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High trophic similarity in the sympatric North European trawling bat species *Myotis daubentonii* and *Myotis dasycneme*

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Most European bat species are insectivorous and share foraging areas to some extent. Where similar species rely on similar resources in the same foraging habitat, they are likely to interact. This study addresses the trophic niche of the Northern European trawling bat species *Myotis dasycneme* (Boie, 1825) and *Myotis daubentonii* (Kuhl, 1817), occurring in the same habitat, and possible interactions or differences within their dietary behaviour. Dietary data of both species were analysed to draw conclusions on their ecology, possible dietary overlap, hints for coexistence mechanisms and community structure. In this study, *M. dasycneme* and *M. daubentonii* fed mainly on Chironomidae (*M. dasycneme*: 44.4%; *M. daubentonii*: 32.8%) and Trichoptera (*M. dasycneme*: 20.4%; *M. daubentonii*: 22.2%), showing a high trophic niche overlap and similar niche breadth. Nevertheless, there were differences in the diet of the two species concerning the predation of chironomids. Differences also occur regarding the prey types, referring to the terrestrial or aquatic life-cycle of prey groups. This could be evidence for different foraging habitats and a spatial segregation of both species. High resource abundance is also likely to allow the coexistence of both species within the same hunting habitat.

Key words: *Myotis dasycneme*, *M. daubentonii*, diet analysis, faecal samples, trophic niche, coexistence

INTRODUCTION

Bats are the most diverse group of mammals, and this is especially pronounced in regard to their variability in trophic niches (Simmons, 2005). In temperate regions bats generally feed on arthropods, and although temperate communities are less diverse than those in the tropics, they still show a variety of different foraging techniques and hunting behaviours. For example, some bat species that hunt mostly over water show so-called 'trawling' behaviour or gaffing (Siemers *et al.*, 2001*b*; Fenton and Bogdanowicz, 2002). The described behaviour and accompanying morphological adaptations, like proportionally large feet, have now been observed in species of three bat families: Noctilionidae (e.g., Kalko *et al.*, 1998), Phyllostomidae (e.g., Weinbeer and Kalko, 2007), and Vespertilionidae (e.g., Jones and Rayner, 1988). In particular it is very common among the genus *Myotis*, with over 12 species showing the mentioned adaptations (Ruedi and Mayer, 2001; Fenton and Bogdanowicz, 2002).

The European bat community harbours three species of water surface foraging *Myotis* bats: the long-fingered bat, *M. capaccinii*, the pond bat, *M. dasycneme* and Daubenton's bat, *M. daubentonii*, which all hunt for prey directly above the water surface using their hind-feet to scoop prey that flies above or floats directly on the water into their mouth (Jones and Rayner, 1988; Kalko and Schnitzler, 1989; Siemers *et al.*, 2001*a*, 2001*b*; Fenton and Bogdanowicz, 2002). *Myotis capaccinii* occurs in the Mediterranean basin and is absent from the central-northern parts of Europe. *Myotis dasycneme* is distributed throughout the northern part of the Eastern Palaearctic, showing a rather fragmented distribution in Western European Lowlands, higher abundance in Eastern Europe and Siberia with some evidence of its occurrence in the Far East. It is regarded as threatened in most of its Western distribution area. In contrast, *M. daubentonii* occurs in nearly the entire Euro-Siberian zone from the British Isles to Siberia, and also enters the Mediterranean zone in the south. Along its eastern and southern areal borders it is replaced by subspecies and sister species (Matveev *et al.*, 2005; Simões *et al.*, 2007). *Myotis daubentonii* is regarded as among the most common bats in the Palearctic region.

For bats, food and roosts are potentially limiting resources and very likely to be involved in shaping their community structure (Findley, 1993). Information on these limiting factors are crucial to understand the ecology of single bat species, but also to determine factors that might be involved in community structuring.

Data pertaining to foraging ecology and the diet of *M. dasycneme* is scarce and fragmentary (Limpens *et al.*, 1999). Thus far there have been four analyses of different profundity of dietary remains of pond bats (Britton *et al.*, 1997; Sommer and Sommer, 1997; Borissenko *et al.*, 1999; Ciechanowski and Zapart, 2012), where Chironomidae and Trichoptera were identified as the main prey items with an overall low diversity. For *M. daubentonii*, which has been more strongly represented in ecological studies, a similar diet consisting mainly of Chironomids and Trichoptera was shown (Swift and Racey, 1983; Sullivan *et al.*, 1993; Flavin *et al.*, 2001). Even less is known about the interaction of *M. daubentonii* and *M. dasycneme* in their hunting habitats. In areas where they occur in sympatry, which is the case for the Northern German Lowlands, they are frequently observed hunting together in the same habitat (Van de Sijpe *et al.*, 2004). The first study to consider a possible trophic niche overlap of both species was published by Borissenko *et al.* (1999), who discussed that their trophic niche does overlap to some extent. However, Daubenton's bats are thought to be rather territorial (Wallin, 1961). Biscardi *et al*. (2007) suggested that Daubenton's bats are potential competitors for food resources of similar, less common species (e.g., *M. capaccinii* — Biscardi *et al*., 2007). A similar effect has also been described for the common *Pipistrellus pipistrellus*, which is believed to have contributed to the decline of the rare *Rhinolophus hipposideros* by resource competition (Arlettaz *et al.*, 2000).

To investigate these issues of resource competition we used dietary data to characterize the ecological niche of the endangered *M. dasycneme* as well as of *M. daubentonii* in the area of sympatry. We then compared the dietary data of *M. dasycneme* with that of *M. daubentonii* in an attempt to discriminate between their ecological niches on a trophic level. Additionally, we were interested in whether mechanisms enabling the coexistence of both bat species in the same habitat in Northern Germany could be derived from these dietary data.

Material and Methods

Study Area

The study area, the valley of the lower Schwentine River in Eastern Schleswig Holstein, Germany, included three different sites: Rastorf (54°28'N, 10°35'E), Wahlstorf (54°18'N, 10°31'E) and Postsee (54°21'N, 10°21'E — Fig. 1). The Schwentine river connects three major lakes and thus forms a rich wetland area in the moraine-formed landscape of eastern Schleswig-Holstein (Weichselian glaciation), with an overall good water quality, rich woodland in the catchment area, and a high percentage of protected areas (Fauna-Flora-Habitats, Nature Protected Areas) resulting in a rich biodiversity concerning e.g. insect communities (Boettger and Rudow, 1995; Poepperl, 1999). The sampling sites were located in the vicinity of two major roosts of *M. dasycneme* and several roosts of *M. daubentonii*.

Capture and Collection of Samples

Catching and handling of bats was done with the official permission of the State Agency for Agriculture, Environment and Rural Areas in Schleswig-Holstein. Bats were caught in mist nets placed directly over the water surface at sites of commuting and hunting along the Schwentine River. Animals were kept separately in soft cotton bags for a maximum of one hour and released after taking measurements and collecting faecal samples. Additionally, Pond bats were marked with metal rings holding individual numeric codes for monitoring purposes. Daubenton's bats were temporarily marked with nail polish to prevent double sampling. A total of 206 faecal pellets obtained from 206 individuals (*M. dasycneme*: 84; *M. daubentonii*: 122) were collected during five single nights during the reproductive season in May, June, July and August 2009 (Appendix I).

Faecal analysis is still a proven method to gather qualitative insight into the diet of bats, even in the midst of the growing molecular genetic approach (Kunz and Whitaker, 1983; Whitaker *et al.*, 2009; see Clare *et al.*, 2009, 2010; Zeale *et al.*, 2011 for progress in molecular techniques). For the faecal analysis, samples were dried at room temperature and stored at -20°C to avoid coprophagous insects. Before analysis, pellets were soaked 48 hours in 70% ethanol and dissected under binocular vision (× 40–50). Characteristic fragments were separated and mounted in euparal for further examination. 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). Fragments were assigned to prey groups (considering the taxon) and prey type (considering the main habitat of prey).

Data Analysis

Prior to analysis, sample size estimation for the population mean was performed with G-Power 3.1.0 (Faul *et al.*, 2007). Using the 'vegan' package (Oksanen *et al.*, 2010), we generated sample-based prey accumulation curves (based on 84,122 random selections of the sample order of *M. dasycneme* and *M. daubentonii*, respectively) using the occurrence of major prey groups in samples.

Non-metric multi-dimensional scaling (NMDS, using the 'metaMDS' function) was performed to determine differences

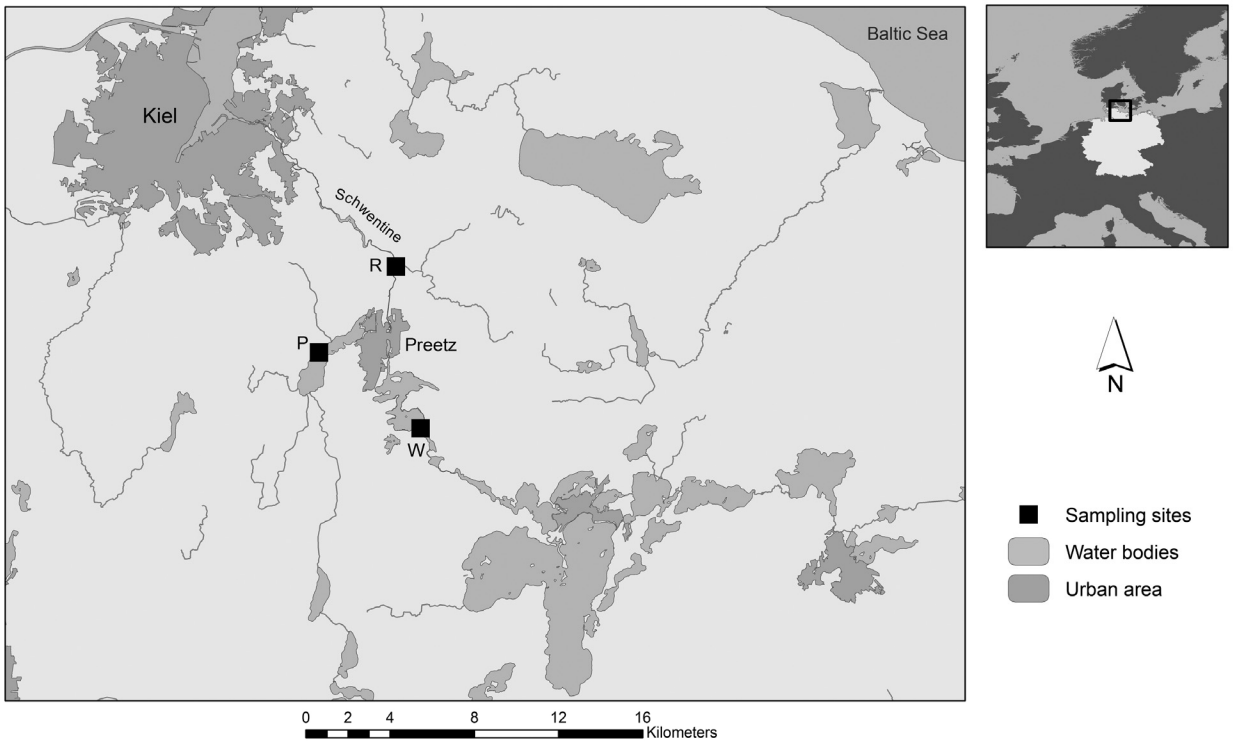

FIG. 1. Geographical overview showing the study area and the three sampling sites in the lake district of Schleswig-Holstein (R — Rastorf, P — Postsee, W — Wahlstorf)

in prey pattern of *M. dasycneme* and *M. daubentonii.* Dissimilarities among fecal samples were calculated using Jaccard distance. To supplement the NMDS analysis, we further conducted a permutational multivariate analysis of variance (ADONIS — Anderson, 2001). Calculations were done in the 'vegan' library in R (Oksanen *et al*., 2010).

To assess dietary niche breadth, we used the reciprocal Simpson's index for diversity and heterogeneity, $1/D = 1/\Sigma(p_i^2)$, where p_i is the relative proportion of a prey item i (with $i = 1 \ldots n$; n = total number of prey items). Thus, a higher index indicates a broader diet with a more evenly proportioned distribution (Lee and McCracken, 2005). Significant differences in dietary niche breadth between the bat species were analysed with one-way ANOVA. For the estimation of diet overlap we calculated the Pianka's index for niche overlap. The Pianka's index is a symmetric measure so that overlap between species A and species B is identical to the overlap between species B and species A. The values range from 0 where no identical resource is used, to 1, indicating a complete resource overlap (Pianka, 1973). The estimation of both indexes was based on the binomial presence-absence data.

For both bat species, occurrence of each prey group was calculated as the relative proportion of all sampled individual bat (*N*) ('percentage occurrence', total > 100 %). We further determined the relative proportion for each prey group of the total of consumed prey groups (Nc) ('percentage frequency', total = 100% — McAney *et al*., 1991; Vaughan, 1997). Variations in the occurrence of prey groups in the diet and prey type among the two bat species were analysed using generalised linear models (GLMs) with a binomial distribution and a logit link function (Zuur *et al.*, 2007). Prey groups were assigned a value of 1 if they were present in the faecal sample or 0 if they were absent. Furthermore, to assess the effect of main foraging habitat on the occurrence of prey groups, prey groups were stratified in aquatic-born and terrestrial types. GLMs were applied for each species separately. All models were fitted using R, version 2.10.1 (R Development Core Team, 2009).

Ethical Standards

The study was conducted meeting the current laws concerning welfare and conservation of the focal species, including an official permission given by the State Agency for Agriculture, Environment and Rural Areas in Schleswig-Holstein (LANU 314/5327.74.1.6). Although dietary studies are a non-invasive method, animals could face stressful situations while catching and keeping animals, thus time of handling and keeping animals, followed international standards and was reduced to a minimum to avoid harmful stress. Nets were guarded through the whole catching event to free bats from the net as soon as possible. Bats were hold in soft cotton bags for a maximum of half an hour. Throughout the whole study no animal was harmed or injured.

RESULTS

Food Habits

The number of different prey items found in each sample varied from one to seven, with a mean of two prey taxa per sample. Both the G-Power test and the prey accumulation curves of both species justify the chosen sample size (Fig. 2).

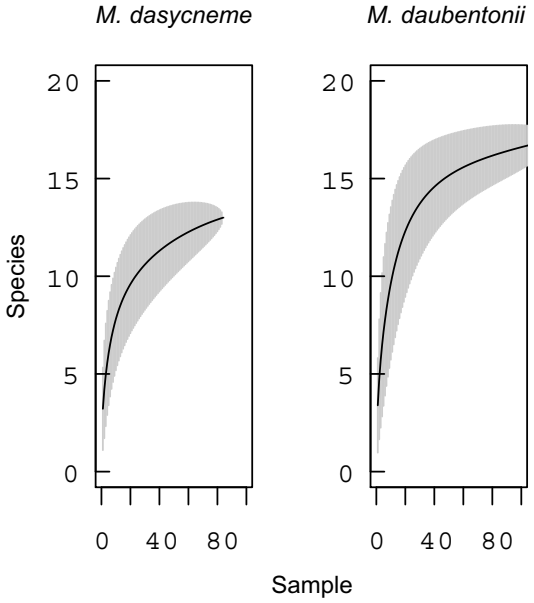

FIG. 2. Prey accumulation curves for prey groups shown in the diet of *M. dasycneme* and *M. daubentonii* based on samples from 84 and 122 bats, respectively. Grey areas indicate the 95% confidence intervals. Both curves turn towards a flattened curve progression just around 20 samples

Overall, 12 prey groups were identified in the diet of *M. dasycneme* encompassing four orders, two suborders, three families, and one genus. For *M. daubentonii*, 17 prey groups were identified, covering nine orders, three suborders, four families and one genus. The calculated frequency of prey groups showed that both species fed mainly on Chironomidae (*M. dasycneme*: 44.4%; *M. daubentonii*: 32.8%) and Trichoptera (*M. dasycneme*: 20.4%; *M. daubentonii*: 22.2%). Also, both species fed on pupae of Chironomidae (*M. dasycneme*: 8.4%; *M. daubentonii*: 4.4%), indicated by parts of pupal cuticles, sometimes with legs and wings still inside as well as the long dense antenna setae, which in most cases were still neatly clumped together. Other items were identified only a few times and therefore only contributed to the diet in low percentages (Table 1). Proportion of main prey groups was rather consistent throughout the sampled time. Due to the limited sampling per month seasonal effects could not be tested (see Appendix II).

Interspecific Variation

The ADONIS indicated significant differences in the diet of the two species (ADONIS: $F_{1, 205} = 2.53$, $P < 0.05$). The NMDS ordination resulted in a two-dimensional solution with a final stress of. Samples of *M. dasycneme* were clustered in the lower left, associated with prey taxa like Chironomidae and chironomid pupae. In contrast, samples of *M. daubentonii* were more evenly spread out in the diagram, but overlapped strongly with the *M. dasycneme* cluster (Fig. 3).

TABLE 1. Results of both percentage occurrence and percentage frequency of prey groups in the diet of *M. dasycneme* and *M. daubentonii*. *z*- and *P*-values, marking significant differences between both species derived from GLM based on the binomial presence-absence data, are shown in addition. Numbers in parentheses identify the number of captured bats, respectively the number of collected faecal samples. Bold numbers denote the main prey groups, whereas an asterisk indicates significant *P*-values

Prey	Percentage occurrence		Percentage frequency		*z*	*P*
	M. dasycneme (*n* = 84)	*M. daubentonii* (*n* = 122)	*M. dasycneme* (*n* = 84)	*M. daubentonii* (*n* = 122)		
Other Diptera	2.4	8.2	1.1	8.2	1.647	0.099
Chironomidae	**95.2**	**82.0**	**43.0**	**34.1**	-2.628	**0.008***
Chironomid pupae	**20.2**	**11.5**	**9.1**	**11.5**	-1.709	0.088
Tipulidae	9.5	10.7	4.3	4.4	0.264	0.792
Other Nematocera	**17.9**	**26.2**	**8.1**	**19.9**	1.400	0.162
Brachycera	4.8	12.3	2.2	5.1	1.772	0.076
Other Hemiptera	–	0.8	–	0.3	0.003	0.997
Corixidae	6.0	5.7	2.7	2.4	1.647	0.948
Gerridae	–	0.8	0.0	0.3	0.003	0.997
Coleoptera	1.2	4.9	0.5	2.0	1.337	0.181
Neuroptera	1.2	4.1	0.5	1.7	1.146	0.252
Aphidoidea	2.4	4.1	1.1	1.7	0.661	0.509
Trichoptera	**46.6**	**50.8**	**21.0**	**21.2**	0.619	0.536
Lepidoptera	**14.3**	**12.3**	**6.5**	**5.1**	-0.416	0.678
Hymenoptera	–	3.3	0.0	1.4	0.009	0.993
Ephemeroptera	–	1.6	0.0	0.7	0.005	0.996
Araneae	–	0.8	0.0	0.3	0.003	0.997

The reciprocal Simpson index (Levin index) showed no statistically significant differences between both species in the diet breadth and the diversity of prey taxa, respectively (*M. dasycneme*: 2.21; *M. daubentonii*: 2.39, ANOVA: $F_{1, 205} = 1.19$, $P = 0.28$). Additionally, Pianka's index for niche overlap indicated an overlap of nearly 100% (0.97). Regardless of sampling time the estimated index showed a similar level of overlap. Additionally, only chironomids differed significantly between the two bat species (Table 1) and this significant difference was not observed if data are grouped for single sampling events through the summer season. Both species displayed differences in prey occurrence regarding the main habitat of prey groups (GLM, aquatic: $z = -0.009$, $P < 0.05$; terrestrial: $z = 0.902$, $P = 0.367$).

Discussion

Food Habits

Our results show that the diets of both *M. dasycneme* and *M. daubentonii* are strongly related both to adult as well as sub-adult chrionomid midges, but other prey groups such as Trichoptera and Lepidoptera also play an important role.

The high amount of relatively small insects (e.g., body length of chironomids = 2–10 mm) caught by *M. dasycneme* is striking considering its larger body size (mean forearm length of 47 mm versus 38 mm in *M. daubentonii*) and lower frequency calls compared to *M. daubentonii* (main call frequency of 39 kHz versus 43 kHz in *M. daubentonii*). This contradicts the hypothesis of increasing prey size with increasing predator size (Barclay and Brigham, 1994; Jones, 1999), but supports the idea that large to medium sized bats, which emit lower echolocation calls, are able to detect smaller prey at greater distances (Jones, 1995*a*; Waters *et al*., 1995; Schnitzler and Kalko, 2001). Considering the swarming behaviour displayed by species like chironomids, caddis flies or mayflies, detection should be even easier compared with that of single individuals. Our results add to the earlier work of Britton *et al.* (1997), Sommer and Sommer (1997) and the more recent analysis of Cechanowski and Zapart (2012) by

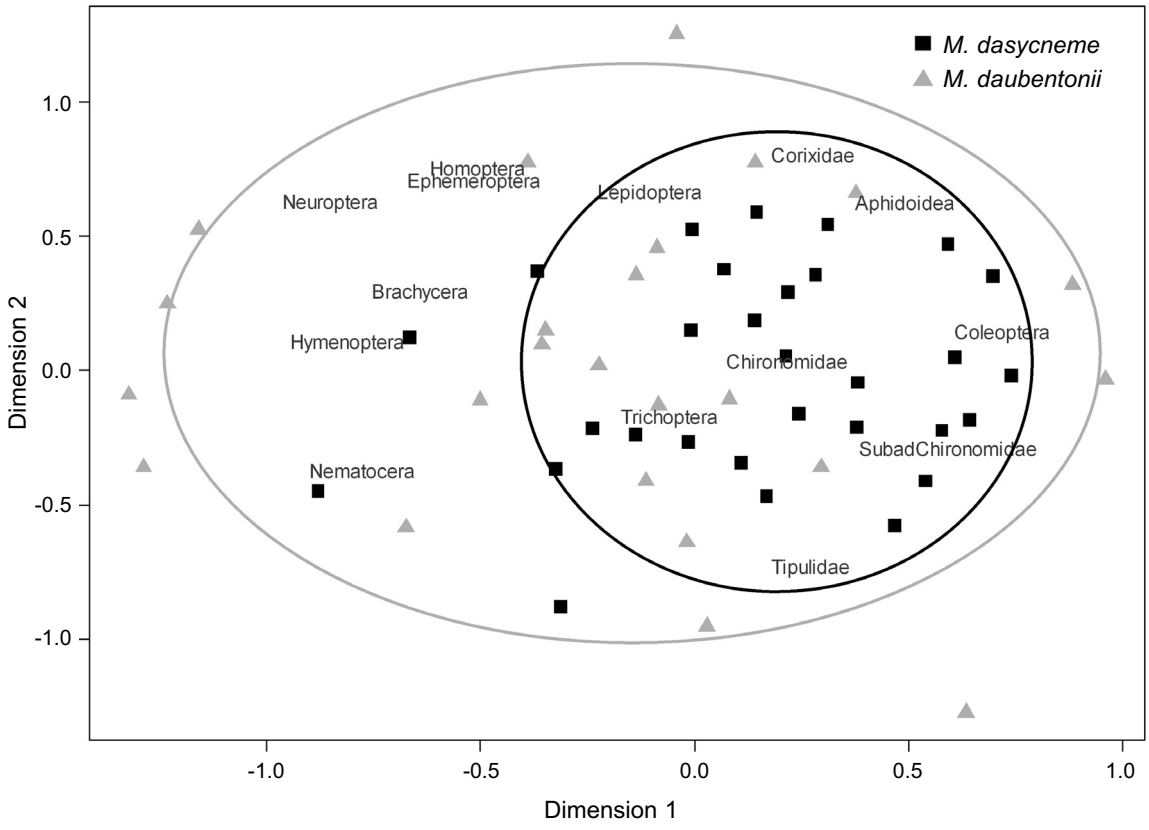

FIG. 3. Non-metric multidimensional scaling (NMDS) ordination of 206 faecal samples showing the diet of *M. dasycneme* and *M. daubentonii*, sampled in North-western Germany. Additionally the identified prey groups are shown associated with their main predator

identifying Heteroptera as prey group, specifically water-boatman (Corixidae). Whether or not Corixidae are captured while leaving the water surface (thus by trawling) or in flight is questionable as they are known to fly and also to appear in the diet of other, non-trawling bat species (Lee and McCracken, 2005). The occurrence of Lepidoptera we observed is similar to that found in other studies (Britton *et al.*, 1997), although our data show a higher frequency compared to Ciechanowski and Zapart (2012) and Sommer and Sommer (1997). This might be related to ecological or traditional differences between subpopulations due to temporal or spatial variation in the availability of this prey group (Aldridge and Rautenbach, 1987; Clare *et al.*, 2010). For *M. daubentonii* we could confirm previous dietary results (Swift and Racey, 1983; Sullivan *et al*., 1993; Flavin *et al*., 2001) where chironomids were identified as major prey item, but a great variety of other, non-aquatic insects were also encompassed in its food spectrum. This may indicate that *M. daubentonii* forage in a larger variety of habitats than *M. dasycneme*.

Our results agree with the dietary findings for other trawling *Myotis* species; they are indeed correlated with aquatic biomes regarding their diet, reflected by a high proportion of arthropods with full or partly aquatic life-cycles. In particular, the high proportion of Chironomidae, which are strongly aquatic in their juvenile stages, and are highly abundant in water ecosystems and throughout their life cycle (Corbet, 1964), has also been shown to be typical for other trawling *Myotis* species like *M. capaccinii* (Almenar *et al*., 2008). Overall dietary results across the group of trawling *Myotis* species are rather congruent compared to our result, with small dipterans as main prey group (Anthony and Kunz, 1977; Robson, 1984; Funakoshi and Takeda, 1998). Among the trawling *Myotis* there are also quite a few species known to prey upon fish to some extent. In Europe, *M. capaccinii* is the only trawling *Myotis* where its strong preference for small subsurface fish species has been shown via both diet analysis and field experiments (Aihartza *et al*., 2008; Almenar *et al*., 2008). *Myotis daubentonii* is also able to catch fish, at least under laboratory conditions (Siemers *et al*., 2001*a*; see also Brosset and Delamare-Debouteville, 1966). Considering the regular presence of ichtyophagous trawling bats in water surface foraging bat communities, it seems likely that either one or both of the northern European trawling *Myotis* species might prey on fish to some extent. However, this could not been shown regarding the samples examined within this study, neither could Ciechanowski and Zapart (2012) find any evidence for this type of ichtyophagous behaviour, despite their great sampling effort.

Interspecific Variation

Comparing the diets of both species, we show that their food spectrum overlaps to nearly 100%. Although the original goal of measuring niche overlap is to evaluate interspecific competition (Schoener, 1974) the high niche overlap does not imply true competition and its absence would not necessarily mean zero competition (MacArthur, 1968; Abrams, 1980). Hence our results do not provide evidence for direct competition.

Both species are water-surface foraging bats that show similar foraging behaviour and follow the same strategy to especially hunt for water emerging insects such as chironomids and caddis flies. These insects are known for high abundance and low weather dependency (Syme *et al*., 2001). Chironomids are known to be particularly abundant at water sites over the whole season, with peaks of abundance for different species at different times of the year and night (Corbet, 1964). Most temperate chironomid species start emerging from water bodies as soon as March and continue to do so throughout the season, with peaks of emergence just after sunset and before sunrise, but emerging throughout the night (Oliver, 1973).

The study area is characterised by high productivity. Based on previous insect monitoring studies from the area (e.g., Orendt *et al*., 2006), a lake of medium size (5 km^2) showed a mean production rate of 2 kg chironomids during the month of May. Overall, other data show that chironomids play a vital role as an energy source in aquatic ecosystems (e.g., Berg and Hellenthal, 1992). Thus, chironomids can be considered an unlimited food resource, leading to low competition albeit high trophic niche overlap. However, studies among other bat communities (e.g., Biscardi *et al.*, 2007), interpreted the high trophic niche overlap, which they detected for Mediterranean *M. daubentonii* and *M. capaccinii*, as evidence for competition between the two taxa. Furthermore they suggested that due to its higher roost specificity *M. capaccinii* could be outcompeted by *M. daubentonii*.

A similar scenario could have lead to the decline of *Rhinolophus hipposideros*, which supposedly competed for food resources with an expanding population of *Pipistrellus pipistrellus* (Arlettaz *et al.,*

2000). Nevertheless, our results cannot support such scenarios for our study species in Northern Germany. Rather, the decline in populations of *M. dasycneme* may be triggered by its synanthropic roost preference and hence interference with humans rather than by competition for food resources (Limpens *et al*., 1999). Despite the high trophic niche overlap we can show slight differences in usage of certain prey groups. *Myotis dasycneme* appears to show a distinct increased predation on adult chironomids and an almost two-fold predation rate on sub-adults (pupae) compared to *M. daubentonii*, even though these prey items are the most important prey groups for both species.

Among closely related species, slight differences in habitat preference are common, as are subtle distinctions between different physical characteristics of the environment (Schoener, 1968; Ricklefs, 1990). Food specialization based either on prey-size or on foraging behaviour can also separate species ecologically (Siemers and Schnitzler, 2004). As foraging behaviour is linked with the morphology of species and vice versa, morphological differences can already be a sign for partitioning. Although echolocation behaviour, search image, foraging strategy and prey perception are very similar (Siemers *et al*., 2001*b*), the studied bat species show significant differences in their morphology. Compared to *M. daubentonii*, *M. dasycneme* has larger wings, higher wing loading and a higher wingtip ratio (*M. daubentonii*: 7 g, 7.0 N/m^2; *M. dasycneme*: 17 g, 10.4 N/m^2), allowing fast and powerful flights above the water surface, but less manoeuvrability (Norberg and Rayner, 1987). Additionally the lower frequency (39 kHz) enables *M. dasycneme* to detect prey from a longer distance. Whereas *M. daubentonii*, being more manoeuvrable and with higher frequencies (43 kHz), hunts in smaller ranges, but due to a higher acoustic resolution also in front of cluttered backgrounds (Kalko and Schnitzler, 1989; Siemers and Swift, 2006). The significantly higher amount of pupae and aquatic insects in the diet of *M. dasycneme* reveals a putative preference for trawling behaviour along the water courses, whereas *M. daubentonii* apparently favours a broader prey spectrum, also hunting along terrestrial habitats. The latter seems comprehensible as numerous authors describe *M. daubentonii* hunting for quite an extensive time in forest habitats (Taake, 1992).

Thus hunting mode and the use of space are influenced by eco-morphological dissimilarities and thus provide a potential mechanism for avoiding competition for food resources (Aldridge and Rautenbach, 1987; Jones, 1995*b*; Safi and Siemers, 2010). Especially foraging in three-dimensional space, which birds, bats or other airborne insectivores exhibit, may facilitate spatial niche partitioning and thus the utilisation of similar resources (Kingston *et al*., 2000). This is also thought to be the case for the sympatric *Myotis myotis* and *M. blythii*. These two species are even more similar in morphology, echolocation and behaviour, as well as sharing roosts. However, they do forage in different habitats apart from each other using different environmental structures and show strong resource partitioning (Arlettaz *et al*., 1997; Jones *et al*., 2011; Siemers *et al*., 2011). As opposed to the case of *M. dasycneme* and *M. daubentonii*, the shared history of *M. myotis* and *M. blythii*, is rather young, as they separated less than two million years ago (Stadelmann *et al*., 2004). Another example of resource partitioning among bats was shown by Hickey *et al.* (1996). In their study they proposed that for *Lasiurus borealis* and *L. cinereus*, which hunt together around streetlights, the partitioning in prey size they observed may be the result of selection to minimize competition between these two sympatric, sibling species.

In the case of *M. dasycneme* and *M. daubentonii* in northern Germany, the morphologically-induced different hunting modes and optimal habitat enables both species the use of the same unlimited food resource in the same area. Additionally, further ecological differences between the focal species are likely to allow sympatric occurrence in the same area. *M. dasycneme* is, unlike *M. daubentonii*, synanthropic and often depends on human buildings for maternity roosts. *Myotis daubentonii* shows more variability, but roosts mainly in tree cavities (Boonmann *et al*., 2000). Whether these differences in turn result from co-evolutionary processes cannot be shown in this study. It is likely that the two species evolved separately, as their phylogeographic past reveals (Stadelmann *et al*., 2004), and became adapted to their environment of origin. Upon meeting in their current distribution area, each species became established in that part of habitat for which they were pre-adapted (Connell, 1980).

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Appendix I

Overview of capture sites with the number of individuals (per sex, per species) from which faecal samples were collected for analysis

Date	Site	*M. dasycneme*		*M. daubentonii*	
		♂♂	♀♀	♂♂	♀♀
25.05.2009	Wahlstorf	10	18	5	5
17.06.2009	Rastorf	5	20	3	12
01.07.2009	Postesee	3	2	9	10
15.07.2009	Wahlstorf	9	13	19	40
27.08.2009	Wahlstorf	1	3	9	10
Sum species/sex		28	56	45	77
Sum species		84		122	
Total sum samples		206			

Appendix II

Percentage frequency of prey groups in the diet of individuals of *M. dasycneme* and *M. daubentonii* conditioned on sampling events in 2009. Numbers in parentheses identify the number of individuals from which faecal samples were collected, bold numbers highlight the main prey groups

Prey	May		June		July		August	
	dasycneme (n = 28)	*daubentonii* (n = 10)	*dasycneme* (n = 25)	*daubentonii* (n = 15)	*dasycneme* (n = 27)	*daubentonii* (n = 78)	*dasycneme* (n = 4)	*daubentonii* (n = 19)
Other Diptera	1.6	0.0	0.0	0.0	1.7	5.0	0.0	0.0
Other Nematocera	18.0	0.0	3.2	0.0	3.4	15.9	0.0	0.0
Chironomidae	**44.3**	**50.0**	**40.3**	**34.2**	**41.4**	**30.8**	**80.0**	**45.9**
Chironomid pupae	**11.5**	**13.0**	**14.5**	**5.3**	**1.7**	**4.5**	0.0	2.7
Tipulidae	1.6	0.0	1.6	11.0	10.3	4.5	0.0	2.7
Brachycera	3.3	6.0	0.0	13.0	3.4	2.5	0.0	0.0
Trichoptera	**18.0**	**31.0**	**29.0**	**26.3**	**17.2**	**19.9**	0.0	**21.6**
Lepidoptera	0.0	0.0	8.1	2.6	10.3	6.0	**20.0**	5.4
Other Hemiptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corixidae	0.0	0.0	0.0	7.9	8.6	2.0	0.0	0.0
Aphidoidea	0.0	0.0	1.6	3.0	1.7	2.0	0.0	0.0
Neuroptera	1.6	0.0	0.0	0.0	0.0	2.0	0.0	2.7
Coleoptera	0.0	0.0	1.6	0.0	0.0	2.0	0.0	5.4
Ephemeroptera	0.0	0.0	0.0	2.6	0.0	0.0	0.0	2.7
Hymenoptera	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0
Araneae	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0
Gerridae	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0