pattern (above 49 °N) has one notable exception, focused around the Pannonic lowland (Horáček and Hanák 1989; Popov and Sedefchev 2003; Lučan et al. 2007; Görföl et al. 2018), a large flat alluvial basin, divided from north to south by two major rivers: the Danube and Tisza. This region



Map template: © Getty Images/iStockphoto

Fig. 3 Schematic overview of the summer distribution of the pond bat (*Myotis dasycneme*). In apricot, the total range is indicated, with a higher density of animals in the summer (i.e., breeding populations or estimates thereof) indicated in red dashed polygons. (Based on IUCN Red List of Threatened Species. Version 2017-2/Limpens et al.

(1999), with higher densities based on Haarsma et al. (2019).) The European continent includes Western Europe as far east as the border of the Asian continent. The Atlantic islands of the Azores, Madeira, and the Canary Islands are also included (Map template: © Copyright Getty Images/iStockphoto)

includes all of Hungary and parts of Slovakia, Serbia, and Romania. Currently, the southernmost breeding location in Europe is in Serbia (Benda et al. 2003). The eastern range includes Ukraine,

Belarus, Russia, Kazakhstan, and Manchuria (Strelkov and Il'in 1990; Golovatch et al. 2018). The boundaries of the European range are not definitive. Anecdotal findings are available for

the United Kingdom (UK) (Crawley et al. 2020; Hutson 2005), Finland (Siivonen and Wermundsen 2003), the Caucasus (Gazaryan 2004), Austria (Reiter et al. 2010), and Luxembourg (Gessner 2012). It is unclear whether these findings reflect the limits of the summer range or are only accidental autumn/winter visits.

Although *M. dasycneme* is relatively rare, it is among the better-documented European bat species. However, complete knowledge of population size and the number of known maternity roosts is sparse (Table 1). The level of detail depends on the investigation effort and methods used. In some regions, such as the Netherlands, Belgium, France, Germany, and Latvia, distribution knowledge is relatively accurate, with areas of known presence and known absence. In contrast, in extensive regions such as Poland, Hungary, Ukraine, and Russia, the number of findings is limited. Due to insufficient surveys in such vast regions, the population size or distribution pattern can only be estimated approximately.

Throughout its range, the pond bat is not a cave dweller. Across Europe, less than 5% of the population is observed during the winter (Limpens et al. 1999; Haarsma 2012, Pētersons and Vintulis 2020). It seems probable that the species may locally avoid underground hibernacula and go unnoticed. In most countries, low densities of pond bats are detected during the winter, even in countries with high summer densities (Table 2).

Description

Size and Morphology

The pond bat is a medium-sized bat. The ears are relatively long (15–17 mm, 1/7–1/8 of the body length). The tragus is unusually short for a *Myotis* species and slightly bent inwards. The muzzle is broad, reddish brown with several inconspicuous warts, and only a small pinkish zone around the eyes. The nostrils are wide and heart-shaped. The wings are relatively long and narrow (aspect ratio 6.8, Norberg and Rayner 1987). Wing loading

varies between 14.3 and 16.3 (N/m²). The wing is attached to the heel. The penis of adult males is clearly club-shaped at the end. The feet are very large (11–12 mm), with long bristles. The dorsal fur is dense (hairs are ca. 8 mm long), pale gray-brown, and sharply demarcated with white or white-gray ventral fur. All hairs are two-colored with a dark, black/grayish basis. The young of the year (YoY) are distinguished by a dark face color in combination with more gray fur. The hairs on the inside lower leg of YoY are thick and downy. Both YoY and reproductive females can have conspicuous bald spots on their backs (Haarsma and van Alphen 2009a). Regrowth of these hairs occurs at the end of the summer (June/July), suggesting the molt of this species starts relatively early compared to other *Myotis*. Age can be estimated based on the color of a chin spot, which changes from dark to progressively paler in the course of time (Haarsma and van Alphen 2009b). Individuals with an above-average age are recognizable by a light brown muzzle, a light chin spot in combination with a completely white nose tip. Cases of melanism have been reported (Dekeukeleire et al. 2013). During winter, in a free-hanging position, the pond bat can be recognized by its long ears, which, depending on the posture of the hibernating bat, often reach beyond the nose, a relatively narrow waist, and clunky broad, purple-colored forearms. The relatively long nose extends slightly beyond the underlip when the bat is hanging on the wall or from the ceiling. The hair zone on the forehead does not end abruptly but rather extends almost to the tip of the nose. Table 3 shows ranges for body measurements, most of which are employed for species identification.

Skull and Teeth

The skull of the pond bat is flat and wide. The skull is similar to that of Daubenton's bat but has a concave forehead, and is much smaller, with a relatively smaller brain zone and a longer rostral section (Lange et al. 1986; Jenrich et al. 2012).

Table 1 Estimated population size of pond bat (*Myotis dasycneme*) in a selection of countries with known breeding populations (updated table based on Limpens et al. (1999)). The European continent includes Western Europe as far east as the border of the Asian continent. The large variation in the estimates is indicative of different

knowledge/survey methods. The number of known roosts for all countries should be interpreted as a minimum. If substantially more roosts are expected, because information is severely lacking, this is indicated with "?". Population sizes are given as follows: * = 1–100, ** = 100–2000, *** = 2000–5000, and **** = more than 4000

Country or part of country	# known maternity roosts	Breeding population size during summer	Nonbreeding population size during summer	References
Belarus	3	**		In Viciebsk Voblasć, Hrodna Voblasć, and Vygonoschanskoje. Dziamianchyk et al. 2004; Shpak et al. 2022
Belgium	3	*	*	3 known (small) maternity roosts in Oostkerke, Boezinge, and Ieper. Verkem et al. 2003; Van de Sijpe et al. 2004; Rotsaert et al. 2017
Denmark (Jutland)	1?	*	*?	Baagøe 2007
Estonia	10?	***		In Palupohja, other locations are not described. Masing et al. 2000, 2004
France	2	*		2 known small roosts in Looberghe and Duinkerke. Parmentier et al. 2005; Arthur and Lemaire 2009
Germany	17	***	**	Approx. 1 maternity roost in Bremen, 9 summer/maternity roost only in Lower Saxony, 6 in Schleswig-Holstein, 1 Mecklenburg-Vorpommern, and 1 in Brandenburg. Boye et al. 2004 with update by Lothar Bach, Labes 1992
Bulgaria	1?	*		Benda et al. 2003. Only one observation (ultrasound recording)
Czech Republic and Slovakia	?		*?	Horáček and Uhrin 2010
Bulgaria/Romania	?	**		Görföl et al. 2018; Benda et al. 2003
Serbia	1?	*	*?	Görföl et al. 2018. Some evidence of breeding, netted sub-adult and postlactating females
Hungary		**		In Tokaj, other locations are only indicative. Görföl et al. 2018; Bihari and Gombkötő 1994; Gombkötő 1998a; Dombi and Szatyor 2007; Estók and Tamás 2008
Kaliningrad (Russian Federation)	?	*	?	Along the Pregolja
Latvia	26	****		Pētersons and Vintulis 2020
Lithuania	0?	?		
Moldova		*	?	
The Netherlands	69	****	***	Haarsma 2012
Poland	2–11?	**	?	Two known large maternity roosts, in Jeleniewo and Lubnia. Furthermore, 6–11 findings which could be interpreted as indicative of a breeding site. Sachanowicz et al. 2006; Ciechanowski et al. 2007; Łupicki and Cichocki 2008

(continued)

Table 1 (continued)

Country or part of country	# known maternity roosts	Breeding population size during summer	Nonbreeding population size during summer	References
Ukraine	5?	**		Vlaschenko 2011; Vorobei et al. 2021; Godlevska et al. 2022
Russian Federation		****	**?	Large breeding population located around the Samara bend. Smirnov and Vekhnik 2014b; Snit'ko and Snit'ko 2017

Adult dentation develops from 2 to 3 months onwards and is expressed by the following dental formula: $2133/3133 = 38$. The three molars are powerful. P^1 and P^2 are located slightly towards the inside. P^2 is hardly visible from a lateral view (Fig. 4).

Physiology

Female pond bats usually select warm roosts during the breeding season (Kapteyn 1995). Preferences for roost temperatures of 35–40 °C are observed during early stages of reproduction (Haarsma 2012). Maternity roosts are sites that permit the storage of heat from the sun during the day. The observed thermal gradient is large, ranging from very hot during warm days and preferably still warm during colder days (Kapteyn 1995; Haarsma 2012). Maternity roosts are also found near spots unintentionally heated by humans, such as near a central heating installation or a boiler room. As all European bats, pond bats can enter torpor (to be a facultative heterotherm) to conserve energy and survive periods of low insect abundance during poor weather conditions. The benefits of using torpor are counterbalanced by its costs, such as, for females, a delay in fetal and presumably neonatal development (Racey and Entwistle 2000), leaving less time for females and their young to prepare for hibernation following weaning (Lausen and Barclay 2006). Energy management to hasten the developmental period of the offspring might be necessary for a short northern summer, especially when migration is also necessary (Haarsma and Siepel 2013a).

Different optimal temperatures during hibernation have been reported, probably also due to

regional differences in winter temperatures. Ranges have been recorded between 2 °C and 7 °C (Strelkov 1958), 2–7.5 °C (Masing 1981, 1982), –2.5–8 °C (Masing and Lutsar 2007), 5–7 °C (Haarsma 2011), and –1.9–12 °C (Gilson 1978). The temperature optimum differs between the sexes: male sites tend to be warmer (mean temperature: 8.1 °C, with an overall range of 2–12 °C) than female sites (mean temperature 6.0 °C, ranging from 0 °C to –13 °C) (Haarsma et al. 2019). Females tend to reside closer to the main entrance but move longer distances within the hibernacula than males (Smirnov and Vekhnik 2009). In stable sites, pond bats awaken on average once every 10–20 days. When the temperature in a winter site changes, pond bats follow their preferred climate zones (e.g., Bezem et al. 1964; Masing 1987; Korn 2008). There is no evidence of foraging during mild winter days, and the occasional flights seen in winter in the proximity of the roost are due to “light sampling behaviour,” as they are immediately followed by returns.

Genetics

The karyotype is unknown, probably $2n = 44$, similar to *Myotis petax* and *M. daubentonii* (Gorobeyko et al. 2020; Zima and Horáček 1985). Recent molecular studies of the pond bat with sampling localities in Germany, Denmark, Latvia, Russia, and Hungary detected significant genetic differentiation among all populations, probably due to genetic drift combined with a founder event (Andersen et al. 2019). The molecular phylogeny suggested a closer relationship between the Russian and Northern European populations compared to the Hungarian/

Table 2 Data of winter populations of the pond bat (*Myotis dasycneme*) in a selection of European countries (similar selection as Table 1). A distinction is made between observed during visual counting and estimated with mark-recapture during mating swarming. The European continent includes Western Europe as far east as the border of the Asian continent. The large variation in

the estimates is indicative of different knowledge/survey methods. The population estimates should be interpreted as a minimum. If substantially larger population is expected because the information is severely lacking, this is indicated with “?”. Population sizes are given in the following classifications: * = 1–100, ** = 100–2000, *** = 2000–5000, and **** = more than 4000

Country or part of country	Winter population based on visual surveys	Winter population based on estimates (e.g., mark recapture)	References
Belarus	*?		
Belgium	**		Palmans 2022; San Martin and Nyssen 2019 (>50 outside limestones in Wallonia, ~90 Flemish limestone district, >100 in Wallonish limestone district, 50 Antwerp fortresses) Rotsaert et al. 2017
Denmark		****	Møller et al. 2013; Degn 1987; Baagøe 2007, swarm estimates are approx. 4600 in Mønsted and approx. 3400 in Daugbjerg (Baagøe and Degn 2009).
Estonia	***		Masing 1983; Masing and Buša 1983; Lutsar et al. 2000
France	*		
Germany	**		Korn 2008; Boye et al. 2004
Hungary/ Romania/ Serbia	*		
Czech Republic and Slovakia	*		Horáček and Uhrin 2010
Kaliningrad (Russian Federation)	?	?	?
Latvia	**		
Lithuania	*		
Moldova	?	?	Caldari 2022
Slovenia			Matis et al. 2000; Noga 2007
The Netherlands	**	***	Haarsma et al. 2019; Haarsma 2012
Poland	**		Wojtaszyn et al. 2014; Ciechanowski et al. 2006; Piksa and Nowak 2013
Ukraine	*		Vlaschenko 2006, 2014
Russian Federation	**	****	Large winter population focused around the Urals and Samara bend. Il'in and Smirnov 2000; Strelkov 1958; Snit'ko and Snit'ko 2017, Belkin et al. 2015; Bol'shakov et al. 2005

Romanian population, implying that the latter belongs to an older, ancestral population.

To date, only one study of pond bat genetics is available (Andersen et al. 2019). Hence, levels of

genetic variability between populations or colonies in smaller areas or between populations on a larger international scale are not yet known, and possible risks of inbreeding cannot be judged.

Table 3 Body measurement ranges of an adult pond bat (*Myotis dasycneme*). Measurements were taken from Roer (2001), except for those marked with an asterisk which were taken from Dietz and von Helversen (2004) and Norberg and Rayner (1987). A double asterisk indicates recalculated values. Note that the only specimen used by Norberg and Rayner (1987) to calculate the aspect ratio for this species had an extreme weight of 11.4 g. The average weight should be between 15 and 20 g. The recalculated value is more representative of the species. More measurements for this species, concerning wing area, aspect ratio, and wing loading, are advisable

Measurement	Range
Forearm length**	43–50.1 (mm)
Fifth finger**	57–65 (mm)
Third finger*	72–77 (mm)
Head to toe (during winter)	570–670 (mm)
Ear length	15–17 (19) (mm)
Weight males**	14–20 (18–22 pre-winter) (g)
Weight females**	16–23 (20–26 pre-winter) (g)
CBL	16.6–17.1
CM3	5.9–6.5 mm
Skull length	16.8–18.1 mm
Wing loading**	14.3–16.3 N/m ²
Aspect ratio **	6.8

Life History

The average age of females at first reproduction is 2.2 years (Haarsma and Siepel 2013b). Females tend not to participate in reproduction in their first autumn. Timing of birth, as in other species, depends largely on the age and post-hibernation weight of the mother, environmental conditions, and corresponding food availability (Linton and Macdonald 2018; Barclay et al. 2004), as well as ambient temperature of the roost. Young females tend to arrive later at the maternity roost, and if they become pregnant, they give birth much later in the year. In the Netherlands, the first pregnancies are observed at the beginning of April and the last at the end of June. Lactation is observed from the beginning of May until the beginning of August (Haarsma and van Alphen 2009b). Gestation is ca. 50 days, and weaning is ca. 31.5 days. The weight of the newborn is ca. 5 g, which is ca. 27% of the weight of the mother, with a forearm length at birth of 17.5 mm. The litter size is

1.1; twins are rare and can be fatal for the mother (Verbeek 1998). In the Netherlands and Germany, the first flying offspring are expected around the beginning of June (Haarsma and Tuitert 2009; Dolch et al. 2001). Large differences, up to 9 weeks, between the first- and last-born pup are common. As in other species, late births have a much lower chance of survival (Lausen and Barclay 2006). Geographical differences in timing, reproductive rate, and litter size are expected (Barclay et al. 2004; Roer 2001; Reusch et al. 2022).

Spermatogenesis begins in August, and in September, males have a visibly full epididymis. In the Netherlands, the mating season starts at early July and last till the end of September (Haarsma 2011). Pre-hibernation weight is 20–23 g (up to 26 g) for females and 18–20 g for males (Daan 1973; Korn 2008, Šuba et al. 2011; Fjederholt 2013; Haarsma et al. 2019). After a period of intermittent mating and torpor during unfavorable weather periods, hibernation starts from September onwards (Degn et al. 1995; Daan 1973; Masing and Buša 1983; Haarsma 2013). The population at one site increases until the end of November (Fjederholt 2013), and the peak of observable bats is between December and the end of January. Hibernation is repeatedly interrupted by brief active periods used for winter mating (Roer and Egsbeak 1969), drinking, or roost switching (Daan 1973). Detailed observations of 21 pond bat winter matings by Korn (2008) showed that matings lasted between 30 and 240 min. The first females leave the hibernacula from the end of February/beginning of March (Korn 2008), depending on the latitude of the hibernacula, while males seem to leave later (Baagøe and Degn 2009). Pond bats can be observed in their hibernacula as late as April (Korn 2008; Baagøe and Degn 2009; Haarsma 2013). Weight at this moment is 17 g (females) and 15 g (males) (Daan 1973). Females store spermatozoa until ovulation, which occurs between the beginning of March and the end of April.

The observed average age, without survival of YoY considered, is 5.0 years. The maximum observed age is 20.5 years (Sluiter et al. 1971; Haarsma and Siepel 2013b) (Fig. 5).

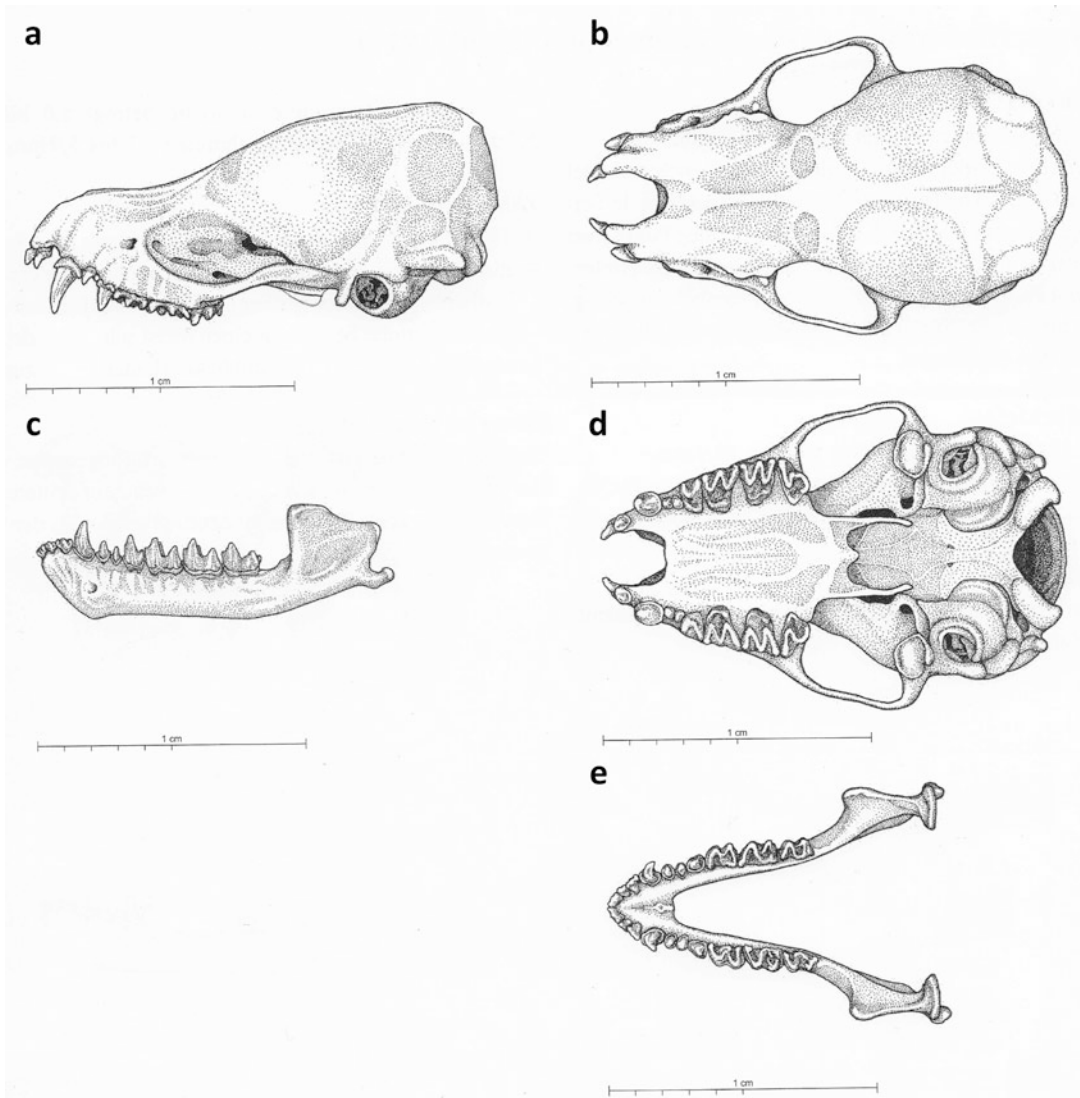


Fig. 4 Skull of *Myotis dasycneme*; (a, b, d) lateral, dorsal, and ventral view of skull; (c) lateral view of left mandible (view from outside); (e) dorsal view of mandible (© Franz Müller with kind permission)

Habitat and Diet

Foraging Habitat

Large, slow-moving, freshwater bodies are favorable (approximately 75% of their time) foraging habitats of the pond bat. Water bodies include canals (> 2.5 m wide), rivers, lakes, swamp/marshland areas and ponds. Reproductive females typically include more larger waterbodies in their home ranges than males (Ciechanowski et al.

2017; Smirnov and Vekhnik 2014b; Table 4). The high productivity of aquatic habitat in terms of insect biomass is crucial for the pond bat. Ciechanowski et al. (2017) showed that pregnant and lactating females select their foraging habitats. While pregnant females selected eutrophic and avoided mesotrophic lakes, mesotrophic lakes were preferred, and eutrophic lakes were avoided during lactation. In the Netherlands females are mainly found in peatlands with shallow water (<2 m), while males not only live in

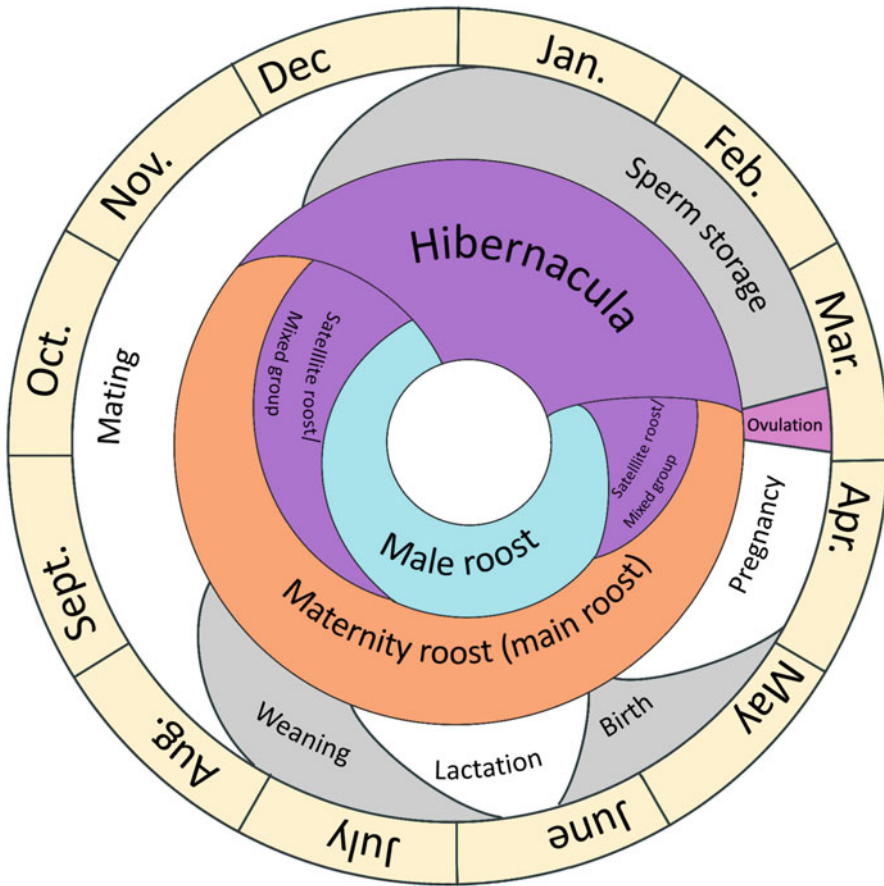


Fig. 5 Generalized life cycle diagram of reproduction and roosting for the pond bat (*Myotis dasycneme*). The 12 months of a calendar year are indicated in the outer circle. The alternating reproductive phases of females are indicated in the second outer circle in two different shades of gray with ovulation indicated in pink. The beginning

and end of each phase can shift in time, as indicated by the curved lines. Male and female pond bats use separate roosts (indicated in red for females in blue for males) during summer. Outside this period, both sexes often use the same roost, sometimes even in mixed groups (indicated in purple) (After Haarsma and Tuitert 2009)

Table 4 Size and number of open water bodies within the essential home range of the pond bat (*Myotis dasycneme*) in the Netherlands, expressed as the habitat where 80% of the entire group hunts 80% of its time). Large is defined as

>20.000 m². Data were collected in the summer months, between 15 May and 15 July, over a period of 15 years and refer to 70 male roosts and 38 female roosts identified through radiotracking (A.-J. Haarsma, unpublished data)

	Number of water bodies (large and small) in home range				Size of large open water within home range (km ²)			
	Min	Max	Mean	SE	Min	Max	Mean	SE
Female	177	5299	795.5	141.2	0.9	40.5	14.1	1.6
Male	11	1114	169	21.1	0.05	36.0	2.9	0.6

SE standard error of the mean

similar habitat as the females, but also occur on other soils (Haarsma et al. 2023 in press).

Because of their fast flight speed, foraging areas for pond bats need to be relatively large

and unrestricted by obstructions. Although the species forages in relatively open landscapes and above large water surfaces, it is mostly found hunting in the shelter of the bank, with occasional

sightings hundreds of meter from the shore of larger lakes or rivers. A few rare observations are available of pond bats hunting above brackish water in estuaries near the Waddenzee, North Sea, and Baltic Sea (Dijkstra 1997; Limpens et al. 1999; De Jong and Gylje 2005; Ahlén et al. 2009).

Pond bats spend approximately 25% of their time above terrestrial habitats (such as meadows/reedbeds and forest edges (Hörn 2012; Christensen 2021; Haarsma et al. 2023 in press). Visual observations of pond bats hunting above reed vegetation are known from both the Netherlands and Denmark. Flight height during these hunting trips is unknown. Anecdotal observations suggest that the pond bat forages between 2 and 7 m in height (e.g., Mostert 1997; Baagoe 1987; Christensen 2021). During cold or windy nights, pond bats tend to hunt in more sheltered habitats, for example, along woodland edges or near the bank of a channel.

Summer Roost

In the summer, males and females live in separate roosts. During birth and weaning periods, maternity colonies tend to use a limited number of main roost sites, sometimes connected to a network of satellite roosts (on average 2–7 sites). Main/satellite sites can be ranked according to the preferences of the bats that use them, varying in the distance from hunting grounds, volume, and/or microclimate. Other factors are important as well, such as the presence of predators, light in the vicinity of the exit, and noise. Only some of the satellite sites will be suitable for the entire nursery colony. The main summer roosts are used from March to the end of October (Haarsma 2012; Pētersons and Vintulis 2020), and most satellite roosts are used for a shorter period. Pond bats show a high site fidelity and use the same main roost for more than 50 years (Haarsma 2012). The size of the maternity colony varies between 30 and 750 animals (Dietz and von Helversen 2004).

Maternity colonies can use a wide range of roosts. The species frequently uses a combination of several building structures, such as a roof and a wall. Temperature gradient in roosts allows the bats to select a preferred ambient temperature which

matches the bats' current needs (Bochove 2007). Roosts have been found under roof tiles (Göttsche 2006; Haarsma 2012), in flat-pitched rooftops (Mundt 1999; Haarsma 2012), house attics (Mundt et al. 2010; Estók and Tamás 2008; Vorobei et al. 2021; Rachwald and Fuszara 2015; Vlaschenko et al. 2016; Ciechanowski et al. 2007; Shpak et al. 2022), hollow double brick walls (Haarsma 2012), and church attics (Il'in et al. 2003; Ciechanowski et al. 2007; Haarsma 2012; Pētersons and Vintulis 2020). Roost preferences differ across different countries and probably also reflect the geographical differences in building structure.

From April to September, males live alone or in groups, and from the end of June onwards, adult females and YoY from maternity colonies in the vicinity tend to join these male groups. Exchanges between female and male groups (>40 km) have been observed (Haarsma pers. data). Such mixed-sex groups show no or very limited breeding activity and their size varies during the season, with an average of 7 bats ($N = 70$, Haarsma 2012), yet, large groups up to 65 (Haarsma 2002) – 140 (Dense et al. 1996) are no exception.

Mixed groups, mating groups, or satellites of the main roost seem very opportunistic in their roost selection. They often use roost types similar to those of maternity groups (Vlaschenko et al. 2016; Haarsma 2002; Godlevska et al. 2022), but also use bat boxes (Schmidt 1998; Boshamer and Lina 1999, Grimmberger 2002; Göttsche and Gloza-Rausch 2010; Baranauskas 2010), tree cavities (Haarsma 2002; Il'in et al. 2003; Hörn 2012; Baagøe 2007; Ciechanowski et al. 2007; Godlevska et al. 2022), bard sheds (Dolch et al. 2001; Hörn 2012), hollow wooden bollards (per obs. Haarsma), bridges (Dolch 1995; Ciechanowski et al. 2007; Kmiecik and Kmiecik 2015), and natural caves and second world war bunkers (Šuba et al. 2008; Haarsma et al. 2019).

Winter Roost

Hibernacula include natural caves as well as human-made underground sites such as mines (limestone and minerals) and bunkers. Pond bats hibernate in buildings and churches, for instance, in hollow walls, in the space under the roof tiles or

under the roof edge. Observations of pond bats have also been made in collapsed mines, steep rock faces, or the walls of an open stone quarry (Frauke Meijer, personal communication, Van Schaik et al. 2015; Vlaschenko and Naglov 2005; Vlaschenko 2014). Most surveys of hibernacula are performed with a visual inspection, but alternative methods, such as captures of swarming bats, can be used to discover new hibernaculum types and make accurate predictions about the local population size. In most swarming studies, the numbers of animals recorded are much larger than those recorded during hibernation (Vlaschenko and Naglov 2005; Šuba et al. 2008; Baagøe and Degn 2009; Vintulis and Šuba 2010; Piksa et al. 2011; Van Schaik et al. 2015; Ciechanowski et al. 2006). An alternative observation method involves installing an infrared light barrier (Degn et al. 1995; Lefevre et al. 2022; Krivek et al. 2023). Light barriers can estimate the population size and trends of bat assemblages with large accuracy, as long as large-scale entrance modifications are not needed.

Hibernacula and underground swarming sites are widely distributed throughout the species' range. Usually, the numbers of hibernating pond bats in each site are low (Ciechanowski et al. 2007; Wojtaszyn et al. 2014; Pētersons and Vintulis 2020; Masing 1983, 1987). Sites with >30 hibernating bats are very rare. The highest densities in Europe have been recorded in:

- Sikspārņu caves (Latvia). During the first discovery in 1980 (Busha 1986), approximately 150 hibernating pond bats were found. Altogether six dolomite caves and holes have been discovered in this area. Since 1980, census of hibernating bats at these caves has been conducted every year. The population size of pond bats observed with winter census monitoring is decreasing (82 in 2020, Vintulis 2020).
- The caves of Piusa (Estonia). Long mines built from 1922 to 1966. The total length of all passages is approximately 10 km. The site is surveyed since 1949, the first pond bat was discovered there in the 1980s, and the population increased to 172 individuals in 1999. Recently, the increase seems to stagnate; in 2017, the total number of pond bats at all sites was 887, and in 2018, it decreased to 741 (Lutsar et al. 2000). Increasing tourism could be a factor.
- The bunkers in Meijendel and Veluwe (the Netherlands). These artificial sites were built in 1940, the first pond bat discovered was discovered in the 1980s, and the population increased to 503 individuals in 2015 (Haarsma et al. 2019; Glas and Kaal 2022). The sites are relatively small (17–870 m, Haarsma and Kaal 2016), but large clusters of 30 or more pond bats are common.
- The mines of Daugbjerg and Mønsted (Denmark) (Baagøe and Degn 2009; Baagøe 2007). Mines quarried since the Middle Ages. Lime exploitation ceased late 1970s. The mines are made of several km of galleries of varying size (up to 14 m in height). The mines have been surveyed for bats since 1825 (Fjederholt 2013). During the last 70 years, several extensive studies took place in these sites (Degn et al. 1995; Baagøe et al. 1988; Baagøe and Degn 2009; Fjederholt 2013) combining monitoring count, infrared monitoring, and harp trap capture. Population size is between 4000 and 5000 pond bats according to mark recapture estimates.
- Natural caves in the Urals (Golovatch et al. 2018). Smolinskaya is a natural cave with a total length of ca. 630 m. Monitored since the 1950s (Strelkov 1958; Bol'shakov et al. 2005), the site contained 1724 pond bats. In 1999, the population size remains at approximately 1700 pond bats (Bol'shakov and Orlov 1999). Large clusters of bats (up to 30 individuals) are common here.
- The Kalkberg Bad Segeberg (Germany) is a natural cave. The cave's total length is at least 6000 m; large sections have not been completely surveyed. The number of observed pond bats during winter surveys is limited, between 20 and 50 bats, while infrared camera recorded at least 700 entering pond bats (Göttsche, personal communication). No information on the population trend of the pond bat is available for that site.

Pond bats often hang or lie solitary or in small aggregations of 2–10 individuals in the hibernacula (Smirnov and Vekhnik 2009; Lindenschmidt and Vierhaus 1997), sites with clusters of more than 30 individuals are an exception (Haarsma et al. 2019; Smirnov and Vekhnik 2014b; Lutsar 2020). Pond bats may hang or lie almost everywhere from the ceiling to the floor, in exposed positions or more or less protected in holes and crevices. Closer to an entrance, they have a small preference for sheltered positions, while deeper in a site, they can be found hidden, half-sheltered, or in free-hanging positions (Daan 1973; Gilson 1978; Haarsma 2011).

Pond bats are loyal to their hibernacula (Haarsma et al. 2019). Observations of individuals moving between summer and winter roosts are scarce (Haarsma 2006). Pond bats captured during swarming in front of hibernacula are often found hibernating in the same hibernacula in a later period of the year (Vintulis and Šuba 2010; Haarsma 2003b). The young of the year occasionally switch hibernacula (Daan 1973; Møller et al. 2013; Haarsma et al. 2019).

Diet

Pond bats mostly feed on nonbiting midges (Diptera: Chironomidae) (Britton et al. 1997; Sommer and Sommer 1997). Nonbiting midges (Diptera: Culicomorpha) and moths (Lepidoptera) are in fact the most frequently observed prey groups (respectively 95.6% and 40.5% of the samples from adult females) (Haarsma et al. 2023 in press). Besides this staple food, the diet includes up to 10 different arthropod orders (Ciechanowski and Zapart 2012; Krüger et al.

2012; Smirnov and Vekhnik 2014a). Other frequently observed prey are dung flies (Diptera: Scathophagidae), dung beetles (Coleoptera: Scarabaeoidea), and water beetles (Coleoptera: Dytiscidae (and Hydrophilidae)). In the second half of the summer (July), nonbiting midges are replaced by caddis flies (Trichoptera) as dominant prey type, as seen in Russia (Samara bend) (Smirnov and Vekhnik 2014a) and northern Poland (Ciechanowski and Zapart 2012). Ciechanowski et al. (2017) linked this diet shift to the different breeding conditions and habitat selection. Pregnant pond bats are more dependent on small prey and pupae of nonbiting midges and mosquitos (Diptera: Chironomidae and Culicidae) than lactating females (and males) (Haarsma et al. 2023).

Behavior

Ranging Behavior

Commuting

Pond bats show high fidelity to their foraging sites and commuting routes (Haarsma and Siepel 2013b). Flight speed during commuting ranges between 7 and 12 m/s (Baagøe 1987; Britton et al. 1997). During foraging, flight speed is similar but can slow to 2–3 m/s. Hunting territories of maternity groups are usually established within 3.7 km of the roost (Table 5), although distances of up to 11.7 km are also recorded. The home range size varies greatly across different areas. Most commuting routes follow linear waterbodies, such as waterways, canals, or rivers. Pond bats may also take routes over land (e.g., following a tree line, road, slope of a dyke, or

Table 5 Home range expressed as the habitat where 80% of the entire group hunts for 80% of its time. Data were collected for several years in the Netherlands in the

summer months, between 15 May and 15 July. Based on unpublished telemetry data from Haarsma obtained from 70 male roosts to 38 female roosts

	Home range (km ²)				Distance to foraging habitat along commuting route (km)			Direct route, as the crow flies, to furthest point within home range (km)			
	Min	Max	Mean	SE	Min	Max	Mean	Min	Max	Mean	SE
Female	13.4	303.4	89.5	10.0	0.06	11.7	3.7	3.7	28.1	11.3	0.7
Male	1.8	90.2	18.4	2.8	0.08	15.4	2.8	1.3	15.4	5.3	5.3

SE standard error of the mean

fence line vegetation), sometimes up to several km (e.g., Ciechanowski et al. 2017). Pond bats may fly underneath bridges and through underpasses below highways and railways, of which minimal sizes are 4 m wide and 1.5 m high (Limpens et al. 2005; Haarsma 2010; Boonman 2011). Lower and narrower bridges are also used but can pose problems under high bat densities (>10 animals within 5 min), as some will tend to fly over. In absence of a bridge pond, bats often cross a road flying very low (up to 0.5 m high) (road hugging). Incidental collisions of pond bats with cars are known (Lesiński 2007; Ciechanowski et al. 2007). In an illuminated environment, they tend to make a short upward maneuver, followed by a quick downward maneuver, often flying low for 3 m before reaching the water bank (road evading).

Migration

Summer populations often live separately from other summer populations because of unsuitable habitat (e.g., mountain ranges); however, populations do sometimes use the same hibernacula (Andersen et al. 2019; Hutterer et al. 2005; Steffens et al. 2004). Hence, migration between summer and winter habitats is perhaps important to conserve genetic diversity. Hibernacula type (e.g., cave, bunker, and house) and their locations differ according to the country and probably also reflect the available variation due to geographical differences in the landscape. As a result, migration patterns can be different for each population, both in terms of distance and direction.

The Dutch/Belgium/West German population tends to migrate 200–340 km south and east (Fairon 1967; Sluiter et al. 1971; Haarsma et al. 2019; Pinno 1999). Bats from Denmark and northern Germany tend to migrate only short distances of between 17 and 57 km (Egsbaek et al. 1971; Götsche and Gloza-Rausch 2010). Pond bats from eastern Germany tend to move to both the east and west (Ohlendorf 2004; Steffens et al. 2004). Some bats marked in Estonia moved in a southeast direction (Masing et al. 1999).

Overall, the pond bat is considered a long-distance migrant (Hutterer et al. 2005; Steffens et al. 2004). Movements of about 200–300 km between summer and winter roosts were also

found in the European part of Russia (Strelkov 1974; Panyutin 1980). A recent study showed that migration patterns can change within a few decades, and at least the male part of the population may become nonmigratory if new suitable hibernacula (built in 1940) are available near the summer roosts (Haarsma et al. 2019).

Foraging Behavior

The pond bat is a highly adapted water trawling bat (e.g., Boonman et al. 1998; Siemers et al. 2001, 2005; Fenton and Bogdanowicz 2002; Almenar et al. 2006). This prey is caught by hunting in a “two-dimensional plane.” The bats fly a few centimeters (10–60 cm) above the water surface (Baagøe 1997; Britton et al. 1997; Van de Sijpe 2008), from which they regularly take prey with their feet and wing membranes during targeted dips. Trawling *Myotis* will not recognize prey if prey echoes are embedded in clutter, such as water surface ripples (<3 cm high) (Mackey and Barclay 1989; Rydell et al. 1999), duckweed (Boonman et al. 1998), or other organic matter (Vaughan 1997).

In some conditions, pond bats tend to prefer a combination of trawling and aerial hawking, which uses more of the “three-dimensional plane” (Fig. 6). This technique includes a faster, more linear search flight, regularly interrupted by sudden rises (aerial hawks). Van de Sijpe and Holsbeek (2007) proved that this three-dimensional technique allowed the pond bats to successfully hunt and capture moths. The auditory systems of many large species of Lepidoptera (e.g., Noctuidae, Geometridae, Notodontidae, Pyralidae, and some Sphingidae) is sensitive to ultrasound in the range of 15–60 kHz capable of detecting the echolocation calls of most aerial hawking bats (Waters and Jones 1996; Rydell and Young 2002; Ter Hofstede and Ratcliffe 2016). In European moth species, the stimulation of the auditory system triggers a variety of escape responses, such as complex loops, spirals, and dives (Roeder 1962; Waters and Jones 1996). Pond bats seem to counter the moths' escape reactions by changing both their search flight and their echolocation call structure. During moth hawking modus, pond bats typically alternate



Fig. 6 Hunting behavior of the pond bat (*Myotis dasycneme*) over large linear waterways, left typical trawling to catch emerging pupae from the water surface and right fast hawking with a sudden rise to follow a moth,

followed by a quick drop to catch it (Photographs: Marc Van de Sijpe in Van de Sijpe and Holsbeek (2007). Reproduced with permission from Marc Van de Sijpe, 4 January 2022)

between echolocation and sequences of silences, creating a discontinuous call pattern (Van de Sijpe and Holsbeek 2007). During the echolocation phase associated with moth hawking, they switch between two distinct echolocation signals, the first predominantly frequency-modulated (FM) and the second having a more pronounced quasi-constant frequency (QCF) ending.

Social Behavior

Bat swarming is a poorly understood behavior observed in several species of bats seen in Europe and North America. Unfortunately, there is no complete consensus on both the definition and the function (Saucy 2019). Pond bats show two distinct and easily recognizable forms of social behavior: (1) mating swarming and (2) dawn swarming. Some studies suggest swarming plays a role in the assessment of the suitability of a site and/or the social information transfer regarding its location (Veith et al. 2004; Piksa et al. 2011; Stumpf et al. 2017).

Swarming and Mating

Swarming in bats consists of intense flight activity during which bats chase each other around an underground site entrance and in and out of it. Unlike other bat species, pond bats tend to spend little time swarming in front of the entrance

of an underground site. After arriving at a swarming site, they tend to quickly enter the site. Pond bats seem to make “patrol” flights, including long (>500 m) back and forward flight movements between a point at some distance from the hibernacula and the entrance itself (Haarsma et al. 2019). Unlike other species (Parsons et al. 2003), pond bats tend to roost inside the hibernacula during the day (Šuba et al. 2011), seemingly forming temporary harem-like groups of up to 10 individuals (Korn 2008; Baagøe and Degn 2009; Šuba 2014; Haarsma et al. 2019).

Sunset Emergence and Dawn Swarming

Timing of emergence follows a day and night rhythm, with variation during a single season (Voûte 1972, 1974) caused by variation in light intensity and weather conditions, most notably cloud cover. Emergence will occur between 30 and 90 min after sunset depending on the size of a colony and the number of exit points. The bats return in the early morning, when it is still dark, and within 30 min, most individuals are back to the roost. Pond bats also perform dawn swarming, i.e., a set of behavioral displays performed during dawn, when bats circle outside the roost entrance, often repeatedly feigning entering by landing and leaping off. Each bat performs some minutes of dawn swarming before entering. In the case of larger roosts, this can result in a spectacular sight involving many circling bats (Fig. 7).

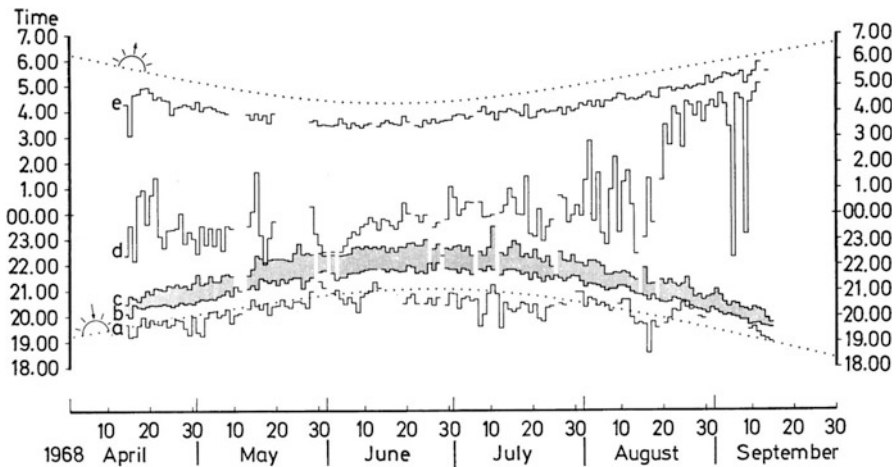


Fig. 7 Nocturnal activity of individual *Myotis dasycneme* occupying a large summer roost. From bottom (sunset) to top dashed line (sunrise): a. first individual moving to exit,

b. first exit, c. last exit, d. first return, and e. last return. (Voûte 1972) (Reproduced with permission from Aldo Voûte, 1 March 2022)

Social Organization

A pond bat nursery colony may occupy one main roost and sometimes a network of satellite roosts. In spring, the first animals arrive in the main and/or satellite site to establish the colony. As the colony grows, the number of satellite sites used dwindles and vice versa at the end of the breeding season. Before and after the breeding season, exchanges between colony groups occur (Haarsma 2003a, 2012), while during the breeding season such exchanges are rare.

Males and females live in strictly segregated habitats. One of the meeting points is given by swarming sites and roosts of mixed groups. In the pond bat (Andersen et al. 2019), female bats from several colonies visit the same swarming sites as seen in several other bat species (Kerth et al. 2003; Veith et al. 2004; Burns et al. 2014).

Echolocation

FM (frequency-modulated) pulses are the basis of pond bat's echolocation. In open habitats (e.g., broad waterways, lakes), the species often uses relatively long echolocation pulses with a QCF component (Ahlén and Baagøe 1999). The pond bat can be recognized by its characteristic rhythm

(pulse interval between 8 and 130 ms) with loud plopping sounds with a pulse length of 8–25 ms and a peak frequency of 35 kHz (Fig. 8). With this echolocation type, the pond bat is able to echolocate over long distances while still noticing its immediate surroundings (Britton et al. 1997; Limpens 2001). Pond bats adapt their echolocation behavior in relation to the perceived distance to landscape elements (e.g., the banks of a canal). Pulse duration and interval increase significantly with increasing distances to landscape elements (Boonman 1995; Verboom et al. 1999). In a cluttered environment, such as woodland, rural areas, or small waterways, the pulse interval becomes shorter (5–7 ms) and pulses also shorten (< 8 ms). In this situation, structural overlap with Daubenton's bat echolocation calls is possible. A clear overview of how to differentiate between the species is provided by Van de Sijpe (2011), Barataud (2015), and Russ (2021).

Social Calls

Pond bats can be extremely loud when captured or otherwise in distress, a sound previously described as the “alarm call of a blackbird.” Interactions between females and offspring sound like audible, high-pitched chattering. During the

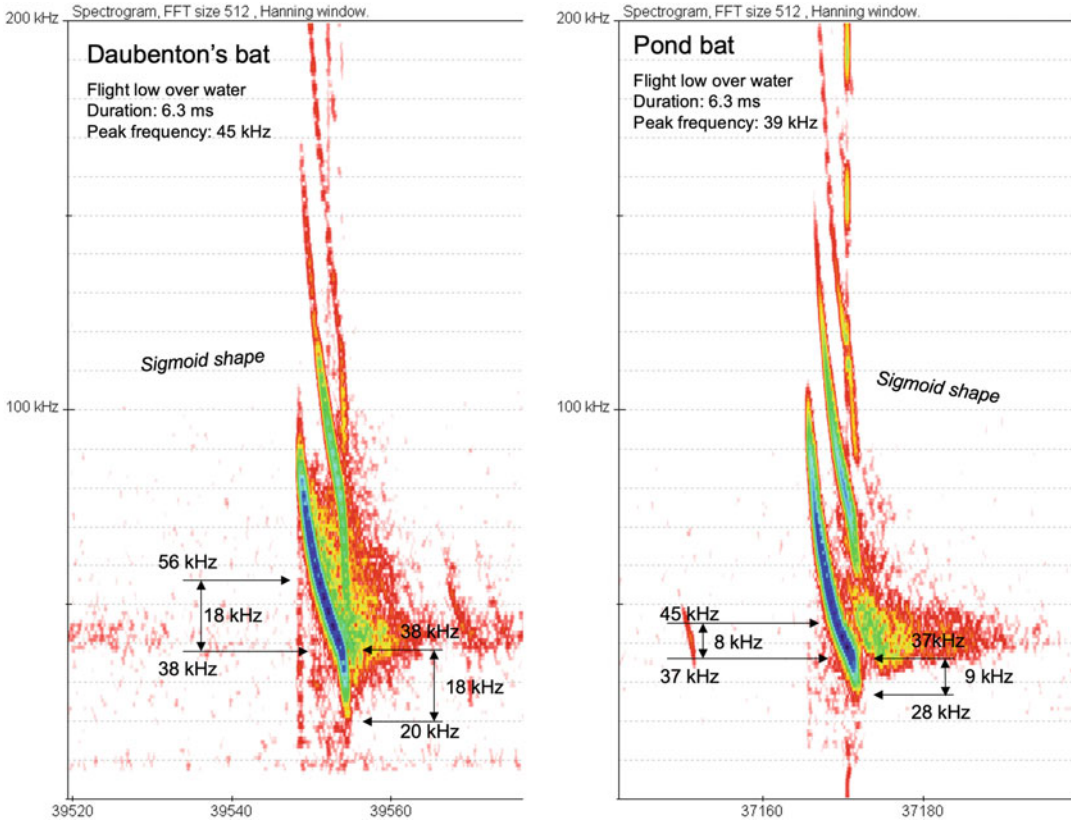


Fig. 8 Echolocation pulses of two bat species: Daubenton's bat (left) and the pond bat (right). These species hunt above large bodies of water under similar weather conditions, and while their pulse duration and peak frequency are similar, their pulse shapes are quite distinct. The pulse of the pond bat has one sharp decline, almost at the end of the pulse, while the pulse of a Daubenton's bat has two declines. Just above the decline in the pulse of a Daubenton's bat, the frequency decreases

so slowly that a QCF-part is formed at around 35 kHz. In contrast, the pulse of a Daubenton's bat has two sharp declines, at the beginning and end of the pulse. Above the lowest decline, the slope is much steeper than in the pulse of the pond bat. Although Daubenton's bat can reach a pulse duration of 13 ms, a QCF is never formed. Additionally, the end frequency is lower in the pulse of a Daubenton's bat (20 kHz) than in the pulse of a pond bat (28 kHz) (Drawing made by Marc van der Sijpe)

flight, pond bats rarely make social sounds. Social calls are described as special, low-frequency sounds with obvious harmonics (Britton et al. 1997; Skiba 2003).

Parasites and Diseases

Parasites

Many ecto- and endoparasites have been recorded in this species, including bat bugs, ticks, fleas, flies, louse flies, and mites. A high parasite load

is not associated with decreasing body condition. Overall males tend to have fewer parasites (Zahn and Rupp 2004). Reported arthropods for *Myotis dasycneme* are *Cimex pipistrelli* (Van Rooij et al. 1982; Aukema 1989, Křištofik and Danko 2012), fleas *Ischnopsyllus intermedius* (Brinkman 1976; Van Rooij et al. 1982), *Ischnopsyllus octactenus*, *Ischnopsyllus simplex* (Van Rooij et al. 1982), *Ischnopsyllus hexactenus* (Jaunbauere et al. 2008), flies Nycteribiidae and Hippoboscidae (Schuurmans Stekhoven 1969; Orlova et al. 2015), ticks *Ixodes vespertilionis* (Brinkman 1976), mites *Macronyssus corethroproctus*

(Orlova et al. 2012), *Macronyssus flavus* (Brinkman 1976), *Spinturnix dasycneme* (Brinkman 1976; Krištofik and Danko 2012; Dekeukeleire 2013; Siepel et al. 2018; Sachanowicz et al. 2017), Trombiculidae (Brinkman 1976; Jaunbauere et al. 2008), *Steatonyssus* (Brinkman 1976), and *Penicillidia monocerus* (Haensel 1985). Frank et al. (2015), Krištofik and Danko (2012), and Orlova and Zapart (2012) provide extensive overviews of all known parasites of *Myotis dasycneme*.

Diseases

Diseases include *Besnoitia besnoiti* (Hornok et al. 2015) and *Neorickettsia* sp. (Hornok et al. 2018). Five (4%) of the 129 specimens tested from the Netherlands were positive for the European bat lyssaviruses (EBLV) antigen (Poel van et al. 2005). *Pseudogymnoascus destructans*, the fungus causing the White Nose Syndrome (WNS) in North American bats, was first identified in Europe in 2008–2009 (Wibbelt et al. 2010). Historical records indicate the fungus has always been widely present among the pond bat population (Feldmann 1984; Korsten et al. 2009), suggesting that it is native to Europe (Puechmaillie et al. 2011), where it does not cause mass mortality unlike in North America.

Population Ecology

Population Dynamics

Based on winter hibernacula surveys, the pond bat shows an increasing or stable overall trend in most European counties (Korn 2008; Haarsma et al. 2019; San Martin and Nyssen 2019; Vintulis 2020; Palmans 2022). Roosts that are not disturbed by people seem to have the largest increase (Berthinussen et al. 2014) whereas disturbance or an alteration of roost microclimate lead to decreasing population trends (Kervyn et al. 2009; Haarsma 2011; Lutsar 2020). Declines of the summer population have been reported for several countries. In the Netherlands, the

population has shrunk over 39% in the past 10 years (Haarsma and Janssen 2022). In Germany (Göttsche and Gloza-Rausch 2010; Meinig et al. 2009, 2020), the species is very rare and has experienced a decline (M. Göttsche, personal communication). Populations are also declining in Latvia (Pētersons and Vintulis 2020) and Estonia (Lauri Lutsar, personal communication). It is noted that the decreasing trend in summer coincides with decreasing average numbers of animals per roost, instead of local extinctions. In 2012, the average roost size in the Netherlands was 165 animals ($N = 65$), and currently it is only 100 ($N = 65$) (Haarsma 2012; Haarsma and Molenaar 2020).

The discrepancy between winter and summer trends could be caused by a change in migration patterns and the concentration of animals from a large range to well protected winter hibernacula (Haarsma et al. 2019).

Predators

In Europa, dietary studies and anecdotal observations reveal that two owl species occasionally feed on pond bats: the barn owl (*Tyto alba*) (De Vries 1960; Ruprecht 1979; Schmidt 2005; Obuch et al. 2016; Roulin and Christe 2013; Sieradzki and Mikkola 2020) and the tawny owl (*Strix aluco*) (Boonman 1996; Obuch 2011; Sieradzki and Mikkola 2020). A worldwide review of all cases of predation by diurnal birds showed that most bats are caught near their roosts, as bats typically live in dense aggregations which can attract predators (Mikula et al. 2016). A delay in the typical emergence time is considered a response to the presence of a predator. Avoiding light and moonlight stems from this avoidance behavior. Furthermore, pond bats are known to switch roosts after frequent visits by an owl (Kováts et al. 2008; Leonov et al. 2019).

Other predators of pond bats include the domestic cat (*Felis catus*) (Bekker and Mostert 1991; Vintulis and Šuba 2010) and the wood mice (*Apodemus sylvaticus*). In the Netherlands, wood mice were observed to actively search for and kill a considerable number of hibernating

bats, including many pond bats (Haarsma and Kaal 2016).

Conservation Status

Over its entire range, the pond bat is considered a rare habitat specialist, with a decreasing population trend, hence the listing by the International Union for Conservation of Nature (IUCN) as “Near Threatened” (Piraccini 2016). The pond bat is the subject of a European-wide action plan for conservation (Limpens et al. 1999). The pond bat is included in Annexes II and IV of the EU Habitats and Species Directive, thereby requiring special protection measures for both roosts and its essential habitats. In Europe, a total of 573 sites list the pond bat among the species they should protect (<https://natura2000.eea.europa.eu/> and <https://eunis.eea.europa.eu/species/1480>). Most of those sites are foraging habitats and hibernacula, with the exception of two maternity roosts in Poland. Other international treaties of relevance are the Agreement on the Conservation of Populations of European Bats (Bonn Convention, 1994) and the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention, 1982).

Management

Buildings used as roosts play a central role in the life history of the pond bat. Bats are sometimes not welcome and forced to move (Russo and Ancillotto 2014; Simon et al. 2004). Because of its preference for relatively warm, poorly isolated houses (Haarsma and Molenaar 2020), the pond bat faces additional problems. This type of house is frequently insulated, renovated, or demolished (Horáček 1984; Gombkötő 1998b; Limpens et al. 1999; Haarsma and Molenaar 2020). As the number of suitable alternative sites is dwindling, relocation to other roosts leads to a downward spiral of causes and consequences, often starting with less optimal thermal conditions in the new roost, leading to a decrease in thermoregulatory efficiency, culminating in a decrease of both the size

of the breeding colony and the size of the population to which it belongs (Fig. 9). National and international laws protect the species, its roosts, and foraging habitats. Enforcement of these laws is often lacking, however, and should be promoted (Marnell and Presetnik 2010). This includes proactive protection measures to prevent disturbance of summer roosts, several years before it is expected to happen, instead of reactive law enforcement, where pond bats are only protected after a severe negative incident occurred such as closing the entrance followed by death of an entire colony.

Underground habitats used for hibernation and mating may be threatened by changes in internal climate, changes in use, or increased disturbance. The grilling of important sites is advised to prevent unauthorized entry. However, grilling and other forms of closure should be custom-made to prevent severe climatic changes in a hibernaculum. Bat species often have different preferences regarding entrance orientation (Glover and Altringham 2008) and climatic needs. Reducing the size and number of entrances can lead to benefits for some species while harming others (Daan 1967; Daan and Wichers 1968; Kervyn et al. 2009; Voigt and Kingston 2016; Baranauskas 2006; Álvarez et al. 2012).

Activities during the swarming/mating season (both pre- and post-hibernation) should be avoided, as pond bats tend to roost inside hibernacula during the day. Activities often include speleologists, geologists, and archaeologists, sometimes with a permit but also trespassers. Guided tourists (Alsina 2014) and activities such as Christmas markets, cave biking, storing of cheese (Søgaard et al. 2005), paint ball events, abseiling, and music festivals (Haarsma 2011) are among the many activities currently organized in hibernacula. Sensitive species, such as pond bat, Bechstein’s bat, and whiskered bat, decline because of the direct or indirect consequences of these activities (Weinreich and Oude Voshaar 1987; Ciechanowski et al. 2006; Kervyn et al. 2009; Haarsma 2011; Apoznański et al. 2018).

Currently, all pond bat hibernacula are under legal protection by both national and international laws. Protection against microclimate alterations,

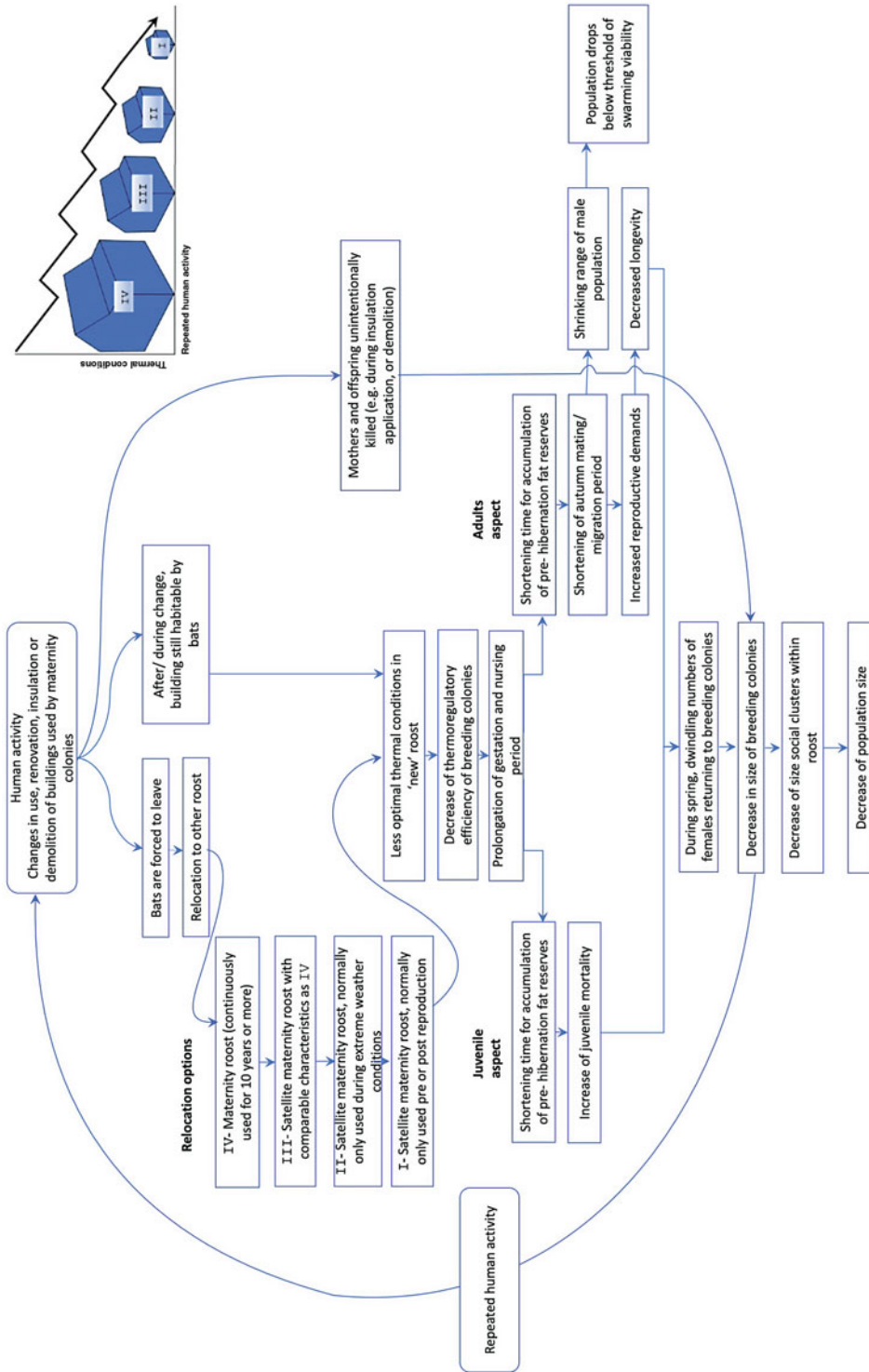


Fig. 9 A sketch of the causality chain of population decline in Europe caused by human activity in the maternity roost of the pond bats (Adapted from Horáček 1984)

changes in use, or disturbance are not always effective. Furthermore, the inclusion of areas used during swarming/mating are needed in most national legislations. For example, swarm zones, located in front of underground hibernacula, could be protected by keeping those zones dark and sheltered from wind.

Toxic residues, such as heavy metals, pesticides, PCBs, PAKs, etc., can accumulate in pond bats feeding on aquatic insects which develop in polluted environments (Reinhold et al. 1999). Hallmann et al. (2017) found a significant correlation between neonicotinoid pesticide use and the decline of insectivorous birds. Aquatic insects are also sensitive to high levels of neonicotinoid pesticides (Morrissey et al. 2015). The use of wood preservatives can cause problems as well. In 1974, a large number of dead juvenile pond bats was found in a maternity roost (Leeuwangh and Voûte 1985), killed by a combination of lindane (γ -HCH) and pentachlorophenol (PCP) preservatives. Long-banned dichloro-diphenyl-trichloroethane (DDT) and other pesticides tend to persist over several decades and are often still detectable in church lofts and other places used by bats (Bayat et al. 2014; Guldmond et al. 2016; Haarsma and Koopmans 2017). Residues of such pesticides are known to be deadly for *Pipistrellus pipistrellus* (Shore et al. 1991) and are likely to be so also for the pond bat.

Pond bats tend to avoid artificial light (Kuijper et al. 2008), especially in situations where bats fly towards the light (instead of cutting the light beam along a perpendicular route). Changing the light color can decrease the level of disturbance (Limpens et al. 2011). In general, it is advised to avoid the use of artificial light (of all colors) along commuting routes essential to pond bats.

Foraging, commuting, and migration habitat include waterbodies, terrestrial habitat types such as meadows, and offshore coastlines. Ecological corridors placed in strategic locations can prevent habitat fragmentation (Haarsma 2018). Although pond bats are not seriously threatened by wind turbines, collisions can occur if turbines are located in critical portions of a colony home range (Göttsche and Göbel 2007). In the vicinity of maternity roosts, turbines should not be placed

in the water along the bank of large water bodies to avoid collisions.

Changes in water quality may affect insect prey and the distribution patterns of pond bats (van de Sijpe et al. 2004). During pregnancy, pond bats prefer slightly eutrophic waterbodies (Ciechanowski et al. 2017). Extremely eutrophic water is avoided, as pond bats have difficulty at detecting prey from clutter. Agricultural intensification often coincides with high levels of pesticides. In the Netherlands, management programs to improve water quality seem to have negative consequences for the pond bat, as this decreases prey abundance (Haarsma and Molenaar 2020). A gentle balance is needed between improving quality up to a certain level and lowering pesticide levels.

In contrast, the (re)introduction of beavers as a management tool, might improve habitat quality for water trawling bats (Ciechanowski et al. 2011). The standing water pools created by beavers are only suitable during the springtime (but highly valuable for pregnant females, as is shown by Haarsma et al. 2023 in press), as they quickly cover with duckweed. Ciechanowski et al. (2011) hint that pond bats might benefit from a change in the spatial structure of a forest, as beavers cut and remove trees, especially near the water edge.

Although the species has been recorded foraging over brackish water, intensive foraging over brackish water is not expected (Walters 2014). A sea level rise may affect water quality in a wide range of lowland wetlands within the distribution range of the pond bat (Finlayson 2018). Local extinction of the species with a sea level rise of 1.35 m, as proposed for the twenty-first century, might be imminent.

Future Challenges for Research and Management

Habitat with shallow water and a large quantity of small bulk prey, preferably catchable as pupae, is needed during reproduction and raising of offspring. Long-term diet studies are needed to better understand and protect regional populations of the pond bat.

Nowadays, buildings suitable for harboring maternity roosts of the pond bat are disappearing. Renovation and demolition of poorly isolated houses to reduce heating costs are promoted in many European countries. The design of alternative maternity roost sites for the pond bat is urgently called for (Berthinussen et al. 2014).

Less than 5% of hibernation sites used by the summer population of pond bats in Europe is known. The unknown winter distribution makes the species very vulnerable, as effective protection of hibernacula is not possible for the entire population. Secondly, incomplete winter monitoring data make it difficult to draw accurate conclusions about annual population trends, especially in countries with incomplete knowledge of the summer distribution. A study focusing on the possibility of hibernation in the summer roosts is desired.

General threats to hibernation sites also affect the pond bat. Hibernating bats and “underground” hibernacula are under constant threat of disturbance by a range of human activities. Inherent to human activities are often structural changes to a site, such as the closing of entrances, hallways, and repairing crevices, which influences the microclimate and thus make a site unsuitable for hibernating bats.

A pilot study showed genetic differentiation between populations of the pond bat from northern and southern Europe (Andersen et al. 2019). A comprehensive genetic assessment of the species across its distribution range, to identify relations between colonies and populations spanning international borders, is highly needed.

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