Avoidance of bats by water striders (*Aquarius najas*, Hemiptera)

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Abstract

Our study showed that one species of water strider (*Aquarius najas*) dominated the insect fauna (>90% of the biomass) on and near the surface of a small stream in southern Sweden, but the diet of Daubenton's bats (*Myotis daubentonii*), regularly feeding over the same stream, contained <1% of these insects. To explain why the bats did not eat water striders in proportion to the apparent abundance of these insects, we tested three hypotheses, with the following results: (1) The water striders did not respond to artificial bat calls and therefore their defence against bats is not based on ultrasonic hearing. (2) Water striders hand-fed to the bats were eaten with similar frequency as palatable controls (caddis flies), so there is no evidence that water striders are unpalatable to bats. (3) Attempted prey-captures by the bats occurred less often than expected within 1 m of the bank of the stream (the bank consisted of a stone wall), indicating that the bats' flight or, alternatively, their detection or capture of insects, was difficult within that area, possibly constrained by clutter. At dusk and just before the bats emerged to feed, the water striders moved away from the open water. They remained motionless close to the bank for as long as the bats were active.

Introduction

Water surfaces are among the most important and frequently used foraging habitats for insectivorous bats throughout the world. Several species of insectivorous bat species are morphologically and behaviourally specialized for foraging over water, where they feed on insects, which they catch on or just above the surface. This is characteristic for many species in the genus *Myotis* (Subgenus *Leuconoë*), e.g. *M. daubentonii, M. dasycneme* and *M. capaccini* in Eurasia, *M. hasselti* in Asia, *M. lucifugus* and *M. yumanensis* in North America and *M. adversus* in Australia (Wallin, 1961; Nyholm, 1965; Belwood & Fenton, 1976; Anthony & Kunz, 1977; Fenton & Bell, 1979; Swift & Racey, 1983; Jones & Rayner, 1988; Kalko & Schnitzler, 1989; Rydell et al., 1994).

Open water surfaces and the air immediately above are good foraging habitats for bats because they are rich in insects and also because of the virtual absence of disturbing echoes (called 'clutter') from calm surfaces, which facilitates detection of insects by echolocation. When a bat is flying close to the surface, echoes from the water tend to be reflected away from the bat, not back towards it. Nevertheless, clutter from water ripples and surrounding obstacles could make detection and recognition of prey items near the surface difficult or even impossible (von Frenckell & Barclay, 1987; Mackey & Barclay, 1989; Kalko & Schnitzler, 1993; Boonman et al., 1998; Rydell et al., 1999).

Semi-aquatic bugs (Hemiptera: Gerridae) are specialized morphologically and behaviourally for life on water surfaces, where they often dominate the animal community. They feed during the day as scavengers or predators on animals that float or drift on the surface. While some species of water striders (e.g. Genus *Gerris*) are found on the surface of ponds and small streams, others (e.g. Genus *Aquarius*) typically occur on larger surfaces of open water such as lakes and rivers (Andersen, 1982; Scrimshaw & Kerfoot, 1987; Krupa & Sih, 1998).

The surface of open water offers little or no protection from predators attacking from below (such as fish; Krupa & Sih, 1998) or from above (such as bats). Nevertheless, water striders have not previously been found in droppings from Daubenton's bats, a species which is specialized for foraging on insects at or near the surface of water, and whose feeding ecology has been studied intensively (e.g. Swift & Racey, 1983; Taake, 1992; Sullivan et al., 1993; Beck, 1995; Boonman et al., 1998). Indeed, as far as we know, water striders have not been found to be eaten by any bat species. Hence, water striders are usually not eaten by bats although their abundance indicates that they frequently should be exposed to these predators. This in turn suggests that water striders may possess some form of active or passive defence against bats. The purpose of this study was therefore to investigate what prevents bats from feeding on these insects.

We tested three hypotheses that may explain why bats do not feed on water striders, specifically *Aquarius najas*, a relatively large (ca. 2 cm body length) species that often inhabits the surface of running water:

(1) Water striders may possess an escape response based on ultrasonic hearing, like many nocturnal insects (for example many Lepidoptera, Neuroptera and Coleoptera; Roeder, 1967; Miller & Olesen, 1979; Forrest et al., 1995). As far as we know, ears have not been found in any Hemiptera, and the response of water striders to ultrasound has never been investigated.

(2) Water striders may be unpalatable to their predators, like several other Hemiptera. Adult Gerridae (including *Aquarius* spp.) have paired metathoracic glands, which produce chemical defences (Scrimshaw & Kerfoot, 1987). In some terrestrial Hemiptera, these substances have a repelling effect on arthropods, but not on birds (Staddon, 1979). Whether the repellents are effective against bats has not been tested.

(3) Water striders feed during the day and may disappear from the open water, where the bats forage, at night. They may then become effectively unavailable either because of 'acoustic concealment' or because they hide in places which are inaccessible to bats.

The first two hypotheses involve active defence mechanisms that may include morphological specializations in one form or another and which therefore probably have evolved as a direct consequence of bat predation. The third hypothesis represents a passive from of defence against bats (or rather avoidance of them) that may or may not have evolved as a direct consequence of predation from bats.

Materials and methods

Study site

Field tests were conducted in the upper part of the Tidan river system in southern Sweden (57° N, 38° E) during August and September 1997 and 1998. The study site was a ca. 300 m long, 5–10 m wide and about 0.5 m deep stream, connecting two oligotrophic lakes. The stream was lined for ca. 100 m with artificial vertical stonewalls about 1 m high and an old stone bridge, at which the stream was split in two parallel furrows by the arches. One of the furrows was shut off because the arch had caved in, and a lagoon (about 5 × 7 m) with backwater had formed above the shut-off. Adjacent to the lagoon was a ditch overgrown with *Elodea canadensis, Lemna minor* and other water plants, but higher plants were generally absent from the surface of most of the lagoon, the stream and the stonewalls. Surrounding the study site was mixed coniferous and deciduous forests and farmland. For a more detailed description of the site, see Rydell (1986) and Rydell et al. (1999).

Foraging behaviour of bats

Our study site has been used during earlier studies (e.g. Rydell, 1986; Rydell et al., 1999), so the general behaviour of bats at the site was well known at the onset of this study. To determine in detail which parts of the surface were used by the bats and which were not, we made intensive observations of foraging bats during two nights (15th and 16th August 1997). We did not extend these observations further in time because they confirmed many nights of observations made in previous years (Rydell et al., 1999). We used two bat detectors (D-960 and D-200; Pettersson Elektronik AB, Uppsala, Sweden), set at approximately 35 kHz. The surface between the bridge and ca. 50 m upstream was scanned from various position at the stone wall. Immediately after a detector observation of a foraging bat ($n = 178$), we also observed it visually for a few seconds in the light of a 12 W halogen headlight (Silva AB, Sollentuna, Sweden). The light was switched off between the observations. The short observation time was necessitated by the risk of seriously influencing the bats' behaviour with the light and to avoid attracting insects to the area where the bats foraged. When we heard 'feeding buzzes' (dramatically increased pulse repetition rates, indicating attempted prey captures; Griffin et al., 1960), we es-

timated visually the bat's distance to the stone wall: <0.5 m, 0.5–1.0 m and >1.0 m, respectively. To facilitate these observations, we glued small reflective markers to poles in the water 0.5 and 1.0 m from the wall. The poles did not interfere with the bats' foraging, since the poles remained entirely below the surface. Daubenton's bats foraging over water usually fly 0.1–0.3 m above the surface (Jones & Rayner, 1988; Kalko & Schnitzler, 1989; Rydell et al., 1999). We therefore ignored occasional bats that flew higher because such bats were probably commuting rather than feeding (Rydell et al., 1999), and in any case they were presumably of no immediate threat to insects on the surface. The bats were not individually marked, so we probably observed each individual more than once.

Mist netting of bats

To collect droppings and perform a palatability test, we captured eight bats (one juvenile and three adult females and four adult males) on two nights (2nd and 3rd September, 1998, four bats each night) in a 9 m mist net placed across and immediately above the water. The net was set up during ca. 30 min each night, during which it was attended continuously. If no bat was caught within 5–10 min, we moved the net slightly, since the bats rapidly learned its position.

To collect droppings for faecal analysis, we kept the bats separately in small bags of rough cloth suspended indoors until the following night or morning. The four individuals from the first night were also used in the palatability test conducted on the second evening after the droppings were collected. We released the bats under the stone bridge the night after they were captured. We did not feed the bats, except for the insects provided during the palatability test (see below).

Faecal analysis

We softened the pellets in a water-ethanol solution (50/50) and analysed them under a dissecting microscope (Olympus SZ4045, Olympus Optical Co. GmbH, Hamburg, Germany; at 6.7–40×). The fragments were identified to insect order or family, using Nilsson (1996, 1997) and Shiel et al. (1997). We counted compound eyes or antennae to obtain a minimum number of individual prey items in each pellet (Swift et al., 1985). The pellets from one of the bats (a male) did not contain any compound eyes or antennae that

could be used for quantification, so we excluded this individual from the analysis.

Estimate of insect biomass

We roughly estimated the insect abundance (wet weight; Sartorius BP 110S, Sartorius AG, Göttingen, Germany) at dusk (850-0 lux (lx) incident light level; Gossen Mastersix light meter, Gossen GMBH, Erlangen, Germany, directed towards the open sky) by hand netting on and above the water. The insect sampling coincided roughly with the time and light intensity that the bats normally emerge and start to feed over the stream. We took one sample of aerial insects, one of surface dwelling and one of drifting insects (see below) during each of three evenings (2nd, 3rd and 17th September, 1998).

To sample non-drifting surface dwelling insects, including water striders, in the middle of the lagoon, we pulled the hand net through the water surface from below. We estimated the biomass of insects that drifted on the surface (flow rate = 0.7 ± 0.1 m s^{-1}, in the middle of the stream beside the lagoon) by placing a hand net (0.4 m diameter) in the water with the net ring perpendicular to the surface during 30 min. For insects in the air, we swept a hand net (0.5 m diameter) 60 times (2.3 m/sweep) immediately above the surface, the sweeps covering both the lagoon and the stream. As the bats forage both on the surface and in the air immediately above, we summed up the insect biomass from the water surface with that of the air above (mg insects per m^2 of water surface plus mg insects per m^3 of air). The biomass estimates of water dwelling insects refer to the lagoon only and that of drifting ones refer to the stream only. Therefore, before these estimates were added to the estimated biomass of flying insects, the former were divided by two because they refer to only about half the area sampled.

Water strider reaction to ultrasound

We exposed *A. najas* to artificial bat calls, using an electronic dog whistle ('Pet Trainer') calibrated to 26 kHz, 110 dB sound pressure level (re. 20 μPa, root mean square measured at 1 m; the second harmonic attenuated >30 dB compared to the fundamental; Rydell et al., 1997). This ultrasound device is very simple but nevertheless elicits normal evasive responses from tympanic moths (Rydell et al., 1997). The frequencies emitted are also included in the echolocation calls used by *M. daubentonii* (Rydell et al., 1999), so if the wa-

ter striders could hear Daubenton's bats, they would presumably react to the dog whistle as well. In the laboratory, where we tested the water striders individually, the distance between the sound source and the insect was 0.5 m ($n = 17$) or 1.5 m ($n = 10$). In the field, where we tested them as they occurred naturally (in schools), the distance was 0.5–2 m. In daytime (incident light level >6000 lx), the size of the school varied between 5 and 50 individuals, while at night (0 lx), the schools consisted of 10 to >100 individuals.

We pressed the button on the dog whistle manually about 10 times in 1–2 s to simulate echolocation calls from foraging bats. The pulse repetition rate was not exactly the same for all samples due to the manual handling. If the striders could hear ultrasound, we expected to see a distinct and, for striders in schools, simultaneous, movement immediately following the sound burst.

Palatability test

We presented live insects in front of a bat, by holding the bat gently in one hand and the insect in the other. We used caddies flies (Trichoptera), which are frequently eaten by Daubenton's bats (Swift & Racey, 1983; Sullivan et al., 1993), as palatable controls. We collected the caddis flies on a 125 W mercury vapour lamp placed near the stream. The water striders (*A. najas*) were caught in the stream using a hand net. Four bats were each fed four individuals of each type of insect. The insects were presented alternately, always starting with a caddis fly. The food was presented to the bat at their normal foraging time, i.e. at the beginning of the night (2100–2200 h Central European Summer Time, CEST).

Spatial distribution of water striders

We photographed the distribution of water striders (mostly *A. najas*) at different places from the shore or the bridge using a Nikkormat camera on a tripod, with a 105 mm lens, an electronic flash, and 24 × 36 mm black and white Kodak T-Max 400 ASA film. We used a cable release to minimize disturbance. Photos and light measurements (as described above) were taken every fifteen minutes throughout the evenings of 16th August 1997 (air temperature 23–18 °C), 2nd September 1998 (12–7 °C), and 27th September 1998 (13–10 °C), starting at ca. 1700 h and continuing until 1–2 h after dark (see Fig. 2). We included the reflective poles (see above) in the photos to mark the distance

Table 1. Biomass (wet mass) of insects sampled from the surface and the air above the surface of a stream in south Sweden. 'Other insects' are >90% Diptera, mostly Chironomidae. *N* is the number of samples

	A. najas	Other insects	Total	*N*
Surface (g m^{-2})				
(a) drifting	0	1.0×10^{-5}	1.0×10^{-5}	3
(b) surface dwelling	0.85	3.2×10^{-2}	0.88	3
Air (g m^{-3})	0	5.1×10^{-4}	5.1×10^{-4}	3
Total biomass (g m^{-3})	0.85	3.3×10^{-2}	0.88	
%	97	3	100	

Table 2. Prey items found in droppings from seven *M. daubentonii*. The number of insects are minimum values; % refers to the frequency of the total number of prey

Bat no.	1	2	3	4	5	6	7	Total	%
No. of droppings	15	10	7	12	12	13	8	77	100
No. of Chironomidae	52	53	31	42	16	38	12	244	98
No. of Trichoptera	0	0	0	0	1	2	0	3	1
No. of Gerridae	0	0	0	0	1	0	0	1	<1

from the stone wall (0.5 and 1.0 m, respectively). The number of water striders positioned within 0.5 m and between 0.5 and 1.0 m from the wall were counted from the photos.

Results

Water striders dominated the insect fauna on and immediately above the water surface (>97% by wet mass; Table 1). Diptera such as non-biting midges (Chironomidae), constituted <3% of the biomass. The mass of the drifting insects was negligible compared to those of the non-drifting, surface-dwelling and flying insects.

In contrast, faecal analysis (77 droppings from seven bats) showed that the bats foraged mainly on chironomids (98%) and sometimes also caddis flies (Trichoptera; 1%), whereas water striders only were taken very occasionally (Gerridae; <1%). We found chironomids in droppings from all seven bats, caddis flies in those of two, but water striders only in droppings from one individual (Table 2).
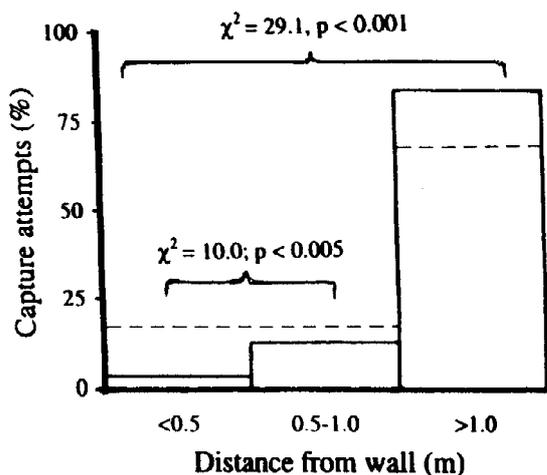
Figure 1. Distribution of prey capture attempts ($n = 178$) by *M. daubentonii* foraging over a stream in south Sweden, in relation to the distance to the stone wall bordering the stream. The dotted lines mark the expected percentage if the capture attempts had been distributed evenly over the surface. The expected numbers detected >1 m from the bank was higher than at <1m from the bank because the former area was larger.

We found no evidence of ultrasonic hearing in *A. najas.* They did not respond in any way to the artificial bat calls, independently of the situation, group size and light conditions. The bats ate both *A. najas* and the palatable control (Trichoptera) presented to them. All the 16 controls were eaten. One bat (juvenile female) rejected one *A. najas* and ate only half of another one, after having eaten two previously. The other three bats each ate the four *A. najas* presented to them without hesitation. Hence, although the samples are too small for a meaningful statistical analysis, the results suggest that the chemical excretions of water striders do not function effectively against Daubenton's bats.

The study site was regularly used as a feeding site by 10–20 Daubenton's bats. Their foraging activity was intense during the study nights in August and early September, but the bats were absent in late September. The bats appeared to be unevenly distributed over the surface, although we did not quantify this. However, as shown in Figure 1, the bats made significantly more capture attempts than expected >1 m from the wall ($n = 149$ observations). There were also fewer capture attempts within 0.5 from the wall ($n = 6$), as compared to the strip between 0.5 and 1 m ($n = 23$). Hence insects became increasingly exposed to bat predation the further they were from the bank.

The distribution of water striders on the surface before and after the bats arrived in the evening (bat arrival indicated by arrows in Figure 2a,b), differed significantly ($X^2 = 91.41$, $p < 0.001$, Fig. 2a; $X^2 = 17.11$, $p < 0.001$, Fig. 2b). Before the bats arrived, the water striders either stayed >0.5 m from the wall ($X^2 = 4.41$, $p < 0.05$, Fig. 2a), or were randomly distributed over the water ($X^2 = 3.81$, $p > 0.5$, Fig. 2b). In contrast, after the bats' arrival, they consistently stayed close to the wall (<0.5 m; $X^2 = 54.18$, $p < 0.001$, Fig. 2a; $X^2 = 5.22$, $p < 0.025$, Fig. 2b).

In late September, when no bats were present at the stream, we compared the distribution of water striders before and after the light intensity had fallen to the level that coincided with bat arrival (<50 lx) in August and early September. The distribution differed significantly before and after ($X^2 = 39.60$, $p < 0.001$, Fig. 2c; $X^2 = 7.87$, $p < 0.01$, Fig. 2d), just as it did earlier. The water striders were evenly distributed on the surface when the light intensity was >50 lx ($X^2 = 1.89$, $p < 0.5$, Fig. 2c; $X^2 = 1.10$, $p < 0.5$, Fig. 2d), but they later stayed within 0.5 m of the wall (<50 lx; $X^2 = 30.42$, $p < 0.001$, Fig. 2c). At one of the photography sites used in late September (Fig. 2d), water striders were sometimes absent, which means that a statistical test could not be made for this sample. Their absence in the photos (Figs 2b and 2d) indicates that they had climbed the wall, rocks in the water or nearby vegetation.

After having spent 1–2 h near the bank, the water striders usually started to move back towards the open water. Generally, few if any foraging bats were present over the stream and the lagoon at this time in the middle of the night.

Discussion

Water striders dominated the insect fauna on and immediately above the water surface, but were only occasionally eaten by the bats. The discrepancy between the abundance of these insects on the surface, where the bats foraged, and their infrequent occurrence in the bat droppings was great and we find it very unlikely that it was entirely a result of biases in the insect sampling or in the analysis of the bat diet. Although the insect sampling was very limited, we are confident that at least part of the discrepancy was real.

Water striders respond to fish strikes by fast escape movements (Andersen, 1982). However, such responses presumably require that the approaching predator can be detected from some distance, i.e. by vision or through detection of pressure changes in the
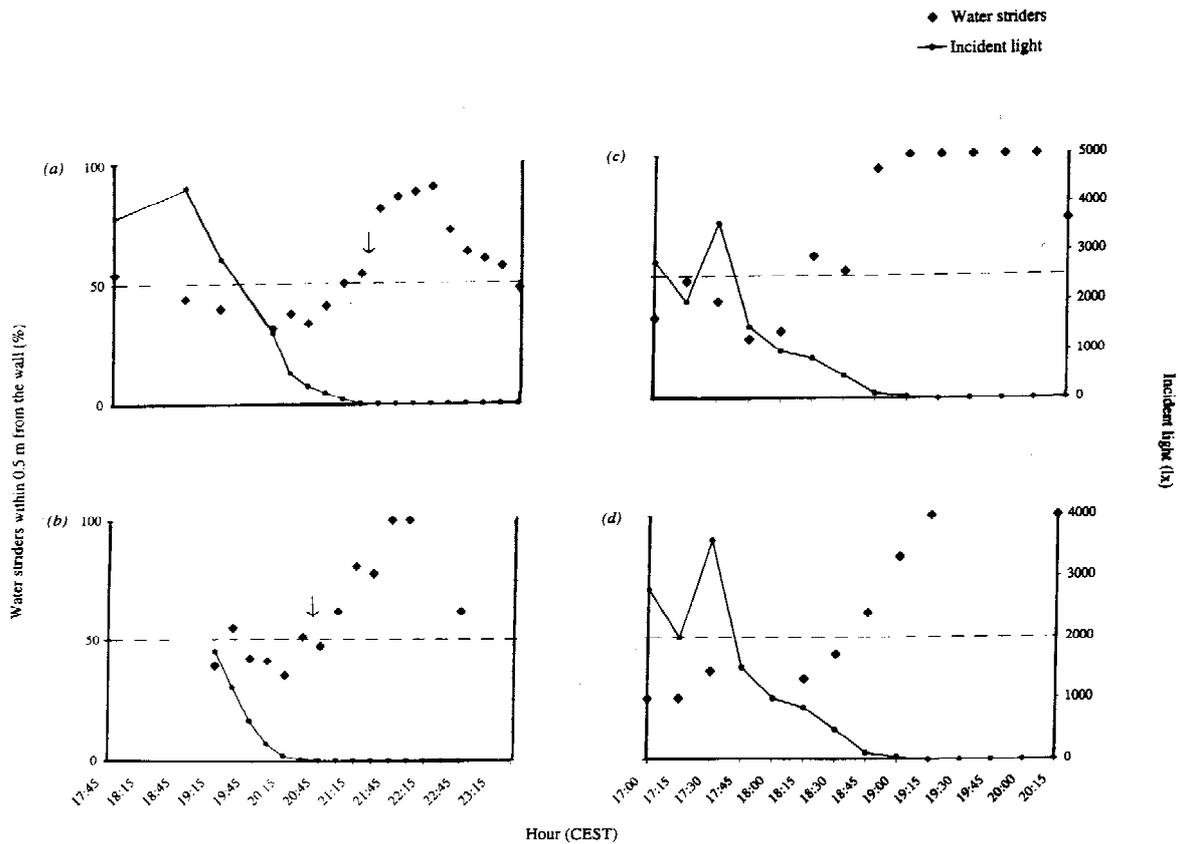
Figure 2. Total number (*n*) of *A. najas* on the surface within 1 m of the bank (a stone wall), and the percentage located within 0.5 m; (a) 17th August, (b) 3rd September, in both cases with bats foraging over the stream, (c) and (d) 27th September (2 sites), when no bats were present. The total number of strider observations are 12 467, 390, 363 and 57 for a, b, c and d, respectively. The dotted lines mark an even distribution on the surface (i.e. 50% within 0.5 m of the bank). The arrows denote the time when the first bats arrived. The hour refers to Central European Summer Time (CEST).

water. To detect an approaching bat from a distance may be another matter and hearing the echolocation calls would probably be the most straightforward way to do this. Ultrasonic hearing and associated responses have been found in a large and increasing number of nocturnal insect taxa, including moths (Lepidoptera; Roeder, 1967), beetles (Coleoptera; Forrest et al., 1995), lace wings (Neuroptera; Miller & Olesen, 1979) and praying mantids (Orthoptera; Yager & Hoy, 1986), but not so far in hemipteran bugs, as far as we know. The electronic dog whistle that we used is a very simple device, but nevertheless elicits normal anti-predator responses in moths (Rydell et al., 1997, 2000). It would presumably have done so in the water striders as well, if they had been sensitive to ultrasound. However, we found no indication that they reacted to the ultrasound. This is consistent with the water striders' withdrawal behaviour, which occurred independently of the presence of bats.

If a fast escape response cannot be used as defence against bats, the water striders may perhaps rely on its presumed unpalatability in this case. Water striders emit secretions from metathoracic glands (Andersen, 1982; Scrimshaw & Kerfoot, 1987) and it is often assumed that the primary function of these chemicals is predator defence. However, because most water striders handfed to the bats were eaten without hesitation, the chemicals did not seem to function as expected. On the contrary, the apparent inefficiency of the chemicals against bats suggests that water striders primarily must rely on other forms of defence against mammals.

It seems unlikely that the water striders were too small or acoustically inconspicuous to be detected by echolocating bats. In fact, most of the prey items actually eaten were much smaller. It also seems unlikely that the bats avoided the water striders actively. For example, Barclay & Brigham (1994) have shown that

M. lucifugus and *M. yumanensis*, two nearctic species that forage over water in a way very similar to that of *M. daubentonii*, usually feed unselectively, and sometimes even catch leaves floating on the surface. Hence, it seems unlikely that Daubenton's bats feed selectively, and ignored water striders for energetic or other reasons. Although Daubenton's bats and its relatives may catch more or less anything that floats on the surface, they typically avoid foraging close to vegetation or rocks (von Frenckell & Barclay, 1987; Boonman et al., 1998) and they also avoid ripples whenever possible (Wallin, 1961; Rydell et al., 1999). The preference for unobstructed and calm surfaces could occur because flight may be less constrained in such places, but also because of the absence of acoustic clutter, which otherwise complicates the detection and recognition of prey items (Mackey & Barclay, 1989; Rydell et al., 1999).

An alternative explanation for the behaviour of the water striders around dusk is that their own performance is constrained by the darkness. In water striders, visual stimuli are probably important in prey location, and necessary during fast locomotion on the surface (Andersen, 1982). Water striders may therefore be unable to forage efficiently after dark. However, our observation that the striders moved back to the open water at midnight, when the bats usually were absent, speaks against this hypothesis.

The movement of the water striders towards the vegetation or rocks at dusk occurred independently of the presence of bats and may have been triggered by the falling light level. However, the movement back to the open water before midnight was presumably not triggered by this kind of stimulus, so the mechanism behind the latter behaviour remains unknown.

It is presumably energetically advantageous for non-foraging striders to avoid moving water, and seek shelter in the backwater near the bank. However, this explanation for the withdrawal behaviour is not entirely applicable to our case, because most of our observations were made in the lagoon, where the water striders had no current to fight in any case. Nevertheless, it remains possible that gathering near the bank at dusk is a general behaviour of *A. najas*, a species that often inhabits running waters (Andersen, 1996).

Our results strongly suggest that the principal reason why bats that forage over water do not eat water striders, which often are the most abundant insects in this habitat, is that the behaviour of the insects is such that they become largely unavailable to echolocating bats at night. They become unavailable following their withdrawal from the open water. The evolution of this behaviour is another matter; the avoidance mechanism may or may not have evolved because of the predation pressure executed by bats (Speakman & Rydell, 2000). Hence with the current information we cannot conclude that the withdrawal behaviour of the water striders was shaped by predation from bats, but it seems fair to conclude that the withdrawal behaviour has the consequence that these insects are rarely captured.

Whether it is important or not to understand how a certain behavioural trait evolved depends on the questions that we are asking. For example, such understanding seems irrelevant if we just want to know (in an ecological sense) which surface-dwelling insects are available as food for bats and which are not. Nevertheless, the consistency and the almost perfect timing of the disappearance from the open water relative to the appearance of the bats suggest that predation from bats could have been involved. Possibly, the water striders use the water surfaces near vegetation and rocks as refuges, since they consistently move towards these areas at dusk. If so, they may exploit shortcomings in the bats' echolocation system, i.e. through 'acoustic concealment', like some other insects (Lewis et al., 1993; Rydell, 1998). In any case, our study illustrates that predator defence in insects can be highly efficient even when subtle, and not necessarily associated with spectacular behaviour or sophisticated morphological specializations.

Our observation highlights a serious problem in studies of the feeding ecology of insectivorous bats, namely that bats and humans sample insects differently, so the apparent abundance of insects may have little or no relationship to what is actually available as food for bats. Availability is to a great extent a function of the efficiency by which particular insects can (a) be detected and recognized by echolocation and (b) be captured by bats.

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