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DOES WATER QUALITY MATTER? FORAGING ACTIVITY OF DAUBENTON'S BAT (*MYOTIS DAUBENTONII*) OVER THREE LAKES WITH DIFFERENT TROPHY

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Abstract

The trophic parameters of water bodies, especially the content of biogenic components, may have an impact on invertebrate communities, both those strictly aquatic and those using the water bodies periodically. Among this group, insects are highly relevant, the density of which can affect the attractiveness of the water body as foraging habitat of water-surface forager bats. The present paper presents the results of a study measuring the foraging activity of *Myotis daubentonii* (Kuhl, 1917) in linear transects over three water bodies: an oligotrophic, eutrophic, and dystrophic lake located within a 1.5 km radius. The research has a repeated measures design, with the consecutive surveys carried out in 1995, 1996, and 2001 in the lactation period (end of June–beginning of July) and in the post-lactation period (end of August–beginning of September). The activity of *M. daubentonii* over the oligotrophic lake varied between 0.0 and 15.9 ind/km, while over the eutrophic lake it was 3.9 and 16.7 ind/km, and over the dystrophic lake was 3.4 and 30.5 ind/km. The study found that the foraging activity above the dystrophic lake was almost twice as high (13.1 ± 6.11) as over the two others lakes: oligotrophic (6.0 ± 4.17) and eutrophic (8.0 ± 3.19). By contrast, in the case of *M. daubentonii,* there was no statistically significant difference in the foraging activity over either of the foraging areas (eutrophic and oligotrophic). The foraging activity in bats in the lactation period was higher than in the post-lactation period. Our results indicate that the differences in the foraging activity of the bats in the present study do not depend on the trophic status of the lake and are linked directly to opportunistic foraging strategy of the species. The higher foraging activity recorded over the small dystrophic lake may be explained by the isolation of this lake from adverse weather conditions (e.g. wind). Hence, the observed slow increase in the number of *M. daubentonii* over the past 20 years cannot be attributed to, as previously suggested, eutrophication, but, on the contrary, seems to be a result of a progressive improvement in the environment.

Cite as

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Чи має значення якість води? Кормова активність нічниці водяної (*Myotis daubentonii*) над трьома різними за трофністю озерами

Малгожата Стржалка, Катажина Козакевич, Томаш Постава

Резюме. Трофічні характеристики водосховищ можуть впливати на їхню привабливість як кормових біотопів для кажанів, що полюють над поверхнею води. У цій статті представлено результати дослідження кормової активності кажанів *Myotis daubentonii* (Kuhl, 1917) на лінійних ділянках трьох водойм: оліготрофних, евтрофних і дистрофних озер, розташованих у радіусі 1,5 км. Дослідження виконано за схемою повторних досліджень, послідовно у 1995, 1996 та 2001 роках у період лактації (кінець червня — початок липня) та у постлактаційний період (кінець серпня — початок вересня). Активність *M. daubentonii* над оліготрофним озером варіювала між 2,7 і 9,1 ос./км, над евтрофним — 6,8 і 9,9 ос./км, а над дистрофним — 6,4 і 18,0 ос./км. Дослідження показало, що харчова активність над дистрофічним озером була майже вдвічі вищою, ніж над двома іншими озерами: оліготрофним та евтрофним. На противагу цьому, у випадку з *M. daubentonii* не було статистично значущої різниці в харчовій активності над жодною з кормових зон (евтрофною та оліготрофною). Активність кажанів у період лактації була вищою, ніж у постлактаційний період. Наші результати вказують на те, що відмінності у харчовій активності кажанів у цьому дослідженні не залежать від трофічного статусу озера, а безпосередньо пов'язані з опортуністичною стратегією харчування виду. Вищу харчову активність, зафіксовану над малим дистрофічним озером, можна пояснити ізольованістю цього озера від несприятливих погодних умов (наприклад, вітру). Таким чином, повільне зростання чисельності *M. daubentonii*, що спостерігається протягом останніх 20 років, не може бути пов'язане з евтрофікацією, як припускали раніше, а, навпаки, є результатом поступового покращення стану навколишнього середовища.

Ключові слова: *Myotis daubentonii*, кормність озер, трофічна активність, Національний парк «Вігри», північно-східна Польща.

Introduction

Lakes and rivers are favourable foraging habitats for many bat species, most of which belong to the genus *Myotis* (Chiroptera: Vespertilionidae) [Zahn & Maier 1997; Warren *et al.* 2000; Ma *et al.* 2006]. Generally, 'trawling' bat species, which hunt above or close to the water surface, prefer to forage over calm and open waters [Jones & Rayner 1988; Siemers *et al.* 2001], and avoid turbulent water [Frenckell & Barclay 1987; Rydell *et al.* 1999; Warren *et al.* 2000], or water covered by floating plants, particularly duckweed [Boonman et al., 1998].

All these bat species catch prey either by seizing it with their feet or scooping it by means of the interfemoral membrane [Jones & Rayner 1988; Kalko & Schnitzler 1989]. Water-surface forager bat species feed on insects flying close to the water surface, emerging chironomids (which often sit on the water surface), or floating large arthropods, e.g., moths [Siemers *et al.* 2001]. In some cases, however, aerial insects [Todd & Waters 2007] constitute a significant part of their diet. Foraging efficiency, in turn, is further influenced by prey abundance or/and insect biomass. Although the correlation between hunting activity of bats and insect abundance in the environment has been reported in several studies [Warren *et al.* 2000; Akasaka *et al.* 2009], in some cases, the choice of water bodies cannot be explained by prey abundance [Van de Sijpe *et al.* 2004]. Another factor that influences insect density, and therefore the attractiveness of feeding ground, is bankside vegetation, which protects the feeding ground from strong wind [Zahn & Maier 1997; Warren *et al.* 2000].

Water habitats, both flowing (riverine) and standing (lakes, ponds) are threatened by many factors such as degradation of riparian vegetation, drainage, or pollution. In turn, the quality of water affects insect communities (to different degrees; [Lambert & Sommer 2007]), and, as a result, the foraging activity of bats [Vaughan *et al.* 1996; Wickramasinghe *et al.* 2004]. Vaughan *et al.* [1996] found that the activity of *M. daubentonii* was affected positively by sewage effluents. On the other hand, Van de Sijpe *et al.* [2004] showed that water nutrient enrichment had a negative impact on the hunting activity of *M. dasycneme*. However, this did not apply to *M. daubentonii*. The effect of water eutrophication on foraging bats is still unclear [Racey 1998], especially that most research concerned flowing waters (streams, rivers); studies on standing waters (ponds, lakes) are much less common.

Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) is a one of most common European bat species associated strictly with aquatic environment [Bogdanowicz 1994]. *Myotis daubentonii* is widely distributed in most of the Palearctic. Its geographic range spans from Spain and the British Isles throughout Europe up to the latitude 60°N and the Ural Mountains [Encarnação & Becker 2023] in the east. During summer activity, this species mostly uses tree hollows as daytime shelters [Boonman 2000], less frequently artificial shelters such as fissures under road and railway bridges [Ignaczak & Manias 2004; Gottfried & Gottfried 2014], and only occasionally attics (our data) or caves [Zahn & Hager 2005]. Daubenton's bat feeds mainly on Chironomidae [Swift & Racey 1983; Beck 1995], although Trichoptera and Lepidoptera can also constitute a significant part of its diet [Arnold *et al.* 2001; Flavin *et al*. 2001; Vesterinen *et al.* 2013].

The species *Myotis daubentonii* leaves its daytime shelters between 30–60 minutes [Bogdanowicz 1994] and 90 minutes [Rydell *et al.* 1996] after sunset. The average distance between breeding colonies and feeding grounds is about 1.5 kilometres [Swift & Racey 1983], although it can be up to 8–10 km [Arnold *et al.* 2001]. The IUCN/SSC Chiroptera specialist group [Hutson *et al.* 2001] has placed the species in the lower-risk group on the index of animals threatened with extinction. Over the last 30 years, the species has been getting more abundant in winter shelters [Stubbe *et al.* 2013; Barlow *et al.* 2015; Verhees *et al.* 2022]. Eutrophisation of waters is, according to some researchers, the main cause of changes in the numbers of hibernating *M. daubentonii* [Kokurewicz 1995]. On the contrary, Daan [1980] considered water eutrophication as the main cause of decline of Daubenton's bat abundance in winter shelters.

The Wigierski National Park (north-eastern Poland) is particularly rich in water bodies of different trophic character, which provides an opportunity to assess their attractiveness as foraging areas for Daubenton's bat. The aim of the study is to determine the foraging activity of *M. daubentonii* on three neighbouring lakes of different water quality (oligotrophic, dystrophic, and eutrophic) and to answer the following research questions: whether water quality can determine bat activity, and whether activity can depend on the phenological period (lactation vs post-lactation periods). We expect that if the polluted water is more attractive to *M. daubentonii*, the highest bat activity will be recorded the on eutrophic lake, and the lowest on the oligotrophic; whereas if water quality proves to be secondary, then the largest activity should be observed on the dystrophic lake.

Materials and Methods

Study area

The Wigierski National Park is situated in the north-east of Poland (Mazursko-Podlaska Land, Kondracki, 2001), ranges from 53°56'N to 54°10'N and from 22°57'E to 23°15'E. The area is 15 086 ha, including forests (62.7%), waters (19.3%), and others (18%). The dominating forest communities are: *Tilio–Carpinetum alamagrostietosum* (46.2%), *Peucedano–Pinetum typicum* (28.4%), *Tilio–Carpinetum* (14.7%), *Ribo nigri–Alnetu* (3.2%), *Peucedano–Pinetum* (2.7%), and others (ca. 5%). The climate is known to be the most severe in lowland Poland. Mean temperatures in winter range from –6.7°C to –2.7°C and 16–18°C in the summer; ice is present for up to 130 days. Mean annual rainfall equals approximately 593 mm, with a range from 442 to 743 mm. The area has a postglacial character, with 42 lakes in the National Park of different trophic status: eutrophic, mesotrophic, dystrophic and oligotrophic.

Methods

The studies were conducted in three summer seasons: 1995, 1996, and 2001. In the first two years, the data were collected during the lactation and post-lactation periods: from 26 June to 12 July and from 17 August to 9 September in 1995, from 3 July to 17 July and from 14 August to

25 August in 1996. In the last season, in 2001, data collection took place only during lactation: from 2 July to 16 July. The activity of Daubenton's bat recorded during the lactation and post-lactation period applies only to the local population, excluding the migrating individuals [Ciechanowski *et al.* 2010].

Daubenton's bat (*Myotis daubentnii*), in contrast to the other water-surface forager bat species, *M. dasycneme*, avoids open water surfaces. Preliminary observations conducted in July 1994 showed that *M. daubentonii* feeding areas are restricted to a narrow littoral zone with a width of 15–20 m and of variable length. Three lakes with different nutrient states were chosen (water parameter after: [Czeczuga *et al.* 2001; Szczęsny & Majecki 2002]):

- Białe Lake (BL): an oligotrophic lake of 100.2 ha, depth: 34 m, low biogen concentrations and high content of Ca^{2+} (23.6 mg/dm^3), high transparency (4.05–9.05 m), well oxygenated bottom parts, conductivity of 178 µS/cm, and pH = 7.1–7.3;
- Wigry Lake, Słupiańska Bay (WL): a eutrophic lake of 211.83 ha and a depth of 73 m (one of the largest and deepest in Poland), with high biogen concentrations and medium concentrations of Ca^{2+} (40–43 mg/dm^3), medium transparency (0.5–5.3 m), conductivity of 300–317 µS/cm, and pH = 7.2–7.6;
- Suchar Wielki Lake (SWL): a shallow, dystrophic lake with a small surface area (8.9 ha) and limited visibility (0.5–1.1 m), characterised by a high concentration of humic acids and low level of Ca^{2+} (3.2–7.6 mg/dm^3), low conductivity (21.0–22.4 µS/cm), and low pH (5.0–5.8).

Linear transects were established along the banks of the selected lakes (Fig. 1), their lengths: 1040 m for Białe Lake, 780 m for Wigry Lake (Słupiańska Bay), and 590 m for Suchar Wielki Lake. The edges of the lakes along transects are covered with mixed coniferous forest, the littoral zone is free from water vegetation: duckweed (*Lemna* sp.) and reed (*Phragmites* sp.). Observations were made with Pettersson bat detectors D–100, D–200 and D–220 with a preset frequency of 45kHz.

Foraging bats were localised by preset bat detectors and counted using headlamp light. Monitoring was carried out with the dinghy, sailing on each transect with a similar speed. This methodology allows to determine preying *M. daubentonii* on transect, and also allows to distinguish it from other 'trawling' bat species, *M. dasycneme* (which is a visibly larger bat). Due to the disagreement in the literature regarding the beginning of the transect, it was determined on the basis of the observations collected under the present research. The presence of Daubenton's bats over the studied lakes was recorded about 30 min after sunset, gradually increased over about 60 minutes, and stabilised after that time. The bat's activity remained stable for the next two hours. A similar distribution of activity was obtained by Bartonička and Zukal [2003]. Therefore, counting was conducted an hour after sunset during the time of the highest activity: in June and July at 10 p.m. and in August and September at 9 p.m. The transects were checked twice—there and back through each one, which took about half an hour each way. The animals were counted separately and the mean was calculated and estimated per kilometre of transect. Observations were not conducted during strong wind or rain.

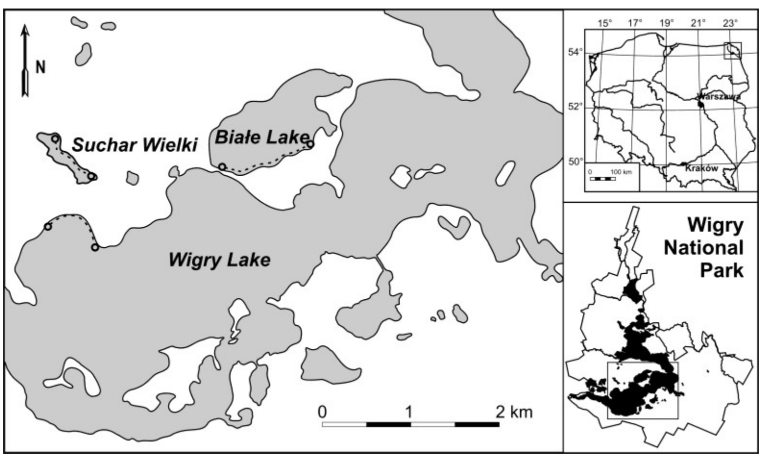

Fig. 1. Distribution of field transects surveyed in Wigry National Park (NE Poland) in the three years of research (1995, 1996, and 2001).

Рис. 1. Розподіл ділянок польового обстеження у Національному парку «Вігри» (північна Польща) у ході досліджень (1995, 1996, 2001).

Transects were scored by two separate teams on two different lakes at the same time: Wigry–Białe, Wigry–Suchar Wielki, and Suchar Wielki–Białe. When the first observation was conducted independently by two teams on one lake, no differences were found between the two teams. The use of feeding buzzes for activity assessment of *M. daubentonii* was omitted in this study because of the controversies concerning this method [Racey *et al.* 1998].

Transects were situated in a radius of 1.5 km, hence the activity of the bats should correspond to prey abundance. Some of the data collected during research in 1995 and 1996 has already been published [Kozakiewicz *et al.* 1995], yet the data analysis in these studies proved to have been based on incorrect lengths of the transects. This work presents the corrected analysis of the data collected in the previous seasons together with one more season (2001).

Data analysis

A two-way (or three-way) ANOVA with unequal sample size was conducted due to the value of the association between the activity of *M. daubentonii* and trophic state of lakes and the period (lactation/post-lactation). To test the relationships between *M. daubentonii* activity, the type of trophic lake, and the period (lactation/post-lactation), a two-way ANOVA with unequal sample sizes was used. Due to the incomplete season in 2001 (no data from post-lactation period) the ANOVAs were performed separately for:

a) the difference between lakes with different trophy land years of research, separately for the lactation and post-lactation periods;

b) the difference between the lactation and post-lactation periods and the year of study, separately for each lake.

Furthermore, a *post hoc* multiple comparison Tukey's test for the average activity of *M. daubentonii* for each pair of lakes was conducted (lactation period and year). All hypotheses were tested at a two-sided significance level of $p = 0.05$. Means ($x \pm SD$) are reported in tables and in the text, F-values and significance are given for ANOVAs. All analyses were carried out using RStudio, version 4.1.0 (R Core Team, 2020).

Results

The total research effort for the three years of research was 105 transect-nights (Table 1). Each of the factors, lake trophy and period, is represented in the sample to a similar extent. The highest variance in the activity of *M. daubentonii* was found on the dystrophic lake (SWL: 3.4–23.8 ind./km), while on the oligotrophic and eutrophic lakes the values were lower: 2.4–15.9 ind./km (BL) and 5.8–11.5 ind./km (WL), respectively.

Differences between the three trophy type lakes

During the lactation period, the average activity of the bats varied from 8.0 ind./km on the oligotrophic lake (BL), through a slightly higher (8.9 ind./km) on the eutrophic lake (WL), to 15.0 ind./km on the dystrophic lake (SWL).

Table 1. The number of transects surveyed on the oligotrophic (Białe Lake), dystrophic (Suchar Wielki Lake), and eutrophic (Wigry Lake) lake over in the three years of research

Таблиця 1. Кількість трансект, проведених на оліготрофних (оз. Біле), дистрофних (оз. Сухар Великі) та евтрофних (оз. Вігри) озерах за трирічний період досліджень

Year	Period	Oligotrophic	Dystrophic	Eutrophic	Total
1995	lactation	3	5	4	12
	post-lactation	7	4	7	18
1996	lactation	10	11	10	31
	post-lactation	10	10	10	30
2001	lactation	4	5	5	14
Total		34	35	36	105

Over this period, the recorded activity of bats was significantly different between the lakes, while no significant differences in the overall activity of the bats have been recorded between the consecutive years of research, and, similarly, there was no significant difference in bat activity between the lake and year of interaction (Table 2a). The greatest foraging activity of *M. daubentonii* was observed on the dystrophic lake and was significantly higher than over the oligotrophic (15.0 ± 6.02 vs 8.0 ± 3.42; p = 0.0003) and eutrophic lake (15.0 ± 6.02 vs 8.9 ± 3.50; p = 0.0006) (Tukey *post-hoc* test). In turn, the oligotrophic and eutrophic lakes were characterised by similar activity of bats (no significant difference between the activities of bats over the two lakes: (8.0 ± 3.42 vs 8.9 ± 3.50; p = 0.837).

During the post-lactation period, the average activity of bats varied from 4.1 ind./km on the oligotrophic lake (BL), through a higher value (7.0 ind./km) on the eutrophic lake (WL), to 10.4 ind./km on the dystrophic lake (SWL). Similarly, as in the case of the lactation period, there was a significant difference in bat activity depending on the type of the lake. Additionally, differences between the years of research were found, however, there was no significant difference in the lake and year of interaction (Table 2b). A significantly higher activity of *M. daubentonii* was recorded over the dystrophic lake: activity on this water body was larger than on the oligotrophic lake (10.4 ± 5.58 vs 4.1 ± 4.16; p = 0.0003). On the other hand, there were no significant differences in bat activity between the eutrophic (WL) and both the dystrophic (7.0 ± 2.68 vs 10.4 ± 5.58; p = 0.096) and oligotrophic lakes (7.0 ± 2.68 vs 4.1 ± 4.16; p = 0.062). The average bat activity recorded in 1995 was significantly higher than that recorded a year later, in 1996 (8.0 ± 5.40 vs 5.3 ± 3.27; p = 0.033) (Tukey *post-hoc* test).

Differences between the lactation and post-lactation periods

The activity of *M. daubentonii* was significantly different between lakes and between periods, but not between years. None of the interactions is significant (Table 2c). The highest bat activity was recorded on the dystrophic lake, and it differs from the activity on both the oligotrophic (12.9 ± 6.48 vs 5.9 ± 4.50; p = 0.0001) and the eutrophic lakes (12.9 ± 6.48 vs 7.8 ± 3.22; p = 0.0002). In turn, no differences were found between the oligotrophic and eutrophic lakes (5.9 ± 4.50 vs 7.8 ± 3.22; p = 0.236). During the lactation period, the bat activity was higher than during the post-lactation period (11.0 ± 5.83 vs 7.0 ± 4.85; p = 0.0002) (Tukey *post-hoc* test).

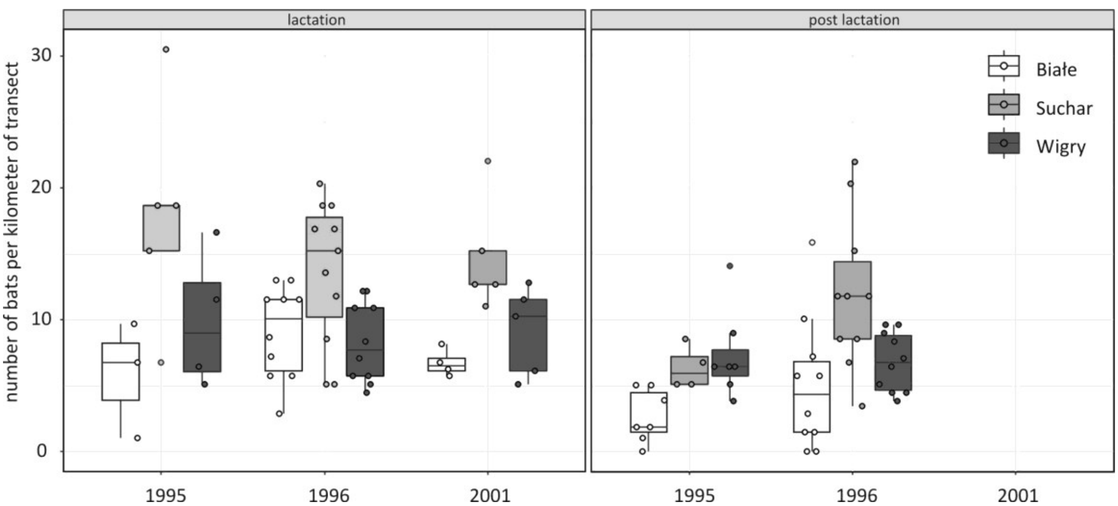

Fig. 2. The activity of *Myotis daubentonii* over three lakes of different trophy in the Wigierski National Park (NE Poland). White—oligotrophic lake (Białe Lake), light grey—dystrophic lake (Suchar Wielki Lake), dark grey—eutrophic lake (Wigry Lake).

Рис. 2. Активність *Myotis daubentonii* у трьох різних за трофністю озерах у Вігерському національному парку (північна Польща). Чорний колір — евтрофне озеро (озеро Вігри), сірий — дистрофне озеро (озеро Сухар-Велькі), білий — оліготрофне озеро (озеро Біле).

Table 2. The results of ANOVA provided for: a) lactation period for three years: 1995, 1996, 2001, b) post-lactation period for two years: 1995 and 1996, c) periods: lactation and post-lactation, for two years: 1995 and 1996 of research

Таблиця 2. Результати дисперсійного аналізу а) періодів лактації у 1995, 1996 і 2001 роках, б) постлактаційних періодів у 1995 та 1996 роках, в) періодів лактації та постлактації у 1995 та 1996 роках

a) lactation/1995, 1996, 2001	df	Sum Sq	Mean Sq	F	p-value	significance
Lake	2	575.2	287.6	13.4	0.00002	***
Year	2	17.6	8.82	0.411	0.665	
lake * year	4	86.2	21.6	1.01	0.414	
Residuals	48	1029	21.5			
b) post-lactation/1995, 1996	**df**	**Sum Sq**	**Mean Sq**	**F**	**p-value**	**significance**
Lake	2	307.9	154.0	9.50	0.0004	***
Year	1	50.9	50.9	3.14	0.084	
lake * year	2	65.2	32.6	2.01	0.147	
Residuals	42	680.8	16.2			
c) 1995, 1996	**df**	**Sum Sq**	**Mean Sq**	**F**	**p-value**	**significance**
Lake	2	779.8	389.9	19.4	<0.0001	***
year	1	16.8	16.8	0.835	0.364	
period	1	268.9	268.9	13.4	0.0005	***
lake * year	2	55.2	27.6	1.38	0.259	
lake * period	2	30.6	15.3	0.76	0.470	
year * period	1	54.7	54.7	2.73	0.103	
lake * year * period	2	102.5	51.2	2.55	0.084	
Residuals	79	1585.9	20.1			

Note. Significance: *** <0.001, ** < 0.01, * < 0.05

Discussion

During the lactation period, the foraging activity of Daubenton's bat was the highest on the distrophic lake (SWL) and was significantly higher than on both the eutrophic lake (WL) and the oligotrophic lake (BL). In turn, the bat activity on the eutrophic and oligotrophic water bodies was similar. However, in the post-lactation period significant differences in activity were noted only between SWL and BL (higher over SWL), while the remaining differences proved to be insignificant. A significant effect of the year of the study was also recorded. Furthermore, foraging activity of Daubenton's bat during lactation was significantly higher than in the post-lactation period. Despite the differences between the periods, the activity of bats follows a similar pattern in each of the periods studied: the dystrophic lake was more attractive than both the eutrophic and oligotrophic lakes, with no significant difference in bat activity over the last two.

The majority of the diet of *M. daubentonii* consists of insects that are active above the water surface (up to 75%), which live mainly on the water surface either permanently or periodically: midge larvae and pupae of Chironomidae, preadult Trichoptera. It also includes the insects that accidentally fall into the water. However, they constitute a smaller part of the bat's diet (up to 25%) [Flavin *et al.* 2001]. The number of flying terrestrial insects also influenced the foraging activity of Daubenton's bat; however, a stronger relationship was found with the number of adult aquatic insects (but not with their biomass) [Akasaka *et al.* 2009]. The diet of this species is dominated by insects of the Chironomidae (Diptera) family [Bogdanowicz 1994; Beck 1995], although in some periods (or different regions), other insects such as Trichoptera, Lepidoptera, and Aranea comprise a significant part of the bat's diet [Vaughan 1997; Flavin *et al.* 2001; Arnold *et al.* 2001; Nissen *et al.* 2013]. Seasonal changes in diet composition are significant and are related to the life cycle of insects [Sullivan *et al.* 1993; Flavin *et al.* 2001].

Water quality in aquatic ecosystems can influence the activity of Daubenton's bat to some extent, although study results published to date are often mutually exclusive.

According to stomach contents analyses of *M. daubentonii* and a high density of Chironomidae over eutrophicated waters, Kokurewicz [1995] hypothesised that eutrophic water bodies are more attractive to this bat than oligotrophic ones. This hypothesis, however, can be treated as anecdotal evidence, as it was based on a single sample from a eutrophic channel, with no comparison to an oligotrophic water body. Eutrophic waters contain aquatic pollutants (mainly nitrogen and phosphorous), which, in turn, affects aquatic life, i.e., the growth of floating and littoral vegetation [Lampert & Sommer 2007]. In turn, *M. daubentonii*, prefers rivers and lakes without aquatic vegetation [Boonman *et al.* 1998]. Moreover, Chironomidae occur within a wide range of pollution levels, from clean water, through a moderately to heavily polluted water, they are also used as indicators of the trophic level of aquatic ecosystems [Saether 1979; Armitage *et al.* 1999]. For example, the three most common Chironomidae species that occurred in the diet of *M. daubentonii—Microtendipes pedellus*, *Glyptotendipes cauliginellus*, and *Procladius ferrugineus* [Vesterinen *et al.* 2013]—are typical for unpolluted streams [de Bisthoven & Gerhardt 2003]. In addition, Trichoptera, which also constitute a significant component of the bat's diet, prefer waters of good biological quality to mild pollution [Wiederholm 1984].

Similar insect density over either eutrophic or oligotrophic rivers was found by Racey *et al*. [1998]: the differences referred to frequencies of insect taxa and their biomass, not to the activity of *M. daubentonii* between rivers. Racey *et al*. [1998] found the largest differences in Trichoptera density: it was twice as high over oligotrophic as over eutrophic water in the rivers. Similar results were obtained during the 4-year studies on trichopteran fauna over Białe, Suchar Wielki, and Wigry lakes: the densities of insects were almost twice as high over Białe lake compared to the two others, while the densities of Trichoptera communities on the eutrophic and oligotrophic lakes were similar, but different from the dystrophic one [Szczęsny & Majecki 2002]. Hence, the higher densities of Trichoptera over the oligotrophic lake compensate for the lower density of insects from other groups, which makes both of the two trophy type lakes similarly attractive as a foraging area. Taake [1992] noted that *M. daubentonii* prefers similar sizes of Chironomidae and other insects, which could explain the ecological flexibility of *M. daubentonii*. Therefore, the small differences in the hunting activity of Daubenton's bat between the eutrophic and oligotrophic lakes confirms the opportunistic foraging strategy of this species. The effects of water pollution and eutrophication on bats remains unclear: different effects are reported for different species and in different areas [Salvarina 2016].

Also, the particularly high activity of *M. daubentonii* over the dystrophic lake (almost two times higher than over the other types) cannot be explained by the trophy type of the water body. Due to the low concentrations of nitrate and phosphorus and similarity of phytoplankton, dystrophic water bodies are considered a class of oligotrophic lakes [Mikulski 1982]. The numbers of Trichoptera over the dystrophic lake falls between those recorded over the eutrophic and oligotrophic lakes [Szczęsny & Majecki 2002], and does not explain the remarkably high activity of bats. Small ponds, like Suchar, are thought to be drinking sites or optional feeding areas when located close to larger, richer lakes [Ciechanowski 2002]. The selected lakes differ in area and bankside vegetation: the area of Suchar Wielki is, in contrast to Wigry and Białe, almost completely protected from wind. Small ponds and parts of rivers that are sheltered from the wind by trees are more attractive as bat-feeding grounds due to the elevated densities of insects [Warren *et al.* 2000; Zahn & Maier 1997]. In turn, the density of insects is correlated not only with the water quality and habitat structure, but also with the relative humidity over the water surface [Payne 2011]. Thus, the high activity of *M. daubentonii* over Suchar may be an effect of isolation of this feeding area from the wind rather than the effect of the trophic status of the lake.

Higher hunting activity during pregnancy and lactation than in the post-lactation period can be attributed to higher energy demands in the reproductive period [Encarnação & Dietz 2006]. Insect phenology is also not insignificant: aquatic insects constituted a considerable proportion of aerial flying arthropods—the variation in insect emergence is mostly explained by water temperature [Salvarina *et al.* 2017]. In turn, the lower bat activity in the post-lactation period is typical for most temperate bat species [Ciechanowski *et al.* 2010]. This pattern is most probably the result of the bats' gradual migration from the feeding areas to swarming/wintering sites.

If this is the case, can the observed increase in the numbers of Daubenton's bat at wintering shelters be the result of changes in water quality in Europe? This species is rather sedentary and rarely migrates further than a few dozens of kilometres [Bogdanowicz 1994]. The slow increase in the numbers of *M. daubentonii* correlates with the increase in the number of other sedentary species of bats: large mouse-eared bat (*Myotis myotis*) and lesser horseshoe bat (*Rhinolophus hipposideros*). Over the past 30 years in Central Europe the use of fertilizers and plant protection measures has dropped considerably, and, consequently, the water quality has improved. In turn, on farms that did not use synthetic fertilizers, pesticides and growth regulators, insect abundance was significantly higher on pastures and in aquatic habitats than in the same habitats on conventional farms [Wickramasinghe *et al.* 2004]. Hence, an increase in the numbers of Daubenton's bat is more likely to be correlated with the improved quality of the environment than the suggested eutrophisation.

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Handling of materials. All manipulations with living animals were carried out using non-lethal techniques and in compliance with the current legislation of Poland.

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