

Strategy-switching in the gaffing bat

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Abstract

Foraging in Daubenton's bats *Myotis daubentonii*, at two altitudinal locations along a river gradient in North Wales was investigated in relation to aerial insect density and to the density of prey on the water surface. Prey capture in Daubenton's bats consisted of aerial hawking, where prey was taken in the air, and trawling, where bats gaffed invertebrates from the water surface. Aerial hawking accounted for 86% of all prey capture attempts, despite aerial insect availability falling close to zero for much of the night. Conversely, prey density on the water surface was an order of magnitude higher than aerial prey density and increased through the night due to aquatic invertebrate drift. At the higher altitude site, *M. daubentonii* switched prey capture strategy to gaffing, possibly to reflect this change in prey availability on the water's surface, but at the lower altitude site, they maintained aerial hawking as the preferred strategy. The switch to gaffing may be inhibited by the significant downstream accumulation of large numbers of inedible exuviae of caddis flies, Trichoptera, at the low-altitude site, which form both acoustic clutter and increase the probability of capturing inedible prey, making foraging less efficient. These small altitudinal differences in foraging strategy should be factored into the design of future altitudinal bat foraging studies and if found to be a widespread strategy, taken into consideration by conservation planners when reviewing the habitat requirements of Daubenton's bats in river valleys within the United Kingdom.

Introduction

Bats occupy a nocturnal aerial niche and the majority of echolocating microchiropteran bats use aerial hawking to catch volant invertebrate prey. Most temperate aerial insectivorous bats show a broadly bimodal activity pattern that generally coincides with peak aerial insect availability at dawn and dusk (Lewis & Taylor, 1964; Racey & Swift, 1985; Rydell, 1993; Swift, 1997). When prey is at low densities in the middle of the night, many species make use of night roosts or go into torpor (Grinevitch, Holroyd & Barclay, 1995). The relationship between aerial prey availability and time appears to be linked to temperature, with fewer potential prey items flying when it is colder. Some bats, however, such as *Myotis evotis*, are able to feed for longer periods by adapting their foraging mode by switching between aerial hawking and gleaning for non-volant prey (Chruszcz & Barclay, 2003). Trawling, or gaffing (see Siemers, Stolz & Schnitzler, 2001b for definitions) has evolved independently in at least three bat families: the Vespertilionidae (e.g. Jones & Rayner, 1988), the Noctilionidae (e.g. Kalko *et al.*, 1998) and the Phyllostomidae (e.g. Weinbeer, Meyer & Kalko, 2006), but it is most prevalent among the genus *Myotis*. For example, in Europe, gaffing of

prey from the water surface is a technique used by *Myotis daubentonii*, *Myotis dasycneme* and *Myotis cappacini* (Siemers *et al.*, 2001b). In Northern America, *Myotis lucifugus* catches insects from the water surface (Barclay, 1991), while *Myotis vivesi* catch fish (Reeder & Norris, 1954). In south-east Asia and Australasia, *Myotis adversus* catches insects by gaffing (Jones & Rayner, 1991) and *Myotis macrotarsus* and *Myotis stalkerii* have large feet, typical of bats that gaff prey (Findley, 1972).

A major factor that may have contributed to the convergent evolution of gaffing in bats is that aquatic habitats such as ponds and lakes are highly productive in terms of biomass and therefore energetically profitable foraging habitats for gaffing bats. Rivers and streams – the prime foraging grounds for *M. daubentonii* – differ from other aquatic environments in having a strong uni-directional flow of water that transports materials from upstream to downstream areas (Johansen, Elliott & Klemetsen, 2000). Although aquatic organisms are adapted to cope with these forces, inevitably many either actively or passively enter the water column or are swept downstream. This event (termed invertebrate drift) has been of interest to stream ecologists since Müller (1954) first reported the phenomenon (see the drift review by Allan, 1995). Invertebrate drift is primarily

aquatic in origin, although terrestrial invertebrates (species that live mainly on the ground and on terrestrial vegetation) and aerial invertebrates (those that spend extensive periods airborne) enter streams accidentally (Bridcut, 2000), and may often dominate the surface drift (Needham, 1930 cited in Elliott, 1967a). It is the surface drift that is of importance to this study as invertebrates play an important role by forming the major link between primary producers and higher trophic levels such as fish (Radar, 1997), birds and trawling bats. The subsequent discovery of drift's increased nocturnal periodicity (Tanaka, 1960; Waters, 1962; Müller, 1963) is of further interest to bat research but has hitherto never been studied in detail in conjunction with temperate bat foraging techniques.

Myotis daubentonii feeds almost exclusively within 1 m of the water surface and uses a mixed foraging strategy where 39% of prey captures are gaffs (Jones & Rayner, 1988), the rest being aerial hawks of insects just above the water. We used this species to test our prediction that bats should switch from aerial to water-borne prey when aerial prey reaches a density too low to make aerial foraging profitable. We also investigated the composition and extent of the aquatic drift throughout the night and the proportion of aquatic/emergent taxa in the drift as potentially important prey for *M. daubentonii*.

Methods

Study sites

The present study was carried out at two locations along the Lledr river, Conwy, North Wales, UK, in July 2001, where *M. daubentonii* was known to forage and had been caught previously in mist nets (V. L. G. Todd & D. A. Waters, unpubl. obs.). The Lledr is an oligotrophic river that is part of the Conwy valley catchment system. Much of the surrounding landscape consists of semi-improved permanent pasture. Site 1 (53°04'20"N, 3°47'25"W) was 200 m long and 12 m wide at an altitude of 40 m above sea level. The higher altitude, Site 2 (53°04'07"N, 3°49'50"W), was 163 m long and 18 m wide at 104 m above sea level. Both sites consisted of straight stretches of river without riffles or obstructions with a channel depth between 0.1 and 0.75 m with trees and shrubs on the banks.

Invertebrate availability – water surface

This study was concerned mainly with surface drift (the neuston) and emergent insects. Sampling was thus aimed primarily at surface fauna, as it is assumed, from observations in the field (Nyholm, 1965; Jones & Rayner, 1988; Kalko & Schnitzler, 1989) and dietary studies (see the review by Vaughan, 1997) and (Flavin *et al.*, 2001), that bats take primarily surface prey, with added possibly of trawling for fauna just beneath the surface. However, the drift were still considered to be primarily 'surface taxa' (see Elliott, 1967a) for the following reasons: (1) inevitably, some terrestrial taxa are either periodically submerged or drowned on or just

beneath the surface; (2) many insects, such as teneral chironomid pupae, are present directly beneath the meniscus when emerging (mainly at night) and are only very briefly present on the water surface before flying away (Mundie, 1959; I. Wallace, pers. comm.); (3) some fish larvae feed just beneath the surface (Bardonnnet, Gaudin & Persat, 1991), periodically breaking the meniscus (D. Palomares, pers. comm.).

As terrestrial insects often dominate surface drift, compared with mid-water drift, a surface or 'neuston net' was used. Three floating neuston nets (see Elliott, 1967a for a full description) were deployed across the river surface to capture invertebrates on or close to the water surface. Each net had an opening of 48 × 20 cm and a nylon mesh of 430 µm and was configured to sample water to a depth of 7 cm. Material was collected at the cod-end of the net in a plastic container with a capacity of 180 mL and preserved on site in 70% alcohol.

The nets were placed equidistantly across the river and the water flow rate at the mouth of the net was recorded using a Digital Stream current meter (Columbia, Great Atlantic Flow Meters, Cornwall, UK) at the beginning and end of the sampling sessions (After Matthaei, Werthmuller & Frutiger, 1998). Elliott (1967b) grouped the flow of an upland stream into four categories, for the purpose of his drift studies: (1) major spate (over 1 ms⁻¹), (2) minor spate (0.5–1 ms⁻¹), (3) normal (0.4–0.5 ms⁻¹), (4) drought (0.1–0.4 ms⁻¹). As severe floods have been shown to reduce drift density (e.g. Sagar & Glova, 1992; Matthaei *et al.*, 1998), no samples were taken the few nights following spates. All observations were carried out in the month of July when the water velocity corresponded to four on Elliott's (1967b) scale (low discharge). Sampling began at 1 h before sunset until 1 h after dawn, with samples being removed from the net hourly on contiguous nights with the exceptions of four nights of heavy rain.

Six nights of data were collected at the low-altitude Site 1 and four nights of data were collected at the higher altitude Site 2, the position of the nets within each site being changed on each night. Invertebrate numbers were converted to density using the flow rate measurements and the depth of water sampled by the neuston nets to allow comparison with the aerial insect availability.

All fauna captured in the net were identified and sorted into two major categories: terrestrial and aquatic. Terrestrial fauna were considered to be either the adult or 'pharate' stage of flying insects including the newly emerged insects with fully pumped-up wings ready to fly. This category also included the immature stages of terrestrial insects such as larvae (e.g. caterpillars or beetle larvae) and all fauna falling from vegetation or banks such as spiders, or slugs. Included here were the surface dwellers such as water crickets, Hemiptera, Heteroptera and Veliidae (as in the study of Elliott, 1967a), which are meniscus dwellers and wingless, but not strictly aquatic. The riffle beetles (Elmidae) would normally be classified as strictly aquatic; however, they float to the surface if disturbed because they are buoyant (Cooter, 1991). Therefore, for convenience, it was assumed that these

individuals were present at the surface as they had probably floated down from the faster-flowing sections of the river and they were therefore classified as terrestrial.

The aquatic component was divided into two sub-categories: (1) those at the surface and (2) non-surface dwellers. (1) were often the larvae of terrestrial species such as emergent pupae of chironomids and empids. A pupa was deemed to be emerging when a distinct split of the thorax was observed, indicating that it was at the surface at the time of sampling. A pilot study showed that newly emerged or 'teneral' Ephemeroptera imago and Empididae were easy to identify and were frequently taken in the drift samples and they were included in this category. The non-surface dwellers (2) were considered more rarely to have broken the surface of the water during the sampling period. These fauna included, for example, fish fry (Cypriniformes) aquatic snails (Prosobranchia) and leeches (Hirudinea).

Invertebrate availability – aerial insects

Aerial insects were captured in a 35.5 cm diameter sweep net. Forty 180° sweeps were made about 1 m above the water surface as close to the centre of the channel as possible. No torches were used during insect capture to avoid attracting or repelling insects. As the net pole and arm described a radius of 1.8 m, each sweep of the net sampled 0.62 m³ of air, 24.8 m³ of air per sample. Air temperature was recorded from a mercury thermometer at the sample location. Sampling was started at an hour before sunset until an hour after sunrise, samples being taken at 30-min intervals for the first 2½ h after sunset and before sunrise, and at hourly intervals throughout the night. Sampling location was altered each night, with six nights sampled at Site 1 and four nights sampled at Site 2.

Bat foraging behaviour

To film prey captures, a Sony DCR-TRV320 Digital 8 camcorder was used with two Sony HVL IRC infra-red lamps with the camcorder operated in 'Nightshot' mode (Sony, Tokyo, Japan). The stereo audio input of the camcorder was configured to accept signals in one channel from a Tranquility II 10 × expanding bat-detector, and the other from a Magenta heterodyne bat detector tuned to 45 kHz. The heterodyne bat detector operated in real time to record the temporal pattern of the bat echolocation calls, and identify approach phase calls and feeding buzzes to indicate prey capture, while the time-expanding bat detector digitally captured the call structure to allow identification of bat species (specifically to separate *M. daubentonii* from *Pipistrellus* species). Bats were tracked with the camera to record all prey captures within the range of the infra-red lights as they foraged over the water surface. Videos were analysed by playing them through a video monitor (Sony Trinitron, Tokyo, Japan), and a feeding attempt was defined as any deviation from normal flight associated with a feeding buzz. Species identification was confirmed by analysing the associated time-expanded audio sequence using Batsound

(Petersson Electronic, Uppsala, Sweden) on a PC and observing the call spectrogram (512 point FFT, Hamming Window). Calls of *M. daubentonii* were separated from those of *Pipistrellus* species by the lower terminal frequency and the lack of a constant frequency tail at the start of approach phase. Bats were filmed over 14 nights, which overlapped with the periods of aquatic and aerial insect sampling.

Data analysis

Data were tested for normality and transformed where appropriate. Two-way ANOVAs were used to test for patterns of aquatic drift with time at each site and to examine temperature variability, and *t*-tests were used to examine aerial insect and foraging strategy differences between the two sites.

Results

Invertebrate availability – water surface

Figure 1 shows the classification of the species documented in the aquatic drift. The four most common orders present on the water surface were nematoceran dipterans ($n = 7333$), trichopterans ($n = 3035$), brachyceran empids ($n = 2283$) and ephemeropterans ($n = 1032$). The remaining 34.6% consisted of a mix of terrestrial species such as hemipterans, hymenopterans and arachnids (total 18.6%) and fully aquatic species, such as aquatic beetles and fish fry (16%), which were generally considered not to be as accessible to bats as the surface and emerging taxa. Invertebrates that are available to foraging *M. daubentonii* bats are termed 'surface drift', and those deeper in the water column as 'aquatic drift'. These totals exclude the floating exuviae of trichopterans, which made up 62% of all items in the nets.

Invertebrate activity showed a clear inverse pattern to the aerial insects, with very little drift occurring before sunset or after sunrise, but with a large level of activity at night peaking between 23:00 and 24:00 h (Fig. 2). Drift differed with time (ANOVA, $F_{8,198} = 9.17$, $P < 0.001$), but not with site ($F_{1,198} = 0.93$, NS). There was also no significant interaction between time and site ($F_{8,198} = 1.96$, NS), indicating that the pattern of drift was the same for the two sites. The mean prey density available for bats was 0.14 ± 0.15 items m⁻² of the water surface at Site 1 and 0.15 ± 0.14 items m⁻² at Site 2.

The floating exuviae of trichopterans showed the same temporal pattern as the rest of the drift invertebrates. The number of exuviae varied with time (ANOVA $F_{8,198} = 27.02$, $P < 0.001$) and site ($F_{1,198} = 10.58$, $P < 0.001$), with Site 1 having about twice the amount of trichopteran exuviae as Site 2 with 4.9 ± 7.54 exuviae m³ at Site 1 compared with 2.5 ± 3.18 m³ at Site 2. There was no significant interaction between time and site ($F_{8,198} = 0.41$, NS), illustrating that the pattern of surface drift was the same at both sites.

The ratio of inedible trichopteran exuviae to surface drift was arc-sine square root transformed prior to analysis. The ratio differed both with time ($F_{8,198} = 16.06$, $P < 0.001$) and

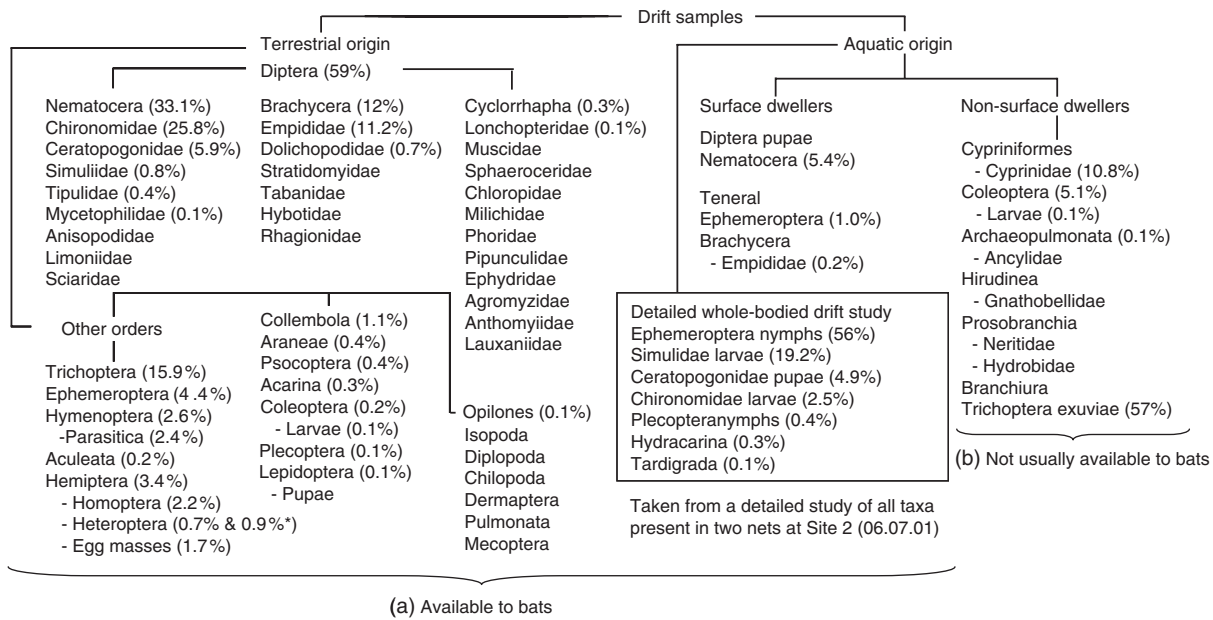


Figure 1 Composition of the drift. Percentages in brackets represent the proportion of that category in the whole drift (excluding Trichoptera exuviae). Categories without percentages were <0.05% present (one or two individuals). The asterisked heteropteran value represents the surface-dwelling bugs such as the water crickets (Veliidae).

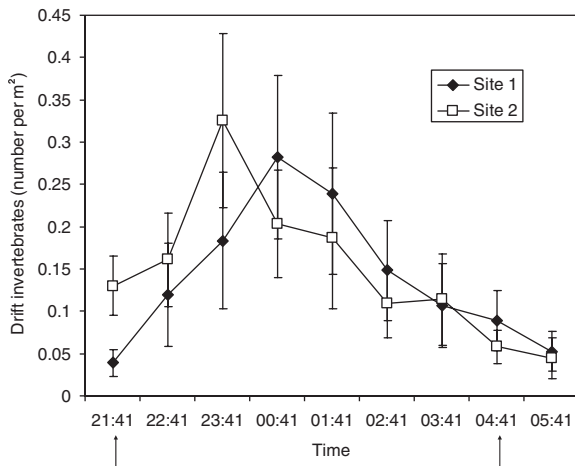


Figure 2 Change in the density of drift invertebrates with time at the two sites expressed as the number invertebrates per m² of the water surface (mean ± 1 SEM). Open squares are for Site 1 (low altitude) and solid diamonds are for Site 2 (high altitude). Sunset and sunrise are indicated by arrows.

Site ($F_{1198} = 18.78$, $P < 0.001$). There was no interaction term ($F_{8198} = 18.78$, $P < 0.001$). At Site 1, trichopteran casts made up 70% of all items in the surface drift, while at Site 2, it comprised only 47% of items.

Invertebrate availability – aerial insects

Aerial insects showed both a low abundance and a low diversity. The most common were the nematoceran dipter-

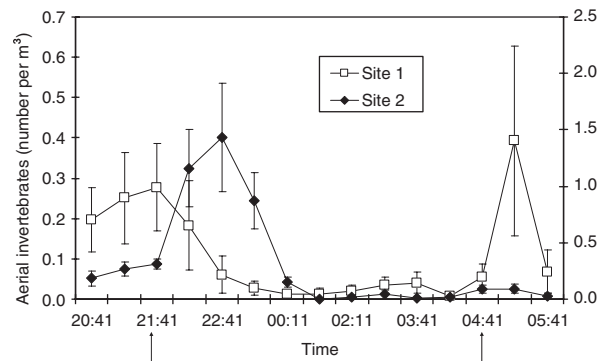


Figure 3 Change in the density of aerial insects available at the two sites with time (mean ± 1 SEM) expressed as the number of insects available per m³ of air. Aerial insects were less abundant at Site 1, and so are expressed on different Y-axes to show similarities of pattern. Site 2 is on the left-hand side and Site 1 on the right-hand side. Open squares are for Site 2, and solid diamonds are for Site 1. Sunset and sunrise are indicated by arrows.

ans (48%, $n = 336$), brachyceran dipterans (39%, $n = 274$) and trichopterans (12%, $n = 86$), with the remaining 1% being composed of the Ephemeroptera, Homoptera, Lepidoptera and Psocoptera. A significantly higher density of aerial invertebrates was caught at Site 2 (0.3 ± 0.53 insects m³) than Site 1 (0.1 ± 0.22 insects m³), $P < 0.005$ ($n = 80$, t -test).

Aerial insects showed a different pattern between the two sites (Fig. 3). At Site 1, aerial insects mainly consisted of Empididae, which showed a general decline in abundance after dusk, with very low numbers through the night,

followed by an increase at dawn. At Site 2, the aerial insects were mainly chironomids, which showed an increase in abundance at dusk, followed by a decline to zero throughout most of the night, with small numbers of individuals reappearing at dawn. At Site 2, the peak aerial insect availability was at 22:41 h, 1 h after sunset, when 1.4 individuals m^{-3} were available to bats (Fig. 3).

There was a significant difference in mean air temperature between sites over the study period, with Site 1 averaging $12.7 \pm 1.49^\circ C$ and Site 2 being warmer at $14.4 \pm 2.12^\circ C$ (ANOVA, $F_{8,49}$, $P < 0.0001$).

Bat foraging behaviour

For the bat activity, we recorded 1157 feeding attempts. Of these, 85.7% were aerial hawks occurring within 1 m of the water surface, the remaining 14.3% being gaffs from the water surface. A significantly higher number of total catch attempts was recorded at Site 1 ($n = 1022$) than Site 2 ($n = 135$), $P < 0.01$ (t -test).

Foraging activity was recorded through the night, with bats arriving at sites within 30 min of sunset and leaving 30 min before dawn. There were often many bats present at each site simultaneously.

Feeding activity peaked 1 h after sunset, with a gradual decline until dawn. At the upstream higher altitude Site 2, the proportion of gaffs is initially low (Fig. 4), when aerial insect availability is high, but as aerial insects become scarce, bats switch to gaffing and at 23:41 h, 2 h after sunset. 71.5% of all prey captures are gaffs. As dawn approaches, the bats once again return to aerial hawking. At the downstream Site 1, this pattern does not occur, with bats making gaffs 8.2% of the time through the night, and not following the availability of insects in the aquatic drift. There was no significant difference in the bat's foraging behaviour (gaffing or hawking) with the neuston nets present or absent during filming (one-way ANOVA, d.f. = 7, $F = 1.085$, NS).

Discussion

The diversity of aerial insects caught in this study is comparable to other riparian insect studies for example (Nelson, 1965; Jónsson, 1987; Warren *et al.*, 2000) and the drift fauna are typical of a British mid-altitude stream (Elliott, 1967a; Elliott, 1968; Bridcut, 2000). Most invertebrate categories, in particular the chironomids, have been recorded in the diet of *M. daubentonii* (Vaughan, 1997; Flavin *et al.*, 2001), and are therefore considered to be potential prey items.

This study shows that *M. daubentonii* clearly spends the majority of its time foraging on aerial insects above the water surface. However, as aerial insect availability falls to zero at the higher altitude Site 2, these bats switch to gaffing prey from the water surface. Prey availability varies throughout the night from times when aerial insects are abundant with very little drift availability, to times when aerial insects are at low levels, when drift invertebrates dominate. If prey detection and capture were equally effi-

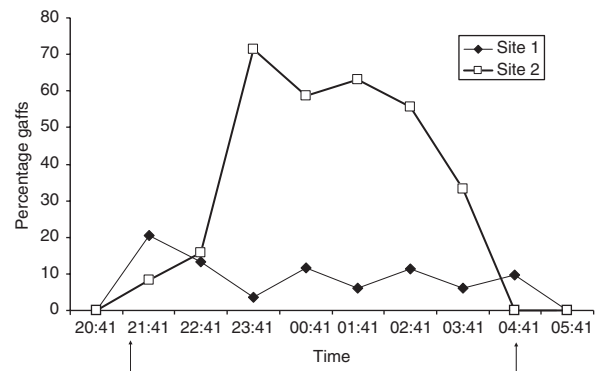


Figure 4 Change in the percentage of prey capture attempts that were gaffs made by *Myotis daubentonii* at the two sites with time. Open squares are for Site 2, and solid diamonds are for Site 1. Sunset and sunrise are indicated by arrows.

cient in both capture modes, then we would expect *M. daubentonii* to switch strategy with changing prey availability. While this is clearly the case at the higher altitude Site 2, where it is paradoxically warmer, and has a higher dusk peak availability of aerial insects, this does not occur at the lower altitude site, where bats continue to hawk aerially despite the availability of water-borne prey and the very low abundance of aerial insects.

Myotis daubentonii may make a decision to adopt a particular capture mode based on relative prey availability, prey detectability and capture success, all of which contribute to net profitability. The bimodal activity pattern most often shown by aerial hawking bats probably represents the underlying activity patterns of aerial insects (Racey & Swift, 1985; Hayes, 1997; Waters, Jones & Furlong, 1999). Gleaners and trawling bats tend not to show this bimodal pattern (Rydell, Entwistle & Racey, 1996; Swift, 1997; Chruszcz & Barclay, 2003), presumably because they are not wholly dependent on volant prey, which are most active at dusk and dawn (Lewis & Taylor, 1964). Here, we clearly demonstrate how well *M. daubentonii* can adapt to dynamics in prey availability, in this case caused by aquatic drift. As far as we are aware, this is the first study to attempt to link both aerial and water-borne prey availability to a temperate bat foraging strategy. One other lacustrine study on a tropical trawling phyllostomid bat species also collected insects from a water surface and aerial prey in conjunction with the filming of bat foraging strategy (Weinbeer *et al.*, 2006). However, in that study, no temporal switch in foraging strategy in relation to aerial/water-borne prey was observed, presumably because the availability of both aerial and surface prey remained high throughout the night (as is typical of tropical areas) unlike the peaks and troughs associated with temperate regions.

While comparisons between prey densities in three-dimensional aerial spaces with those on a two-dimensional water surface are difficult, Kalko & Schnitzler (1989) found that the mean foraging height of *M. daubentonii* was 15.8 ± 6.7 cm above the water surface. They identified two

modes of prey capture: low catches where the bat dives down towards prey, and high catches, where *M. daubentonii* soars upwards and catches prey between 80 and 200 cm above the water surface. Most of the aerial hawks that we observed occurred within one metre of the water surface, suggesting that this is where most prey detection occurs. Thus, we have calculated that at their peak, there will be on average one potential prey item for every 3 m² of the water surface. By comparison, at the peak of aerial insect abundance there is one potential prey item per 0.72 m³ of air-space. However, this quickly falls to zero after dusk at the higher altitude site, and *M. daubentonii* switches to gaffing mode. Prey selectivity patterns, such as the decision for *M. daubentonii* to preferentially hawk an aerial insect over a prey item on the water's surface may be explained, in part, by the specific conspicuousness of the prey to the bat's sensory system as has been demonstrated in greater mouse-eared bats, *M. myotis*, which do not select prey in proportion to their abundance (Siemers & Güttinger, 2006). As water surface-borne insects increase in availability, so do the inedible exuviae of trichopterans, which increase in abundance downstream in a cumulative manner. At the upstream Site 2, they form 47% of all potential prey items, while at the downstream Site 1, 70% of all items on the water surface are inedible. A further factor that may affect the ability of bats to efficiently capture prey from the water surface is acoustic clutter. Boonman *et al.* (1998) found that the presence of duckweed on a pond surface reduced the ability of *M. daubentonii* to capture prey. This is due to the duckweed producing additional echoes that inhibit the bat from identifying prey on the water surface. Thus, although insects on a water surface show a 6.7 dB gain in echo strength over the same target in air (Siemers *et al.*, 2001b), resulting in a greater detection range (Siemers, Baur & Schnitzler, 2005), the benefit of such an increase in detection capability may be outweighed by the confusion of multiple loud echoes from non-edible targets. Moreover, this 'exuviae' clutter may reduce the profitability of foraging, as by chance, 70% of prey captures would yield no energetic reward. Over half of the total drift is inedible exuviae casts of trichopterans. If we assume that *M. daubentonii* is unable to distinguish edible from inedible items, not an unreasonable assumption given that Kalko & Schnitzler (1989) found that bats sometimes mistake inedible objects such as floating leaves for prey, and Barclay & Brigham (1994) found that both *M. lucifugus* and *Myotis yumanensis* attack small inedible prey (beetles and leaves) as frequently as similar-sized edible prey, then over half of all prey captures would result in no food reward. The two effects of reduced detectability due to acoustic clutter and reduced profitability due to inedible prey may make the switch to gaffing uneconomic at the lower altitude Site 1. Prey on the water surface clearly represents a valuable food resource when aerial insects are rare.

When given a preference, *M. daubentonii* appears to prefer to forage aerially, and indeed, even the 'fisherman bat' *Noctilio leporinus* only seasonally specializes in trawling (Brooke, 1994). While not included in the analysis, large numbers of fish-fry were also caught in the drift, and

piscivory has been recorded in *Myotis ricketti* (Ma *et al.*, 2003) and *M. cappacini* (Aihartza *et al.*, 2003). In the latter study, fish accounted for up to 82.5% of faecal volume. In the laboratory, *M. daubentonii* will catch and eat small fish (Siemers *et al.*, 2001a), and fish bones and scales have been recovered from faeces (Brosset & Deboutville, 1966), although these are more likely to have come from dead or dying fish on the water surface (Kalko & Schnitzler, 1989). The ability to switch from aerial hawking to trawling thus means that bats have access to a continuous supply of food throughout the night, thus exploiting a niche unavailable to other aerial hawking bats. They also have the advantage of energy conservation through the ground-effect when foraging low over the water surface (Norberg & Rayner, 1987), and even show adaptations to reduce hydrodynamic drag on their otherwise over-sized feet (Fish, Blood & Clark, 1991). One disadvantage of trawling is that foraging may be more temporally restricted in that emergence times are later than that of other sympatric species such as *Pipistrellus* spp., possibly due to the greater visibility to predators when foraging over a water surface (Jones & Rydell, 1994).

In conclusion, the evolution of trawling has allowed bats to exploit new food resources at times when aerial prey is unavailable. However, the difficulty of detecting these prey in the 'acoustic detritus' on the water surface means that bats will switch back to aerial hawking even at very low prey densities. Strategy switching allows these gaffing bats to exploit a source of prey that is available all night, but appears to be constrained by the levels of acoustic clutter that builds up on the water surface. Even though trawling bats show aerodynamic and other physical adaptations to prey capture from water surfaces, this mode of prey capture appears not to be reliable enough to facilitate the evolution of obligate trawlers and may explain the limited extent of this foraging method among bat species.

Finally, we have demonstrated that small altitudinal differences in bat foraging strategy exist along a river gradient. There is a wealth of literature showing that the ecology of bats and their prey differ with both small and high variations in altitude (Walsh & Harris, 1996; Cryan, Bogan & Altenbach, 2000; Senior, Butlin & Altringham, 2005). Therefore, we recommend that more work be carried out on *M. daubentonii* and other trawling bat species along altitudinal river gradients to see whether this foraging pattern is a more widespread occurrence. If this is the case for *M. daubentonii*, this study should be taken into account by conservation planners when considering habitat management requirements of this species along altitudinal gradients in the United Kingdom.

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