

Ponds in acidic mountains are more important for bats in providing drinking water than insect prey

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Abstract

Ponds, streams and other water bodies are known to attract high numbers of bats of various species and all foraging guilds. The attractiveness of these riparian habitats for bats lies in their providing the required large amounts of drinking water for successful reproduction and a potentially high supply of both aquatic and terrestrial prey insects compared to the surrounding habitats, and in the lower ultrasound interference over water than in forest habitats, important for foraging of open-habitat bat species. The actual abundance of prey depends strongly on the productivity of the aquatic ecosystem, and therefore eutrophic riparian habitats are highly attractive to bats, but little is known about the reasons for the attractiveness of oligotrophic habitats. Here, we compared the bat activity, bat foraging activity and insect abundance around oligotrophic and less-prey-rich ponds in acidic near-natural environments to two structurally similar, simple habitats, that is, clear-cuts and meadows, by simultaneously recording echolocation calls and light trapping of insects. Our generalized linear mixed models showed no differences in prey abundance but higher bat activity at ponds than at meadows and clear-cuts, and all locally indigenous bat species visited the ponds. The foraging activity of bats evaluated as the proportion of feeding buzzes to commuting passes positively correlated with prey abundance at meadows and clear-cuts but not at water bodies. We therefore conclude that ponds in acidic mountain areas are more important to bats as a source of drinking water than as a source of prey. Our results indicate that bat monitoring in such a landscape by bat-call recording and probably by mist netting is highly promising around water bodies, and that bat conservation strategies should maintain a continuous network of water sources as an important habitat feature.

Introduction

In central Europe, forests represent the major natural habitat of bats, yet forest habitats are still underrepresented in scientific studies of bats (Lacki, Hayes & Kurta, 2007). Insectivorous bats show morphological, echolocational and behavioural adaptations to the vegetation structure of their favoured habitat; these adaptations have been used to classify bats into four foraging guilds: open-habitat, edge-habitat, closed-habitat and trawler species (Fenton, 1990; Schnitzler & Kalko, 2001). Within the complexity of forest habitats, the three-dimensional vegetation structure acts as a habitat filter that successively excludes these guilds from forest stands with increasing density (Fenton, 1990; Müller *et al.*, 2012).

The foraging guilds respond differently to variations in prey. Open-habitat foragers hunt exclusively in open areas and aggregate at patches of high prey abundance (Safi & Kerth, 2007; Müller *et al.*, 2012). In contrast, edge- and closed-habitat foragers regularly patrol through their compa-

rably small territory and are able to collect prey not only in open space but also from the ground and leaves (Müller *et al.*, 2012). The few trawler species in Europe, for example, *Myotis daubentonii*, prefer rivers or ponds, but these water bodies are regularly visited by most bat species, which results in a higher diversity and abundance of bats at water bodies than in forest stands; accordingly, bat diversity and abundance are negatively affected if the water supply is short (Kurta, 2001; Russo & Jones, 2003; Menzel, Menzel & Kilgo, 2005; Francl, 2008; Brooks, 2009; Salsamendi, Arostegui & Aihartza, 2012).

Bats prefer water bodies because the habitat complexity over water bodies is low (Mackey & Barclay, 1989) and the ultrasound interference is similar to that of other open habitats, that is, meadows or clear-cuts (Siemers, Stitz & Schnitzler, 2001), which simplifies foraging in forest landscapes. Another reason for the preference is that riparian habitats often provide a higher density of both terrestrial and aquatic prey insects, with Chironomidae (Diptera) being one of the most important groups of aquatic prey. Some aquatic

insects, for example, caddis flies, even provide ephemeral food bonanzas during emergence, which is the main reason for the attractiveness of certain types of riparian habitats for bats (e.g. Fukui *et al.*, 2006; Hagen & Sabo, 2011). The importance of water as a source of prey depends strongly on the productivity and type of the aquatic ecosystem relative to the surrounding habitats. In general, prey biomass is higher at eutrophic than at acidic and thus oligotrophic water bodies (Brodin & Gransberg, 1993; Racey *et al.*, 1998), but the significance of aquatic insects as prey can also be pronounced at less-productive ponds or rivers if the surrounding landscape is especially poor in food. This is often the case along lowland streams that are flanked only by a narrow strip of natural habitat but are otherwise embedded in intensively used agricultural areas (Stahlschmidt, Pätzold & Ressler, 2012).

Bats also seek water bodies as a source of drinking water, which is required in high amounts because of their physiological characteristics. The wings of a bat enlarge its surface area up to sixfold the size of a wingless mammal of the same body mass (Morris, Curtin & Thompson, 1994), which leads to an increased loss of water through evaporation of about 60% of the total water loss (*Plecotus auritus*, body mass 6–9 g; Webb, Speakman & Racey, 1994). In comparison, a shrew loses about 40% of the total water loss through evaporation (*Cryptotis parva*, body mass 5 g; Goldstein & Newland, 2004). The high turnover of water in bats emphasizes the significance of drinking water intake, which amounts to 20–26% of the total water requirement of bats (Kurta, Bell & Nagy, 1989; Kurta, 2001) and only 16% in shrews (Goldstein & Newland, 2004). The need for water depends directly on oxygen consumption and hence on the energy spent on foraging (Webb, Speakman & Racey, 1995).

Among bat species, the dependency on water availability varies. In a water-denial experiment, individuals of the trawler *M. daubentonii*, which is highly associated with open water, lost a higher percentage of their body mass and showed signs of dehydration earlier than individuals of *P. auritus*, which is a typical closed-habitat forager with a lower association to open water (Webb *et al.*, 1994). Some species of bats even partition water resources temporally to reduce competition (Adams & Thibault, 2006).

Although the importance of eutrophic, prey-rich water bodies for bats has been shown in various studies (Russo & Jones, 2003; Menzel *et al.*, 2005; Francl, 2008; Brooks, 2009), the importance of oligotrophic and less-prey-rich water bodies in acidic near-natural environments remains unclear. To investigate the importance of these water bodies as a source of water or of prey for insectivorous bats in acidic mountain forests, we simultaneously measured bat activity by recording echolocation calls, including feeding buzzes, and prey abundance at oligotrophic ponds and in two structurally similar simple habitats, that is, clear-cuts and meadows. We predicted that if bats use water bodies primarily for foraging, prey abundance and bat activity should be higher in the riparian habitats than in the other open habitats. Alternatively, if drinking water is more important than foraging, the proportion of feeding buzzes should be less strongly correlated with prey abundance in riparian habitats than in other open habitats.

Methods

Study site

The study was conducted in the temperate forests of the Bavarian Forest National Park situated in south-eastern Germany (48°54'N, 13°29'E; for details, see Müller *et al.*, 2012). At elevations between 650 and 1430 m a.s.l., the mean annual temperature ranges between 3.8 and 5.8°C, and the total annual precipitation varies between 1200 and 1800 mm. The soils in the region developed essentially from granite and gneiss, resulting in low pH and oligotrophic mountain streams and ponds of low productivity (Bauer *et al.*, 1988; Soldan *et al.*, 2012). The aquatic species composition of most taxa (e.g. Ephemeroptera, Trichoptera) resembles that of lakes of the Tatra Mountains, but the Heteroptera and Chironomidae species compositions are more similar to those of lakes in the Alps and the boreal zone, respectively (Soldan *et al.*, 2012). Forests are dominated by stands of beech *Fagus sylvatica*, spruce *Picea abies* and silver fir *Abies alba* and are characterized by a high level of dynamics in spruce-dominated stands due to natural disturbances such as bark beetle infestation and windthrows. These disturbances as well as over-mature stands provide a high density of bat roosts in the whole area (Ormsbee, Kiser & Perlmeter, 2007; Kanold, Rohrmann & Müller, 2009). In the buffer zone of the national park, salvage logging is allowed and creates clear-cuts. For this study, we selected plots in three open-habitat types – pond, meadow and clear-cut – with six replicates each ($n = 18$). Forest habitats were omitted because the access of less-manoeuvrable species is restricted due to dense vegetation (Müller *et al.*, 2012).

Bat survey and prey sampling

Bat activity was monitored with autonomous bat-call recorders (batcorder 2.0; <http://www.ecoobs.com>), which were placed on a wooden pole at 2.7 m above ground in the centre of each sampling plot. During all surveys, we used the same recording mode ('Auto + Timer') and the same settings (quality: 20; threshold: –27 dB; post-trigger: 600 ms; critical call frequency: 16 kHz). Acoustic surveys ran from 30 min before sunset until 30 min after sunrise during each sampling night. All 18 plots were surveyed seven nights each, from May to September 2009, but only if the probability of rain was low and the temperature was above 0°C. Moonlit nights were avoided (Meyer, Schwarz & Fahr, 2004).

To identify bat species from the recorded echolocation calls, we used the software program bcDiscriminator1.14 (<http://www.ecoobs.com>), which provides for each recording probabilities to which species or species group it may belong. Calls of *Myotis brandtii* and *Myotis mystacinus* as well as calls of *Plecotus austriacus* and *P. auritus* cannot be distinguished from each other by the software because the call properties are highly similar (Parsons & Jones, 2000). Bats, including all species in our study area, recognize a water body by its mirror-like echo reflection (Greif & Siemers, 2010), descend to the surface and dip their chin into the water to drink (Siemers *et al.*, 2001). There are no hints that insectivorous bats in

Europe produce drinking buzzes (V. Runkel, pers. comm.). Therefore, any buzzes, that is, a rapid series of calls, are a clear indication of foraging activity (Grindal, Morissette & Brigham, 1999). We thus categorized all records visually as a commuting pass of a travelling bat or as a feeding buzz.

Abundance of arthropod prey was sampled simultaneously with the bat survey using one light trap per plot. Insects were counted separately by taxonomic groups, but the sum of all trapped individuals per plot and nights serves as an estimate of prey abundance (for details, see Müller *et al.*, 2012). Differences in insect assemblages were not within scope of this study; instead, we focused on the prey effectively available to bats during each survey night.

Data analysis

All statistical analyses were carried out in R 2.13.1 (<http://www.r-project.com>). To examine differences in the abundance of bats and prey between the three habitat types, we fitted two generalized linear Poisson mixed models (GLMM) using the add-on package lme4 with either bat activity (commuting passes plus feeding buzzes) or prey abundance as the response variable and with an observation-specific random intercept to account for overdispersion (Elston *et al.*, 2001). The proportion of feeding buzzes was modelled in a GLMM with a binomial distribution, which estimated the habitat-specific influence of prey abundance (log-transformed). In all three models, plot served as a random factor to account for replicated measurements.

Results

During 126 nights, we recorded 30 480 bat-call sequences, including 1315 feeding buzzes of 13 species and the 2 species groups (*M. brandtii*/*M. mystacinus* and *P. austriacus*/*P. auritus*; Table 1). At clear-cuts, we detected 12 species and 1 species group; at meadows, we detected 12 species and 2

species groups; and at ponds, we detected 13 species and 1 species group. Species that were most abundant at ponds were the trawler species *M. daubentonii*, the edge-habitat foragers *Barbastella barbastellus*, *Pipistrellus pygmaeus* and *M. brandtii*/*M. mystacinus*, and the closed-habitat forager *Myotis bechsteinii*.

The abundance of prey did not differ significantly between the three types of habitat (Fig. 1), but the assemblage of insect orders varied slightly, with Diptera being the most numerous group (Table 2). Total bat activity was higher at water bodies than at clear-cuts (GLMM: $P < 0.001$) and meadows (GLMM: $P = 0.01$; Fig. 2). Our model revealed that at meadows and clear-cuts, the ratio of feeding buzzes to commuting passes clearly increased with increasing prey density

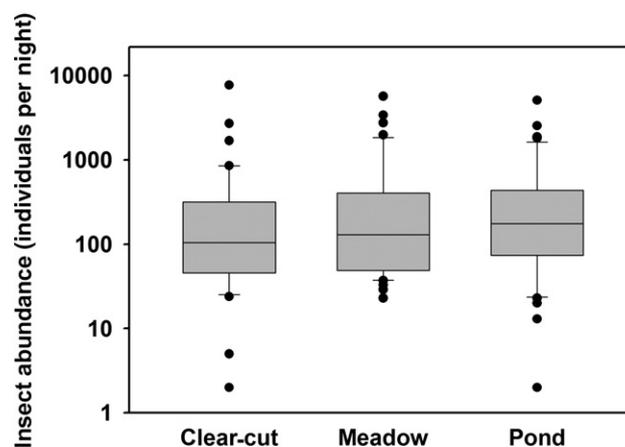


Figure 1 Total number of insect individuals sampled with light traps during 126 nights in three different types of open habitat. The general linear mixed model with plot and observation as random effects showed no significant differences between habitat types. Note that the y-axis is log₁₀-transformed.

Table 1 Total number of recordings of all bat species in each open-habitat type during 126 survey nights

Guild	Species	Number of recordings		
		Clear-cut	Meadow	Pond
Open-habitat	<i>Eptesicus nilssonii</i>	2482	1726	706
	<i>Eptesicus serotinus</i>	0	7	4
	<i>Nyctalus leisleri</i>	3	8	3
	<i>Nyctalus noctula</i>	70	22	26
	<i>Pipistrellus nathusii</i>	44	10	21
Closed-habitat	<i>Vespertilio murinus</i>	62	39	31
	<i>Myotis bechsteinii</i>	2	3	26
	<i>Myotis nattereri</i>	4	1	2
	<i>Plecotus austriacus</i> / <i>P. auritus</i>	0	1	0
Edge-habitat	<i>Barbastella barbastellus</i>	27	20	46
	<i>Myotis myotis</i>	2	6	7
	<i>Myotis brandtii</i> / <i>M. mystacinus</i>	71	634	2415
	<i>Pipistrellus pipistrellus</i>	1232	2976	1678
Trawler	<i>Pipistrellus pygmaeus</i>	2	0	17
	<i>Myotis daubentonii</i>	11	93	346

Table 2 Mean and range of summed up individuals of five insect orders trapped per plot during seven surveys in the three types of open habitats

Habitat	Insect order				
	Lepidoptera	Trichoptera	Diptera	Hymenoptera	Coleoptera
Clear-cut	565 (232–1090)	344 (72–631)	2210 (160–7 569)	77 (34–170)	42 (10–129)
Meadow	614 (199–1147)	187 (23–467)	2799 (265–10 051)	70 (40–115)	49 (10–166)
Pond	549 (213–1316)	350 (178–573)	2480 (112–7 432)	65 (15–115)	26 (6–40)

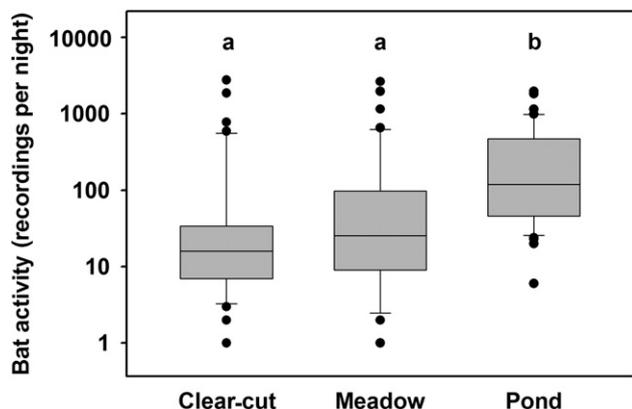


Figure 2 Total bat activity during 126 survey nights in three different types of open habitat. Different letters indicate significant differences as computed in a general linear mixed model with plot and observation as random effects. Note that the y -axis is \log_{10} -transformed.

Table 3 Results of a generalized linear mixed model with a binomial distribution estimating the habitat-specific influence of prey abundance (log-transformed) on the proportion of feeding buzzes. Plot was a random factor to account for replicated measurements

Predictors	Estimate	z-Value	P
Clear-cut: prey	0.69	8.91	<0.001
Meadow: prey	0.52	6.09	<0.001
Pond: prey	-0.09	-1.29	0.20

(Table 3). However, at water bodies, increasing prey density showed no significant correlation with the proportion of feeding buzzes, and the estimator was negative (Fig. 3). We also analysed *M. daubentonii* (the only trawler species) separately from the other species; however, the results remained the same. For *M. daubentonii*, the proportion of feeding buzzes did not significantly correlate with prey abundance in any of the three habitats.

Discussion

Our standardized sampling of bat activity, foraging intensity via feeding buzzes and prey abundance at oligotrophic ponds, meadows and clear-cuts in a forested acidic mountain area showed a higher bat activity at ponds than at meadows and clear-cuts but no differences in insect abundance. All the locally indigenous bat species visited ponds regularly, includ-

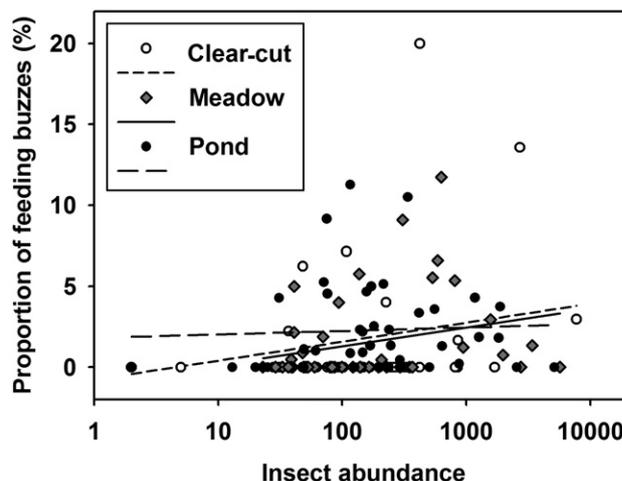


Figure 3 Scatterplot of the proportion of feeding buzzes compared to commuting passes in three open types of habitat in relation to prey density which is only significant at meadows and clear-cuts. The lines are simple regressions for illustrative purposes only. Note that the x -axis is \log_{10} -transformed.

ing *B. barbastellus*, *M. bechsteinii* and *M. myotis*, which are listed under Annex II of the EU Habitats Directive. The mean relative number of feeding buzzes that we detected in all three habitats (ponds 3%, meadows 6%, clear-cuts 6%) were lower than in other studies conducted in non-acidic riparian habitats (10–30% reported by Kalcounis-Rueppell *et al.*, 2007), which indicate a lower capture effectiveness across all habitats as the bats hunted in our mountain habitat. The ratio of foraging activity to prey density suggested that ponds in an acidic mountain landscape are predominantly a source of drinking water rather than of prey. This is in contrast to studies that have found higher foraging activity of bats over water than in adjacent habitats (Grindal *et al.*, 1999; Fukui *et al.*, 2006; Hagen & Sabo, 2011). This difference can be explained by the differences in the habitats studied. The earlier studies were conducted in eutrophic riparian habitats with high insect densities, whereas the ponds we surveyed are acidic and oligotrophic and thus do not provide a higher food supply relative to the surrounding open areas. Also, most riparian forest habitats in lowlands, as in the earlier studies, are narrow linear patches of natural habitats surrounded by highly productive farm land with monocultures and applied pesticides, which reduces the abundance and diversity of nocturnal insects and leads to a relatively high concentration of insect prey in

adjacent riparian habitats (Wickramasinghe *et al.*, 2004; Stahlshmidt *et al.*, 2012). In contrast, the ponds in our study are all embedded in the near-natural forest landscape of a national park, with a high patchiness of forest cover and therefore a generally higher density of prey and bat roosts equally distributed throughout the area (Kanold *et al.*, 2009; Lehnert *et al.*, 2013). In our study area, no correlation of activity of edge- and closed-habitat foragers with prey abundance has been found in the different types of forests present (Müller *et al.*, 2012). Investigations of variables explaining high abundances of nocturnal insect activity in riparian forests have similarly found an increase of insects of all orders with increasing deciduous canopy cover (Ober & Hayes, 2008).

The studies published to date hardly separate between the importance of water bodies for drinking and their importance for foraging. For example, Fukui *et al.* (2006) experimentally reduced the flux of emerging aquatic insects from rivers by fully covering a 1.2 km stretch, but it also limited the access to drinking water. Although earlier studies did not focus on drinking water, some of the results obtained are in line with our results. Menzel *et al.* (2005) found most bat activity below a height of 10 m in riparian habitats but only low bat activity at the same heights in clear-cuts. It is likely that the high activity at low strata in riparian habitats is due to bats attempting to drink. Kalcounis-Rueppell *et al.* (2007) compared insect abundance upstream and downstream of wastewater treatment plants together with bat activity and bat-foraging activity and found, in contrast to their expectations, no response of overall bat activity to differences in insect abundance. Similar results were obtained by Racey *et al.* (1998). Razgour, Korine & Saltz (2010) partially covered ponds in an arid environment and found a stronger decline of species that used the water bodies for foraging than of species that depended on the water bodies as a source of drinking water. All these results could be explained by bats visiting water bodies more often for drinking than for foraging and they corroborate the general importance of natural and artificial water bodies for drinking in dry areas (Adams, 2010; Jackrel & Matlack, 2010).

In general, the physiology and life strategy of bats evoke a higher demand for energy and drinking water than that of flightless mammals of the same size. The energy demands can be re-fuelled by rapid consumption of exogenous nutrients, whereas some part of the required water has to be gained directly from water bodies (Voigt, Sörgel & Dechmann, 2010). This is especially pronounced for lactating females, who must visit water sources six times more often each night than non-reproductive females (Cryan, 2003; Adams & Hayes, 2008). Therefore, maternity roosts are often located near water bodies (Speakman *et al.*, 1991). The high water needs of lactating females even causes reproductive success to decline when water availability decreases (Adams, 2010). Thus, the availability of drinking water is not only crucial to individuals but can also affect the survival of local populations. Our results confirmed the high importance of water – not only all bat species were detected at ponds, but also higher bat activity.

Although we found that the trawler bat *M. daubentonii* preferred riparian habitats, there was no significant correla-

tion between the proportion of its feeding buzzes and the prey density in any of the three habitat types. One explanation could be that the number of calls was too low to detect a statistically significant response. Another reason may be the selectivity of the species for adult aquatic insects (e.g. Chironomids), which were not considered separately in our study. In a comparison of a channelized and a restored part of a lowland river in Japan, the foraging activity of *M. daubentonii* was well correlated with the abundance of aquatic insects but not with the abundance of terrestrial insects (Akasaka, Nakano & Nakamura, 2009). On the other hand, *M. daubentonii* feeds on Diptera, Trichoptera, Hemiptera, Lepidoptera and Coleoptera, almost all of which can be captured by light traps (Boonman *et al.*, 1998). Considering that populations of *M. daubentonii* are greatly increasing due to the eutrophication of waters in Europe (Racey *et al.*, 1998), our acidic ponds are probably not the optimal habitat for this species. This may also explain why in our study area this ‘water bat’ is regularly found foraging far from ponds in mature single-layered forest stands (Müller *et al.*, 2012).

Finally, we would like to draw some implications for conservation and the monitoring of bats in acidic central European mountain forests, many of which under the protection of NATURA 2000. Within this framework, regularly monitoring is conducted, especially of the species listed under Annex II of the Habitats Directive, such as *M. bechsteinii*, *B. barbastellus* and *M. myotis*. In such near-natural forests, monitoring by offering artificial nest boxes is highly ineffective due to the high supply of natural roosts (Bavarian Forest National Park: 0–1 bat individuals per 50 nest boxes during annual monitoring). Instead, batcorders, particularly when located at ponds, represent a promising alternative method. Ponds attract bat species of all foraging guilds, and thereby allow monitoring of the regional species pool. Additionally, drinking from the water surface forces all species to fly down to the ground level on distinctive flight paths that resemble an airport landing strip, which offers opportunities for mist netting of all species, including the generally high-flying open-habitat foragers (Adams & Simmons, 2002). The direct catching of individuals at ponds is especially promising for obtaining proof not only of the occurrence of a species, but also provides information about local reproduction as lactating females visit water sources more frequently (Cryan, 2003).

European bats travel 6–10 km between roosts and foraging habitats each night (Dietz, von Helversen & Nill, 2007). Considering the high importance of drinking water, a continuous network of water sources should be provided within this distance also in acidic mountains as a contribution to the conservation of bats. Even man-made water bodies could contribute to the water network, although this might be undesirable in a protected area. Beavers naturally and readily create new lakes and ponds in the areas where they occur or spread to (Ciechanowski *et al.*, 2011). Furthermore, as forests represent a reliable source of prey, bat conservationists should focus more strongly on forest habitats. In any case, the importance of ponds for drinking must not be underestimated, and at least in acidic mountain areas, ponds are even more important for drinking than for foraging.

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