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Authors: Nissen, Henning, Krüger, Frauke, Fichtner, Andreas, and Sommer, Robert S.

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Local variability in the diet of Daubenton's bat (*Myotis daubentonii*) in a lake landscape of northern Germany

Henning NISSEN[1], Frauke KRÜGER[1], Andreas FICHTNER[1] and Robert S. SOMMER[1]*

[1] *Institute for Natural Resource Conservation, University of Kiel, Olshausenstrasse 40, 24098 Kiel, Germany; e-mail: hnissen@ecology.uni-kiel.de, fkrueger@ecology.uni-kiel.de, afichtner@ecology.uni-kiel.de, rsommer@ecology.uni-kiel.de*

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Abstract. Daubenton's bat *Myotis daubentonii* is one of the most common bat species of Europe, hunting its prey in the surroundings of water bodies, with different microhabitats. To explore the local adaptability to different environmental conditions, we compared the diet of Daubenton's bats at four different sites in a lake landscape in northern Germany with a main focus on prey diversity. Bats were caught (n = 85) in mist nets for collecting individual faecal pellets (n = 276). Pellets were dissected and the occurrence of identifiable pieces of each prey group was evaluated and grouped in five different frequency groups. We found 17 different groups of arthropods among the prey, with a clear dominance of Chironomidae and Trichoptera. There were significant differences among the sampling sites in prey diversity but not in prey richness.The changes in prey diversity were associated with sample sites. We conclude that on a local scale there is low variability in diet of Daubenton's bat caused by hunting in various habitat structures in the surroundings of water bodies. Our results highlight the ecological flexibility of *M. daubentonii*, which could be an explanation for the commonness of *M. daubentonii* across Europe in comparison to the rather rare pond bat (*Myotis dasycneme*), which has similar habitats and main prey group preferences.

Key words: foraging, hunting behaviour, trawling, aerial hawking, prey diversity

Introduction

The analysis of trophical interaction is an important tool to understand the biology and function of single species in their environment. Dietary studies also help to get insights into predator-prey relationships and food-web processes. Additionally results can function as indicators for how species react to environmental changes and if they are adaptable to such changes. In insectivorous bats, diet is mainly triggered by prey availability (Rydell 1992, Walsh & Harris 1996), but might be also influenced by the individual's sex or age. In turn a bat diet can provide information on where it hunts. For vespertilionid bats, among the most diverse bat families, habitats with habitat transition zones, like river banks or forest edges are very important foraging sites (Rydell 1992, Walsh & Harris1996).

Within the vespertilionid bats, Daubenton's bat, *Myotis daubentonii* (Kuhl, 1817), is very common across Central Europe and compared to other bat species it is currently of no special conservational concern. Its distribution is strongly associated with lakes, ponds, rivers and streams. The current knowledge of its feeding ecology and behaviour suggest that *M. daubentonii* forages along waterways and adjacent habitats (Jones & Rayner 1988, Bogdanowicz 1994, Arnold et al. 2000, Warren et al. 2000, Flavin et al. 2001, Ciechanowski 2002, Dietz et al. 2007).

Among the "trawling *Myotis*", which includes all *Myotis* species hunting directly over water and sharing similar morphological adaptations, e.g. relatively large feet (Findley 1972, Siemers et al. 2001a), *M. daubentonii* is thought to be a rather flexible hunter, due to its morphological and echolocation characteristics (Norberg & Rayner 1987, Britton & Jones 1999). It is capable of hunting along edge space, forest interior, open water and free air, using different hunting techniques such as taking prey on the wing (aerial hawking), taking prey from vegetation (gleaning) and grasping prey directly from the water surface (trawling) (Kalko & Schnitzler 1989, Siemers et al. 2001a, Schnitzler et al. 2003, Todd & Waters 2007).

The prey mainly consists of insects, and to a far lesser percentage, also spiders, with a mean size about 7.2 mm (Taake 1992, Dietz et al. 2007). The

* *Corresponding Author*

diet of Daubenton's bats is rather well investigated compared to other European bat species and shows high prey diversity with chironomids and caddies flies representing the most frequent prey items.

The diverse hunting techniques and diet make *M. daubentonii* a fairly adaptable species, thriving in a wide range of habitats. Nevertheless the modern landscapes are heavily altered by humans due to changes in land use, such as urbanisation or agriculture. To gain insights into the adaptability to local environmental conditions as well as prey variability, we compared the diet of Daubenton's bat on a local scale in a lake landscape, typical for the young moraine areas of the European Lowlands. We were interested to see if despite the high quality habitats in the study area we still were able to show differences in the diet of Daubenton's bats regarding its composition and thus showing the high trophic adaptability of this species. As aquatic habitats are regarded as sites with high significance for bat species conservation across many taxa (Racey & Entwistle 2003), we were interested if our small scale approach could show differences between sites within a rather optimal landscape concerning the diet composition.

Material and Methods

Study area

The study was carried out in the nature park "Westensee", which is situated in characteristic North-Eastern European hummocky morainal landscape (Fig. 1). Land use is dominated by agriculture and forestry of different intensity and dimensions. Lake Westensee (7 km²) is central to the investigation area (Fig. 1). Several smaller water bodies such as rivers, streams and little lakes are connected to the lake. These lakes, ponds, streams and rivers are to a certain extent imbedded in woodland patches, meadows, and pasture, often lined by riverine groves. The nature park "Westensee" can be considered optimal for foraging Daubenton's bats due to its expanse of water, offering heterogeneous habitat transition zones between water and other habitats, important for hunting vespertilionid bats (Walsh & Harris 1996). Nevertheless this area is highly influenced by human activities including urbanisation and agriculture. We sampled bats at four different sites (Fig. 1), displaying different habitat structures of typical hunting areas of *M. daubentonii*. The distance of the sampling sites to each other is not far (Fig. 1) and lies within the known commuting distance of *M. daubentonii*.

Still the sites differ in certain environmental features as flow velocity, water type and surrounding: (1) River fast, (2) River slow, (3) Stream and (4) Pond (Table 1).

(1) The sampling site "*River fast"* is a smaller, fast flowing section of the River Eider (width 5 m, depth 50 cm) in a diversified (diverse) agrarian landscape. The stream has a relatively disturbed water surface (shown by undulated water) and is hydro-morphologically altered due to its connection to a water mill with several dammed pools. The shorelines are dominated by few wooded structures, tall herbaceous vegetation and pasture.

(2) Sampling site "*River slow*" is a middle sized, slow flowing section of the River Eider in an urban area. It has a width of 9 m, a depth of 130 cm, its banks are straightened and lined with single trees. Along the urban areas the surroundings are mainly characterized by agricultural use.

(3) Sampling site "*Stream"* is a stream (width 5 m, depth 30 cm) in a light mixed forest connecting smaller lakes. The forest is mainly characterized by European beech. The lake shore lines encompass gradients from forest habitats to lake habitats, offering a diverse structure and thus suitable hunting habitats for vespertilionid bats.

(4) Site "*Pond"* is characterized by artificial, very eutrophic fish ponds in the vicinity of urban area. Here the shorelines are seminatural, dominated by tall herbaceous vegetation and small reed, as well as by a wooded belt. The surroundings are dominated by agriculture and lake Westensee.

Sampling and faecal analysis

Bats were caught in mist nets placed directly over the water surface and were kept separately in soft cotton bags for a maximum of one hour for collecting individual faecal samples (Table 2). Pellets were dried at room temperature, soaked for 48 hours in 70 % ethanol and dissected under a magnification of

Table 1. Description of the sampling sites. Number of the sampling site refers to numbers in Fig. 1.

Sampling site	Water body type	Flow velocity	Habitat structure/land use	
			shore	surroundings
(1) River fast	flowing waters	fast	riverine vegetation/sgl. trees	pasture/agriculture
(2) River slow	flowing waters	slow	riverine vegetation/tree lines	urban/agriculture
(3) Stream	flowing waters	medium	forest	mixed forest
(4) Pond	standing water	none	riverine vegetation/sgl. trees	agriculture

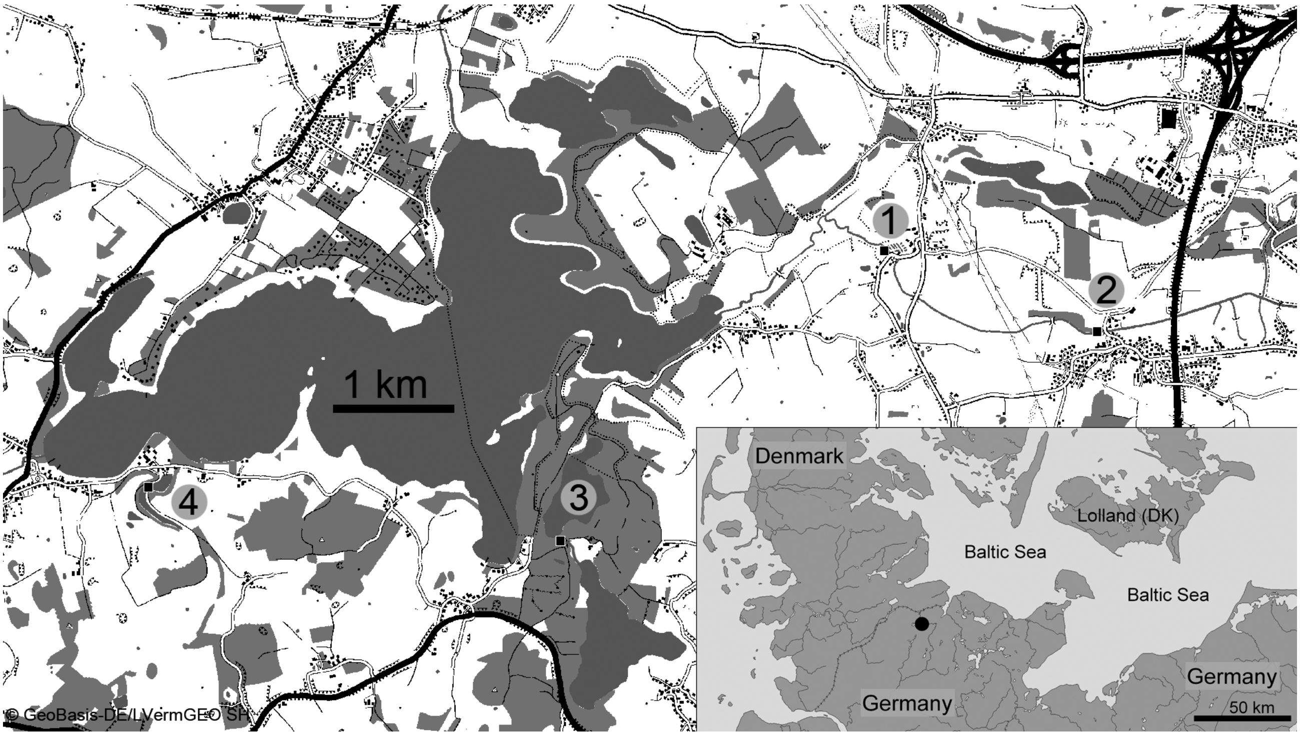

Fig. 1. Structure of the investigation area (with lake Westensee in its centre) and its geographical position in the European Lowlands. Numbers of the sampling sites (black squares) refer to the text. Legend: dark grey = water bodies, light grey = forests or forest patches, white = agrarian landscape (meadows or fields).

10-50×. Identification of taxa to class, order, family, or genus level, was achieved by comparison of fragments with whole collected insects and arthropod identification keys (Shiel et al. 1997). For each sample, identifiable pieces of each prey group were counted and classified in five groups regarding their frequency (1: 1-3 fragments, 2: 4-10, 3: 11-20, 4: 21-50 and 5: 51-80). We further determined the relative proportion of each prey group of the total of consumed prey groups ('percentage frequency', total = 100 %) following McAney et al. (1991) and Vaughaun (1997). Percentage occurrence and percentage frequency were based on the binomial presence absence data.

Table 2. Investigated faecal samples at different sites considering sample dates, sexes and sample size. Number of the sampling site refers to numbers in Fig. 1.

Sampling site	Sampling date	Individuals (female/male)	Sample size
(1) River fast	20.07.2010	5/3	27
(2) River slow	24.06.2010	21/13	147
(3) Stream	27.06.2010	19/-	54
(4) Pond	30.06.2010	18/6	48

Data analysis

We applied an analysis of dissimilarity (ADONIS) to test for differences in prey composition between sample sites (*River fast*, *River slow*, *Stream*, *Pond*) with a Bonferroni adjustment for multiple testing (Anderson 2001). The analysis was performed on a matrix of Bray-Curtis dissimilarities based on the relative abundance of fragments in individual prey groups ($n = 18$).

To analyse the effect of sample site on prey richness and diversity we used a mixed modelling approach with a post hoc performance (Tukey HSD test). Individual was treated as a random component to account for the correlation between samples of the same bat individual (Zuur et al. 2009). Prey richness, quantified as the number of realized prey groups at a given site, was modelled with the log link function and a Poisson distribution. Prey diversity calculations were based on relative abundance data using Simpson's index of dominance:

$$D = 1 - \sum p_i^2 ,$$

where p_i is the proportion of fragments in prey group i (Simpson 1949). The multivariate analysis was performed with the *vegan* library in R (R Development Core Team 2011, version 2.10.1). The generalised linear mixed model (prey richness) and linear mixed model (prey diversity) were fitted to the data with *lmer* function implemented in the *lme4* R library.

Results

We recognised 17 different groups of arthropods among the prey of Daubenton's bat. Imagos of chironomids and pupae of chironomids were differentiated, because pupae were grasped on the water surface and thus it is recorded as a special feeding behaviour. Altogether, estimation of prey percentage frequency showed that Chironomidae (imagos) (22.5 %) and Trichoptera (23.0 %) are by far the main prey groups of *M. daubentonii* (Table 3). Further prey groups are Brachycera (13.1 %), Nematocera (9.3 %), Tipulidae (7.5 %), Coleoptera (6.8 %) and Lepidoptera (4.4 %). The other prey groups with lesser importance are listed in Table 3. Pupae of Chironomidae were recorded with 1.7 %, thus in view of prey turnover, chironomids were the most important taxa with 24.2 %. The results of the four sampling sites are listed in Table 3 (in percentage frequency). On average 3-4 prey taxa were recorded in one pellet. We found a variation in dominance of main prey groups. At site 1 (slow flowing river) the estimation of Chironomidae and Trichoptera were nearly on the same level, whereas a clear variance in dominance with a difference about 7-10 percentage frequency is visible in all other sites. Notably, Neuroptera, with the lowest importance for the diet of *M. daubentonii* in the investigated area, were only consumed in the slow flowing river (Table 3). We could record little stones and plant relics in the faecal pellets of nearly all sites to a certain degree.

The ADONIS indicated that prey composition significantly varied with sample site (F = 3.57, P < 0.001, all pair-wise comparisons $P_{adj.}$ < 0.01). Sample site had a significant impact on prey diversity (F = 5.59, P = 0.002), while differences in mean prey richness values were statistically not significant (χ^2 = 1.49, P = 0.68). Prey diversity increased within the series *River fast* > *Pond* > *River slow* > *Stream* (Fig. 2). These variations were significant for *Stream* vs. *Pond* ($P_{adj.}$ < 0.01), *Stream* vs. *River fast* ($P_{adj.}$ < 0.05), *River slow* vs. *Pond* ($P_{adj.}$ < 0.05), and were marginally significant for *River slow* vs. *River fast* ($P_{adj.}$ = 0.05).

Table 3. Percentage frequency of prey items in the diet of *M. daubentonii* sampled at the four different localities. Most dominant prey groups are marked in bold.

	Frequency of prey groups [%]				
Prey group	River fast (1)	River slow (2)	Stream (3)	Pond (4)	Total
Trichoptera	**26.2**	22.5	**27.0**	19.9	**23.0**
Chironomidae	16.7	**22.9**	20.5	**27.5**	22.5
Brachycera	3.6	14.2	14.1	14.6	13.1
Nematocera	15.5	8.5	0.5	12.3	9.3
Tipulidae	10.7	6.1	10.3	7.6	7.5
Coleoptera	9.5	5.3	11.4	5.3	6.8
Lepidoptera	9.5	5.7	1.6	1.8	4.4
Ephemeroptera	-	2.6	0.5	3.5	2.1
Aranea	-	2.0	4.3	1.2	2.1
Corixidae	1.2	2.6	1.1	1.2	1.9
Chironomidae pupa	1.2	2.4	1.1	0.6	1.7
Formicidae	3.6	1.6	1.1	1.2	1.6
Culicidae	-	0.2	2.7	1.2	0.8
Hymenoptera	1.2	0.8	1.6	-	0.8
Hemiptera	1.2	0.4	0.5	1.8	0.7
Diptera	-	1.0	0.5	-	0.6
Hemerobiidae	-	0.6	1.1	0.6	0.6
o. Neuroptera	-	0.4	-	-	0.2
Total number	100	100	100	100	100

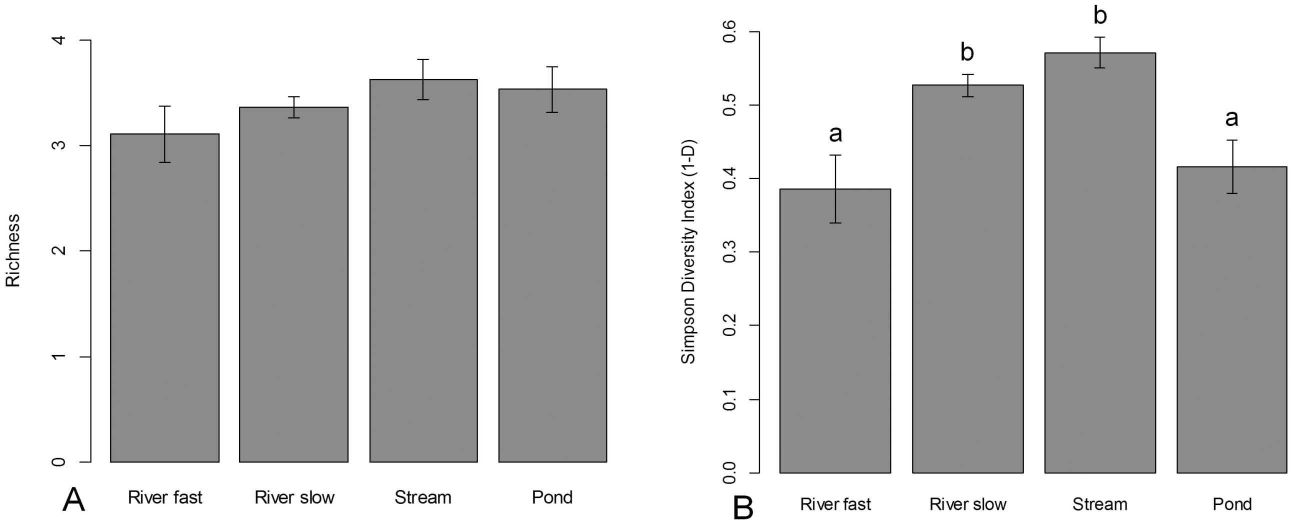

Fig. 2. Effect of sample site on prey richness (A) and prey diversity (B) of *M. daubentonii*. Different letters indicate significant differences between sample sites ($P_{adj.}$ < 0.05 and $P_{adj.}$ = 0.05 for the comparison between the two river habitats, respectively). Variations in prey richness were not significant (χ^2 = 1.49, P = 0.68).

Discussion

The general prey pattern confirms that Chironomidae and Trichoptera are the dominant prey groups with a percentage frequency in sum of about 45 %. This is similar to the data from Ireland with 51 % (Sullivan et al. 1993) and 50 % (Flavin et al. 2001). It also underlines, that our overall findings are not only reflecting a local situation but are comparable to other populations of *M. daubentonii* across its distribution area.

The overall prey groups we could identify reflect the adaptability of *M. daubentonii* concerning its hunting techniques. Besides the prey groups like Trichoptera, Chironomidae (imagos), Brachycera, Tipulidae or Lepidoptera, which are mainly hunted by aerial hawking, some other prey groups are of a special interest. For example Chironomidae pupae are indicators for the particular hunting behaviour involving the grasping of prey directly from the water surface, and thus this species is switching between two very different hunting techniques (Todd & Waters 2007). Whether or not Corixidae (water-boatman) can be also regarded as such trawling-indicator is debatable as they are known to fly and also to appear in the diet of other, non-trawling bat species (Gajdošík & Gaisler 2004, Lee & McCracken 2005). Other prey species are known to dwell along vegetation as Tipulidae or Aranea. Their occurrence in the diet of *M. daubentonii* could be evidence for its gleaning behaviour, grasping prey from any kind of vegetation. The presence of little stones in c. 10-20 % in the dropping samples of all sites and plant relics in three sites could be taken either by error via trawling and gleaning, or as plant matter adhering to prey, still highlighting the importance of trawling and gleaning in hunting behaviour of Daubenton's bat.

When comparing the diversity of prey groups, we found significant differences among the sampling sites (Fig. 2). This pattern of variation may display the adaptability to local prey availability in a lake landscape and highlight the ecological flexibility of Daubenton's bats.

As shown in the results, the dietary diversity is highest among bats caught along the slow river part (2) and the forest stream (3), whereas it is lowest at the fast flowing river part (1) and the pond (4). This can be explained in different ways. The higher dietary diversity at site (2) could be caused by hydro-morphological features like the slower velocity and a wider river bed putatively allowing a richer benthos fauna, thus emerging insects like Chironomidae might be more frequent. The high dietary diversity at site (3) could be explained by occurring transition zones between forest and aquatic habitat. This is known to harbour higher diversity in insects and provide beneficial foraging sites for bats (Rydell 1992, Walsh & Harris 1996, Russ & Montgomery 2002). Lower diversity in diet at the pond site (4) and the fast flowing river part (1) can be related to higher urbanisation resulting in lower insect diversity (Blair & Launer 1997). Intensive agriculture, which is more prominent in site (4) compared to the sites (2) and (3), is also known to have a strong negative effect on insect diversity and richness (Wickramasinghe et al. 2004).

Daubenton's bats are known to use a radius of a few kilometres distance to their summer roosts and the surroundings of the four different sampling sites offer various different habitat structures. Thus, our study gives an insight in variability in diet on a local scale and does not implicitly display the typical prey availability of the habitat where it was caught.

We conclude that there is only a low variability in prey of Daubenton's bats on a local scale, which is visible in changing dominance of both main prey groups Trichoptera and Chironomidae and in diversity of prey groups in the single samplings. Our results illustrate a balanced occurrence of prey groups, displaying different hunting techniques. We have demonstrated the small scale variation in diet of *M. daubentonii* across a typical lake landscape of the European Lowlands. Our dietary results reflect the adaptability of *M. daubentonii* to hunt in different micro-habitat types regarding prey diversity.

The total of behavioural characteristics could offer an explanation for the of *M. daubentonii* across Europe in comparison to comparable, but rather rare species, like the pond bat (*M. dasycneme*), which prefers similar habitats and shows similar main prey groups (Sommer & Sommer 1997, Krüger et al. 2012).

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