ECHOLOCATION ACTIVITY OF DAUBENTON'S BAT (MYOTIS DAUBENTONII) AND COMMON PIPISTRELLE (PIPISTRELLUS PIPISTRELLUS) IN RELATION TO INSECT ABUNDANCE, HABITAT AND ELEVATION IN AN UPLAND RIVER CATCHMENT

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Abstract

Riparian habitats have high insect abundance and consequently provide good foraging opportunities for insectivorous bats. Here we investigate how insect abundance, temperature, season, and elevation affect the foraging behaviour of Daubenton's (Myotis daubentonii) and common pipistrelle (Pipistrellus pipistrellus) bats along the river Wharfe in north Yorkshire. Insect abundance correlated positively with ambient air temperature. Abundance reached a maximum around sunset before dropping to low levels with frequent zero captures throughout the middle of the night. There was often a second smaller peak in insect abundance around sunrise. Insects at all elevation habitats were mainly dipterans, and most (92%) of these were nematocerans. There was a mismatch between peak insect abundance and bat detections, with highest insect detection just before bats arrived in the evening or after they left in the morning. Insect abundance and bat Feeding Buzz Ratios (FBR) did not differ significantly between treeless and tree-lined habitats. Significantly more M. daubentonii detections were recorded in August than in May, but there was no significant difference in the number of mean feeding buzzes between months. More P. pipistrellus FBRs were recorded at lower elevations; however, there was no elevational difference in FBR for M. daubentonii, although more FBRs were recorded for this species. Detections of M. daubentonii were fairly constant throughout the night, while P. pipistrellus exhibited large variations in number of passes per hour. P. pipistrellus arrived c.a. half an hour earlier at tree-lined habitats than tree-less habitats, likely taking advantage of protective tree cover to gain additional foraging time when insects are more abundant. M. daubentonii, on the other hand, generally arrived later. There was no correlation between FBR and number of aerial insects for either species. Bat detections (and therefore presence) is influenced by factors other than the availability of aerial prey.

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ABSTRACT

Riparian habitats have high insect abundance and consequently provide good foraging opportunities for insectivorous bats. Here we investigate how insect abundance, temperature, season, and elevation affect the foraging behaviour of Daubenton's (*Myotis daubentonii*) and common pipistrelle (*Pipistrellus pipistrellus*) bats along the river Wharfe in north Yorkshire.

Insect abundance correlated positively with ambient air temperature. Abundance reached a maximum around sunset before dropping to low levels with frequent zero captures throughout the middle of the night. There was often a second smaller peak in insect abundance around sunrise. Insects at all elevation habitats were mainly dipterans, and most (92%) of these were nematocerans. There was a mismatch between peak insect abundance and bat detections, with highest insect detection just before bats arrived in the evening or after they left in the morning. Insect abundance and bat Feeding Buzz Ratios (FBR) did not differ significantly between treeless and tree-lined habitats. Significantly more *M. daubentonii* detections were recorded in August than in May, but there was no significant difference in the number of mean feeding buzzes between months. More *P. pipistrellus* FBRs were recorded at lower elevations; however, there was no elevational difference in FBR for *M. daubentonii* , although more FBRs were recorded for this species. Detections of *M. daubentonii* were fairly constant throughout the night, while *P. pipistrellus* exhibited large variations in number of passes per hour. *P. pipistrellus* arrived *c.a.* half an hour earlier at tree-lined habitats than tree-less habitats, likely taking advantage of protective tree cover to gain additional foraging time when insects are more abundant. *M. daubentonii* , on the other hand, generally arrived later.

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KEYWORDS: Diptera, Foraging, Insects, Elevation, *Myotis daubentonii* , Yorkshire Dales National Park, *Pipistrellus pipistrellus* , Social calls.

INTRODUCTION

At large scales, insect numbers have been shown to be in rapid decline (Hallman et al. 2017, van Strien at al. 2019), but changes are patchy and habitat-specific, with some studies reporting both decreases and increases in terrestrial and aquatic insects respectively (van Klink et al. 2020). While many studies have focused understandably on invertebrates as providers of pollination-ecosystem services, their abundance is also of crucial importance as a food source for insectivores (Møller 2019). Although total abundance is easier to measure, it is of less use as a metric if insects show high temporo-spatial variation over small scales (McCoy, 1990), and are hence unavailable to predators.

In riparian systems, increasing anthropogenic pressures have resulted in extensive habitat modifications and marginalisation (e.g. eutrophication, pollution, etc.; Salvarina, 2016), yet these regions yield high insect (Cole *et al.* , 2015; Dreyer *et al.* , 2015) and insectivorous bat (e.g., Grindal *et al.* , 1999; Williams *et al.* , 2006) abundance. On several occasions, bat population declines have been correlated to habitat modifications (e.g., Russo and Ancillotto, 2015; Millon *et al.* , 2018) and while it is tempting to use insect availability as a proxy for bat-habitat quality, bat distribution is not always obviously linked to prey presence (Fuentes-Montemayor

et al. , 2013; Salvarina *et al.* , 2018; Carr *et al.* , 2020). Depending on foraging strategy and echolocation specialisation, some bat species favour certain habitat characteristics over others and their ecology can be (at least partially), independent of prey distribution and abundance (Müller*et al.* , 2012; Jantzen and Fenton, 2013; Müller *et al.* , 2013). This is especially salient in small boreal species of insectivorous bat that, in addition to feeding, are subject to thermoregulatory, metabolic, and reproductive constraints (Patriquin, 2001; Smith and Racey, 2005; Boyles, 2007; Masing and Lutsar, 2007; Fabianek *et al.* , 2015), and must also contend with increased temperature vicissitudes (both seasonally and over the diel cycle), exacerbated in habitats that differ in topographical elevation. For example, the small insectivorous Daubenton's bat (*Myotis daubentonii*) and even smaller common pipistrelle (*Pipistrellus pipistrellus*) are known to forage along smooth water sections of rivers, generally with trees along one or both banks, avoiding cluttered and rapid water sections (Warren *et al.* , 2000; Lundy and Montgomery, 2010; Todd and Waters, 2017; Todd and Williamson, 2019), sometimes independent of aerial prey abundance and distribution (Todd and Waters, 2017). This points to understudied, or hitherto unknown abiotic (e.g. temperature, elevation, etc.) and biotic (e.g. prey biology) factors that likely influence both insect and bat distribution and foraging behaviour, demonstrating requirement for further investigations of these species' fine-scale ecology. This is especially salient in upland river habitats in a bid to better understand effects of riparian management.

This study explores both insect abundance and bat activity/feeding attempts throughout the night in relation to elevation along the river Wharfe in the Yorkshire Dales National Park (YDNP). We examine the small-scale temporo-spatial distributions of insects and their potential availability to echolocating bats within this riparian habitat and examine whether insect abundance can predict the foraging behaviour of bats.

MATERIALS & METHODS

Timing & location

Data were collected by two researchers in a paired (simultaneous) sampling protocol between 1st May and 1st September 2000 along a 25 km stretch of the river Wharfe in Wharfedale, North Yorkshire, United Kingdom (UK). The River Wharfe runs through the YDNP, UK. The study area was located between the lower village of Burnsall (54º 3.08' N, 1º 57.14'W) and the highest hamlet of Hubberholme (54º 12.00' N, 2º 6.71' W; **Figure 1**). Sampling locations along the Wharfe have been described, and mapped previously by Todd and Waters (2017) using the same methods presented in Todd and Williamson (2019). Care was taken to ensure that both observers' techniques and equipment were compared with each other in various ways, to obviate observer bias (details below).

Elevation & habitat selection

Three riverine elevation sections along the Wharfe were chosen: (1) High, Hubberholme–Buckden (240–220 m), (2) Mid, Kettlewell area (210 m), and (3) Low, Grassington–Burnsall (163–150 m). In previous studies, bats in this area have been detected most in areas with smooth water (Todd and Waters, 2017); therefore, paired sampling focussed on smooth water sections only. Habitat-type nomenclature has been presented in Warren *et al.* (2000) and Todd and Williamson (2019). This study used habitat one: smooth water with trees both sides, and habitat three: smooth water with no trees, both of which were available in similar amounts throughout the study area (habitat 1 = 3.208 km, habitat 3 = 3.535 km total lengths). Within each of the three elevation sections, twelve suitable study locations were chosen, six of habitat one and six of habitat three (**Figure 2**). Detection of bats using typical *Myotis* and *Pipistrellus* frequencies are generally limited to a range of 20 m or less (Adams *et al.* , 2012); consequently, each habitat was separated by at least 200–500 m to reduce any effects of pseudoreplication between patches (Hurlbert, 1984; Vaughan *et al.* , 1996) and to ensure bats foraging at each habitat type were not in both bat detectors' ranges (i.e. did not influence the paired-sampling protocol).

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Temperature

Air temperature at three elevations along the river Wharfe was recorded between 1st April and 5th September 2000 using three Tinytalk? (TK-0014 Gemini data Loggers, UK) temperature loggers which were calibrated (within an accuracy of 0.5 degC) against mercury thermometers. Loggers were suspended (hidden from view and sun) from overhanging tree branches (*ca.* 3 m above the surface of the water) within the three altitudinal sections along the Wharfe. Loggers were always located over smooth river sections with trees on both sides of the banks and were set to record ambient temperature (degC) every 36 min. Distance between low and mid-elevation loggers was 9.5 km and between mid and high-elevation was an additional 6.5 km.

Paired-insect sampling

In both May and August 2000, the two observers were stationed at paired habitats (e.g. 1a and 3a; **Figure 2**). Sweep-netting is recommended as a method for sampling Diptera (Grootaert *et al.* , 2010), which are the primary prey item for *M. daubentonii* and *P. pipistrellus* (Vaughan, 1997). Insect-capture protocol was the same as previous studies, including Wharfedale for data-comparison purposes (Todd and Waters, 2007; Todd and Waters, 2017; Todd and Williamson, 2019). Prior to experimental sweep-netting, observers were calibrated against each other to ensure sampling procedures were identical, and there was no sampling bias. Two identical, fine mesh (1 mm^2) white sweep nets (Philip Harris, Leicestershire) with a diameter of 355 mm, attached to a 1.2 m aluminium poles, were used and alternated between researchers to avoid net biases.

Netting began as soon as the river target position had been reached and head lamps were switched off to reduce swarming effects induced by positive phototaxis (Jayanthi, 2013). Sampling involved 40 x 180deg sweep netting sessions (per observer) approximately 1 m above the water surface as close to the centre of the river channel as possible at both habitats one and three in each of the three elevations. Trees and riverbanks were avoided to accurately sample foraging space used by *M. daubentonii* . Insect sampling was taken at 30 min intervals for the first two and a half hours, after which sampling occurred every hour until two and a half hours before dawn when sampling at 30 min intervals recommenced from one hour before sunset until one hour after dawn. This variation in netting frequency was to align with timing of bat surveying. Netting took place immediately after bat recordings to avoid interfering with foraging bats. Sampling was undertaken in a range of temperatures, but was not carried out during wind speeds exceeding 1 ms^{-1}, as wind has been shown to affect insect flight (Todd and Waters, 2017). Wind speed was monitored using an anemometer (Wilh. Lambrecht 34, Gottingen, Germany).

Once in the net, insects were sprayed immediately with 70% alcohol, and extracted gently with a soft brush into pre-labelled glass vials. Care was taken not to extract insects that had been attracted to the net post sampling. Insects were counted and identified later in the laboratory with a binocular microscope (Karl Zeiss, Germany) under x10 magnification. Identification was completed to a minimum of order or sub-order using Unwin (1981), Chinery (1993), and Armitage *et al.*(1995). Due to the small values of dry weights and the lack of an accurately measurable mass, insect numbers were presented as a proxy for biomass.

Paired bat detections

All bat-recording equipment had the same specifications as Todd and Waters (2017).At both locations, tripods and time expanding bat detectors were set up one metre away from the water surface, facing the river. The highly directional response of similar designs of detector (Waters and Walsh, 1994) ensured that only bats foraging over the river would be recorded. Tranquility II detectors (Courtpan Design Ltd., Cheltenham, UK) were connected consistently via the right channel to Sony Professional Walkman (Sony, Tokyo, WM-D6C - frequency response: +- 3 dB from 40 Hz–15 kHz) to enable species identification in later analysis. In the left channel of each Walkman, a heterodyne bat detector (Magenta, Staffordshire) was connected, tuned to 50 kHz to record passes and feeding buzzes. Number of passes was counted and a running tally recorded by hand. Recordings were made on 90-minute normal position tapes (BBC, FX 90/type I).

To ensure that bat pass counts were consistent between the two detectors (each of which was used by the same observer throughout), a calibration trial of eight parallel counts of 15 min duration were made from 21:10 – 03:10 on 29th April 2000 at a site on the Wharfe, the day before main observations commenced on 1st May. For this calibration trial, each observer stood on the same side of the riverbank *ca.* 2 m away from each other. Bat pass counts were usually identical, and when different, varied only by one pass. A paired *t* test showed no significant difference $t = 2.36$, d.f. = 7, $P = 0.3$. On this same river system, Senior *et al.*(2005) found that, while *M. daubentonii* commute to a foraging site, once there, they tend to forage repeatedly in one patch of around 100 m or less. While this ensured that we measured bat activity specific to the chosen habitat type, it was not possible to disentangle bat activity, as measured by bat passes, from number of individual bats.

All-night sampling was carried out in May and August 2000. Sampling of elevations was rotated each night to avoid seasonal biases. Habitat locations were never sampled twice within the same month. Observer and habitat were rotated each night to avoid observer-sampling bias. During both months, at habitat types one (smooth water, trees both sides) and three (smooth water, no trees), simultaneous bat detector monitoring commenced one hour before sunset and terminated one hour after sunrise; however, a pilot study11A pilot study using the same procedures, was carried out in August 1999 at habitat type one at Yockenthwaite (2 km upriver from Hubberholme) and Burnsall ($n = 4$ nights/elevation). had shown that bats never arrived at the sites before sunset. Recording sessions continued at 30 min intervals for the first two and a half hours, after which recordings were made every hour until two and a half hours before dawn when sampling at 30 min intervals recommenced. Recordings were made at hourly intervals in the middle of the night, as the pilot study revealed that insect activity was considerably reduced during this period, to reduce unnecessary survey effort. Each bat recording session lasted *ca.* 15 minutes.

In May 2000, each of the six habitats of type one and three were sampled once at each elevation totalling 18 nights for the whole set of experiments ($n = 6$ nights per elevation). The experiment was repeated in August 2000 at the same locations ($n = 18$ nights). Sampling took place on contiguous nights unless interrupted by bad weather. The interval between sampling nights never exceeded seven days.

Data analysis

All data are expressed as means +- Standard Deviations (SD) throughout. Parametric statistical procedures were carried out on all normally distributed data or transformed non-normal data. Non-parametric statistics were used when either numeric +1 log transform or arcsine transformation of the data failed (Zar, 1984).

Bat species identification was confirmed by analysing associated time-expanded audio sequence using Batsound (Petersson Electronic) on a PC and observing the call spectrogram (512-point FFT, Hamming Window).

Calls of *M. daubentonii* were distinguished from those of *Pipistrellus* species by the lower terminal frequency and the lack of a constant frequency tail at the start of approach phase. Calls between the two phonic forms of pipistrelle (*P. pipistrellus, P. pygmaeus*) were distinguished easily from their echolocation calls, as per (Jones and van Parijs, 1993; Vaughan *et al.* , 1997; Rachwald*et al.* , 2016). 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. While separation of calls of *M. daubentonii* from those of other*Myotis* species is problematic (Walters *et al.* , 2012), previous netting surveys at this site had shown that *M. daubentonii* was by far the commonest *Myotis* species (Warren at al. 2000), and so all *Myotis* calls were attributed to *M. daubentonii* unless different significantly in expected parameters.

All combined insects collected each night were counted, placed in an oven for 24 hrs at 60 degC and weighed dry (on a Mettler Af 163 electronic balance) to the nearest 0.01 g and the August insects were identified taxonomically to order and sub order.

One-way and two-way ANOVAs and *post hoc* Tukey's tests were used to compare temperatures at each

elevation. For analysis of temperature variations at each elevation, difference between sunset temperature and minimum nightly temperature before sunrise was calculated.

Bat passes (Fenton, 1970) were counted at each site and converted to bat passes hr^{-1}. Differences in bat pass detection with elevation and season were assessed using Mann-Whitney rank sum tests. Scheirer-Ray-Hare tests (a non-parametric equivalent to a two-way ANOVA with replication, Dytham, 1999) using elevation and habitat type as factors were carried out to assess differences in bat detection with elevation. For *post hoc* tests, when samples were balanced (i.e. equal numbers of observations), Student-Newman-Keuls tests for multiple comparisons were used. With unbalanced data, Dunn's test for multiple comparisons was used. Paired t tests were carried out to test for differences in bat detection between the months of May and August 2000, the data of which were considered to be 'paired', as the same sampling locations were re-tested; the only difference was therefore a factor of time. Spearman's rank order correlations were used to assess patterns in bat passes throughout the night between the two habitat types.

Feeding buzzes were used to quantify feeding rates at each site by foraging bats. These sounds are produced by aerial-hunting and trawling bats when they attempt prey capture (Griffin *et al.* , 1960). As in the study of Vaughan *et al.* (1996), a count of terminal buzzes was used as a measure of foraging effort per unit of time. Number of feeding buzzes was counted and assigned to species based on the bat pass in which they were recorded using the time-expanded recordings. Bat feeding activity was expressed as the ratio of terminal buzzes to bat passes: feeding activity = terminal buzzes/bat passes = feeding buzz ratio (FBR). A FBR of one indicated that an equal number of bat passes and terminal buzzes were heard, or that on average every pass has a buzz (Vaughan *et al.* , 1996). FBR is therefore a measure of foraging attempts per unit of flight activity. The same statistical analysis techniques as bat passes hr^{-1} was applied to FBRs and insect numbers throughout the night.

RESULTS

Temperature

The warmest elevation was the lowest (Burnsall; mean +- SD 11.9 degC +- 4.51 degC; **Figure 3**). Intermediate temperatures were found at Kettlewell (mean +- SD 10.7 degC +- 4.33 degC) and the highest elevation of Hubberholme was the coldest (mean +- SD 10.5 degC +- 4.65 degC). There was a 1.39 degC difference between the high and low elevations and August was the warmest month.

A two-way ANOVA using the mean 24 hr temperature at each elevation and month as factors could not be carried out to investigate temperature differences between the three elevations, because the Burnsall logger was lost for one month; therefore, an interaction term could not be calculated. There was a highly significant difference between monthly temperatures at each elevation from the beginning of April to the end of August (one-way ANOVA, d.f. = 2, $P < 0.0001$). A *post hoc* Tukey's test revealed that there were significant differences in the mean temperatures between all three elevations and that the greatest difference was between the highest and the lowest elevation (**Table 1**).

Insect diversity

There was a general trend for numbers of aerial insects to increase with increasing temperature. Spearman's rank order correlations undertaken on the number of insects (pooled for elevation and habitat type) in May and August revealed that these correlations were significant at the $P < 0.0001$ level (Rs = 0.647, $n = 264$ and Rs = $0.577, n = 340$ respectively).

Scheirer-Ray-Hare tests using elevation and habitat type as factors, revealed that there was a significant elevational difference in the numbers of insects in August only (d.f. = 2, $P < 0.0001$) and a *post hoc* Dunn's test for multiple comparisons revealed this difference to be between Kettlewell and Hubberholme at habitat

one (smooth water with trees both sides) only ($Q = 3.16, P < 005$), where slightly more insects were caught at Kettlewell than at Hubberholme. Habitat type was not significant (d.f. $= 2$, $P > 0.05$). There was no significant interaction factor for both months indicating that pattern of insect distribution at each habitat type at each elevation was the same.

Activity patterns of insects throughout the night in both May and August 2000 (**Figure 4**) were very similar. Insect activity reached a maximum either at sunset or just after sunset and dropped to low levels with frequent zero captures throughout the middle of the night. There was often a second insect peak just before sunrise until after sunrise. This pattern was consistently similar at all three elevations for both habitat types and confirmed the non-significant interaction factor in the Scheirer-Ray-Hare tests; i.e. the pattern of insect activity throughout the night was the same at all elevations.

Insects caught in August 2000 were mainly dipterans (consistently over 90%) at all elevations and all habitat types (**Table 2**), and most (92%) of the dipterans were nematocerans (**Table 3**). Apart from Nematocera, the next most abundant order at all elevations was Trichoptera. All other orders were rare at all elevations, and many (such as the coleopterans, lepidopterans, dermapterans and the neuropterans) were only represented by capture of one individual.

There were no great differences in numbers of different orders or suborders with either elevation or habitat type, with exception of trichopterans. Elevational difference in numbers were significant at the $P < 0.001$ level (Kruskal-Wallis, $H = 23.345$, d.f. $= 2$) and a *post hoc* Dunn's test for multiple comparisons revealed that significant differences lay between the low and the high elevation ($Q = 4.238$, $P < 0.05$) and between the low and the mid elevation ($Q = 4.131$, $P < 0.05$).*ca.* 76% of the total trichopterans caught were at the lowest elevation.

Bat detections

Bat species encountered during both months of sampling were: *M. daubentonii, n $= 10,424$ passes (max $=$ 540 passes hr^{-1}), P. pipistrellus, n $= 9,112$ passes (max $= 586$ passes hr^{-1}), P. pygmaeus, n$= 1,295$ passes (max $= 702$ passes hr^{-1}) and*Nyctalus* spp, $n = 326$ passes (max $= 143$ passes hr^{-1}). Numbers of both *P. pygmaeus* and*Nyctalus* spp. were too low for statistical analysis.

As can be seen in **Figure 5** , for both *M. daubentonii* and*P. pipistrellus* , there was a general trend for bat detections to decrease with elevation at both habitat types and months. Scheirer-Ray-Hare tests using elevation and habitat type as factors revealed that these altitudinal differences were significant for both species in May (d.f. $= 2$, $P < 0.01$ and $P< 0.02$ respectively) and August (d.f. $= 2$, $P< 0.0001$ for both species).

When data were pooled for both habitat types and compared between the two months, detections of *M. daubentonii* were higher in August 2000 than in May 2000 (Mann-Whitney rank sum test: $H = 87467.00, P < 0.001$). There was, however, no significant difference in detection of *P. pipistrellus* between the two months (Mann-Whitney rank sum test: $P < 0.491$).

Figure 6 and **Figure 7** show bat passes in the different habitats and elevations in May and August 2000 respectively. *M. daubentonii* never arrived at foraging sites before or at sunset with the exception of one recording in August 2000 (**Figure 7c**).*M. daubentonii* detections began to increase 30 minutes after sunset, and were highest one to one and a half hours after sunset at all three elevations in both months. Detections of *M. daubentonii*were fairly stable throughout the night with no pronounced peaks or troughs. During May 2000, bats were only detected until one hour before dawn with no detections after this point. This resulted in *P. pipistrellus* having 30 min longer for foraging than *M. daubentoniid* due to their earlier arrival time.

The most noticeable difference between nightly detection of *M. daubentonii* and *P. pipistrellus* during the two months was the more frequent decreases and variability in detection in August 2000 at both habitat types (**Figure 7**). In August at habitat one, neither bat species arrived at foraging sites at sunset (except at the lowest elevation), whereas in May, *P. pipistrellus* was always present at sunset. At 30 min after sunset,

both species were more active than at the same time in May 2000, and it is apparent that detections of *M. daubentonii* were greater at foraging sites 30 min earlier than in May for the same habitat type. Again, *M. daubentonii* detection was more constant than that of *P. pipistrellus* throughout the night, but in comparison with May 2000, peaks in detection were more marked for both species. As in May 2000, maximum detection for *M. daubentonii* was one hour after sunset and generally 30 min after sunset for *P. pipistrellus*.

At high elevation, detections of *P. pipistrellus* reached a pronounced peak one hour after sunset in both May and August 2000 then dropped off throughout the night (**Figure 6** and **Figure 7**). As in May 2000, *M. daubentonii* were detected at a more constant level throughout the night than *P. pipistrellus*. Both species were detected for 30 min to one hour longer than in May, foraging right up until dawn.

Feeding buzz ratios (FBRs)

In May at habitat one (**Figure 8a–c**.) and three (**Figure 8g–i**) the pattern of FBRs of *M. daubentonii* throughout the night was very similar. There were no pronounced peaks in feeding activity, and FBRs were similar at all elevations. For *P. pipistrellus* during the same month, at habitat one (**Figure 8d–f**) and habitat three (**Figure 8j–l**), there were often more pronounced peaks and troughs in feeding activity at each habitat type.

The pattern of FBRs throughout the night in August for *M. daubentonii* at habitat one and three (**Figure 9a–c**) was much the same as in May; however, again bats were feeding for *ca.* one hour longer than in May. There were no noticeable differences in FBRs between elevations. For *P. pipistrellus* during August 2000 at both habitat types (**Figure 9g–i**), the FBRs throughout the night were slightly more constant than in May, but with still the occasional peak after sunset and before dawn.

DISCUSSION

Temperature

It is unsurprising that temperature decreases with elevation since this is the case with the atmosphere in general according to the dry adiabatic lapse rate of 0.98degC/100 m (Rogers and Yau, 1989). The fall in temperature with elevation in Wharfedale was entirely consistent with this rate, even with the influence of other factors such as vegetation cover. Temperature variations operating along a shallow river gradient have important consequences for heterothermic bats, which are heavily influenced by temperature, not only physiologically (e.g., Russ *et al.* , 2003; Hope and Jones, 2012; Wolbert *et al.* , 2014), but also indirectly through effects on activity and abundance of their prey. For example, Todd and Waters (2017) found insect flight cut-off temperature was 4 degC and the average temperature difference between the Wharfedale upper and lower valley was between 1 and 1.5 degC. Furthermore, bats go into torpor when adverse conditions prevent feeding (Dietz and Kalko, 2006); therefore, bats at higher elevations may be forced to enter torpor during the night more often than those lower, resulting in reduced 'effective' foraging time, or simply if there are less insects, by going into torpor do not waste energy expenditure on an scant resource.

Insect diversity

Calculating insect biomass at each stage throughout the night was not possible because insect numbers dropped off rapidly after dusk. Even combining insect numbers into three- or four-hour categories did not produce enough insect mass to provide a meaningful value. For example, total dry mass of all insects combined for the month of August at habitat one at all elevations was 0.9 g. Most fatty substances dissolved in the alcohol solution, resulting in a loss of weight of the insects. Insect numbers are therefore presented here as a proxy for biomass. This is justifiable as most insects were of similar size classes (chironomids and ceratopogonids) at all elevations. Insect activity reached a maximum at or just after sunset with a second

occasional peak around sunrise and very low numbers throughout the middle of the night, similar to findings by Jackson (1988) and Peng et al. (1992).

Adult aquatic insects are most often found in the riparian vegetation adjacent to streams (Cole *et al.* , 2015; Dreyer *et al.* , 2015) and occur in decreasing numbers with increasing distance from streams (e.g., Griffeth *et al.* , 1998). Diversity of insects collected in this study was typical for streams and was representative of the type of prey targeted by *P. pipistrellus* and *M. daubentonii* (Beck, 1995; Todd and Waters, 2017). Nematoceran dipterans - Chironomidae and Ceratopogonidae - can comprise one third of the diet in *M. daubentonii* , another third being mainly trichopterans (Sullivan *et al.* , 1993; Flavin *et al.* , 2001; Nissen*et al.* , 2013; Vesterinen *et al.* , 2013; Vesterinen *et al.* , 2016). There were significantly more trichopterans at the low and mid elevations than higher in Wharfedale, likely related to habitat variables not investigated here, *e.g.* water quality, pH, dissolved oxygen, etc. (Grech *et al.* , 2019; Timm and Haldna, 2019).

Bat detection

In Wharfedale, the most common bats recorded over the water were*M. daubentonii* and *P. pipistrellus* . The results of this study and Warren*et al.* (1997) clearly showed that in Wharfedale, significantly higher detection (of both species) was recorded at lower elevations. Several authors have reported elevational differences in bat abundance (e.g., Grindal *et al.* , 1999; Dietz *et al.* , 2006) and differential use by males and females, with males tending to be found at higher elevations during the summer (Dietz *et al.* , 2006; Nardone*et al.* , 2015). Explanations for the high detection of bats further down the valley may be related to female reproductive state and roosting preferences (Lučan and Radil, 2010). Females are solely responsible for raising young; therefore, reproductive females are under a high energy demand and nightly energy expenditure can peak during lactation (Kurta*et al.* , 1989). Certainly during lactation months (late July/August), female *P. pipistrellus* return to the roost in the middle of the night, presumably to suckle their young, and then leave again for a second foraging flight before dawn (Swift, 1980; Lučan and Radil, 2010). Higher variability and more decreases in detection recorded in August as opposed to May are potential evidence that some bats are lactating in this study area.

In May, temperatures were significantly cooler and weather in general was more variable and windier than later in summer (Todd and Waters, 2017). It is possible that elevational differences in bat detections during this month were only observed in tree-lined habitat types because bats were attempting to gain some protection from stronger winds, which can reduce foraging efficiency (Rydell, 1989). In August, weather was warmer and less windy and trees may not have been as important for cover. Racey and Swift (1985) reported that at low elevation (100 m AMSL) in the early summer, pregnant *P. pipistrellus* foraged only where there were riparian trees and thick undergrowth. Kalko and Schnitzler (1993) also reported that, on windy evenings, *P. pipistrellus* prefer sites which are in the wind shadow of vertical structures such as forest edges.

The most striking difference between detections of *M. daubentonii* and*P. pipistrellus* was the arrival times at sites and how this differed between habitat types. *M. daubentonii* were the latest bats to arrive at foraging sites (usually 30 min later than *P. pipistrellus*). Individuals were never present at sunset except at tree-lined habitats at lower elevation in August. *P. pipistrellus* , on the other hand, always arrived at tree-lined foraging sites at sunset and 30 min later at treeless sites at all three elevations in both months. Dark, protective tree cover may allow earlier evening emergence of this species as refuge from crepuscular predators (see Jones and Rydell, 1994) and diurnal avian predators that have poor visual acuity in darkness (Mikula *et al.* , 2016). Earlier emergence may also provide access to more food, as peaks in insect abundance were recorded closer to sunset. Indeed Jenkins *et al.*(1998) found that *P. pipistrellus* emerged 11 min earlier from roosts with more tree cover potentially gaining as much as 10% of their daily energy requirements in this extra time. Gaisler *et al.*(1998) also reported activity of *P. pipistrellus* to be highest in the first 30 min of the first two hours after sunset. The delayed*M. daubentonii* arrival at foraging locations coincided with lower light levels. As a light-phobic species (Ciechanowski *et al.* , 2007), *M. daubentonii* may not be as dependent on trees for cover from aerial predators. *M. daubentonii* probably emerge later than*P. pipistrellus* as they are slower

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(Baagøe, 1987) which may contribute to a higher susceptibility to predation (Jones and Rydell, 1994; Lima and O'Keefe, 2013). At tree-lined and treeless habitats *M. daubentonii* detection reached a peak one to one and a half hours after sunset, consistent with the findings of other authors (e.g., Rieger, 1996; Gaisler *et al.* , 1998). *M. daubentonii* detection in May was generally constant throughout the night with no pronounced peaks or troughs. *P. pipistrellus* detections usually decreased after the post sunset peak (at a faster rate at the higher elevation), generally to a minimum in the middle of the night compliant with Swift (1980) and Gaisler *et al.* (1998) results. Detection level of this species was also generally lower in the middle of the night at mid and high elevations than that of *M. daubentonii* .

It may be that *P. pipistrellus* emerged from the roosts further up the valley and then dispersed to other areas to forage as soon as the insect density reached a level too low to support aerial hawking. This would explain the peak in detection after sunset and before dawn (Hayes, 1997). The pre-dawn detection peak is probably due to bats exploiting the pre-dawn insect peak before returning to the roosts, on the other hand, could remain in the foraging sites when aerial insect density was low because they can rely on non-volant insects by gaffing – switching to capturing prey from water surfaces as the availability of aerial prey declines (Todd and Waters, 2007). Jones and Rayner (1988) also suggested that capture of prey from the water surface may allow foraging to continue when aerial insects are scarce. This was implied by the more constant number of *M. daubentonii* passes recorded throughout the night than that of *P. pipistrellus* . *M. daubentonii* may take also advantage of slightly warmer temperatures <0.5 m above water surface due to irradiation or convection (Ciechanowski *et al.* , 2007).

In May, *M. daubentonii* returned to the roost one and a half hours before dawn, whereas *P. pipistrellus* foraged for up to an hour longer than *M. daubentonii* . In August, *M. daubentonii* were present in higher numbers 30 min after sunset and foraged right up until dawn, as did *P. pipistrellus* . This may be because at all three elevations, the highest insect abundance was available in the first two hours at the low elevation (93.31% of the nightly total). Rieger (1996) also reported that earlier in the season, *M. daubentonii* arrived at the foraging sites later than later in the season. It may also be that in August, bats may need to feed for longer to meet the energetic demands of lactation.

Levels of detection were more consistent in May relative to August. Detection of both species in August tended to either drop off slightly more after the initial peak, or fall to relatively lower levels in the middle of the night. This may be because in early August, female bats may be returning to the roost to suckle their young. This is certainly the case for *P. pipistrellus* (Swift, 1980; Davidson-Watts and Jones, 2006), and also occurs in *M. daubentonii* (Ruedi, 1993; Dietz *et al.* , 2009; Ruoss *et al.* , 2019).

Bat foraging

In Wharfedale in May, FBRs of *M. daubentonii* and insect abundance did not differ between the three elevations, but *P. pipistrellus* feeding activity decreased with increasing elevation at the tree-lined habitat only. This is consistent with the idea that *P. pipistrellus* probably rely on tree lines to gain some protection from wind ()(which is generally higher in May Todd and Waters, 2017) that can reduce foraging success (Rydell *et al.* , 1996).

P. pipistrellus feeding activity was reduced at higher elevations, but *M. daubentonii* feeding activity was similar at the high and low elevations. *M. daubentonii* mostly feed in a lower airspace than *P. pipistrellus* . The netting procedure in this study was aimed at capturing insects close to the water and not in the 2–3 m airspace above the water where *P. pipistrellus* mainly feed. Volant insects close to the water surface may gain protection from undercut banks (Myers and Resh, 2000) or the boundary layer effect, a discontinuity which can impede adhesion can be found at the interface between an adhesive [air] and substrate [water] (e.g. Taylor, 1974; Chaffin *et al.* , 2013). Finally, abundance of terrestrial and aerial insects collected on river banks and in the surface river drift (available to gaffing *M. daubentonii*) have been shown not to be related to the combination of riparian vegetation and elevation (Bridcut, 2000).

As predicted, variability in insect abundance and feeding activity was greater in May than in August and

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probably reflected the lower temperatures. For example, M. Myers (V. L. G. T. pers. comm.) reported that if the temperature drops below 10 degC then very few, if any, trichopterans are active. May (mean temperature = 10 degC) was on average 4 degC cooler than August (mean = 14 degC). Insect activity was shown to be reduced at lower temperatures, which in Wharfedale, differed by 0.5–1 degC between the highest and lowest elevation. Therefore, in May, slightly elevated temperatures at the lower elevation of Burnsall are unlikely to increase insect abundance (and corresponding bat feeding activity) to any large degree. In August, however, higher mean temperatures (although the $0.5 - 1$ degC difference in temperature between the elevations is the same as in May), may have a greater influence on insect growth and development. This may explain why there was a significant decrease between bat detection and insect abundance with elevation for this month.

More variable temperatures at higher elevation do not appear to affect *M. daubentonii* foraging behaviour to the same extent as that of *P. pipistrellus* . *M. daubentonii* again, are able to continue to feed by gaffing when *P. pipistrellus* either stop or move to other areas (Todd and Waters, 2007). Further down the river, feeding activity of both species was more similar.

There was no significant difference in the pattern of insect activity throughout the night at all three elevations. It was clear that at each elevation, peak insect abundance occurred either just before or just as the bats arrived at foraging sites, illustrating a mis-match between insect and bat-peak presence. At all elevations, aerial insect activity increased around dusk, decreasing sharply in the 30 min after sunset with an occasional secondary peak before sunrise. Wright *et al.*(2013) also reported the biomass of trichopterans to be higher in the beginning of the evening and lowest in the middle of the night.

As with general bat activity (bat passes), the feeding activity (FBR) of *M. daubentonii* was higher and more constant throughout the night than that of *P. pipistrellus* . Although feeding activity was constant in this study, this is not necessarily evidence of food intake. Anthony and Kunz (1977) and Kunz (1974) reported that over 60-80% of the total nightly intake occurred before midnight. FBR of *P. pipistrellus* , on the other hand, generally increased just after dusk, fell in the middle of the night and increased again before dawn emulating the aerial insect-activity patterns.

CONCLUSIONS

A mismatch between times of highest aerial insect presence and highest bat detections was evident. There was no correlation between bat foraging and number of aerial insects for *M. daubentonii* or *P. pipistrellus* . *P. pipistrellus* arrived *ca.* half an hour earlier at tree-lined habitats than tree-less habitats, likely taking advantage of protective tree cover to gain additional foraging time when insects are more abundant, indicating the value of tree-cover in riparian systems for bats. *M. daubentonii* , on the other hand, generally arrived later probably due to a combination of increased risk of predation and ability to take non-volant insects. Bat detections (and therefore presence) is clearly influenced by factors other than purely aerial prey availability, suggesting that both insects and sheltered foraging habitat are important. Detections of *M. daubentonii* were generally more constant throughout the night than those of *P. pipistrellus* , with no pronounced peaks or troughs. Other studies have also reported that bat activity is not always related to insects (Fuentes-Montemayor *et al.* , 2013; Wolbert *et al.* , 2014; de Oliveira *et al.* , 2015; Salvarina *et al.* , 2018) suggesting that a landscape approach that integrates insect abundance with safe foraging spaces is most appropriate.

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TABLES

Table 1: Post hoc Tukey's multiple comparison test (q) of Tinytalk temperature differences (day and night pooled) between the three elevations along the river Wharfe.

Comparison	Diff of Means	p	q	$P < 0.05$
Burnsall vs. Hubberholme	1.392	3	22.62	Yes
Burnsall vs. Kettlewell	1.107	3	17.983	Yes
Kettlewell vs. Hubberholme	0.285	3	5.042	Yes

Table 2: Percentage presence of insect orders at three elevations and two habitat types along the river Wharfe in August 2000. n = total number of insects caught in category. Figures in brackets represent actual numbers of that order caught in samples.

Elevation	Habitat type	n	Ephemeroptera	Trichoptera	Hemiptera	Coleoptera	Lepidoptera	Dermaptera
Hubberholme	1	321	-	1.2% (4)	1.2% (4)	0.3% (1)	-	0.3% (1)
Hubberholme	3	2,186	0.4% (8)	0.6% (14)	0.1% (3)	-	-	-
Kettlewell	1	600	0.3% (2)	1.5% (9)	0.5% (3)	-	-	-
Kettlewell	3	661	1.2% (8)	1.4% (9)	0.9% (6)	-	0.2% (1)	-
Burnsall	1	1,119	0.2% (2)	6.1% (68)	0.3% (3)	-	-	-
Burnsall	3	1,015	0.6% (6)	4.8% (49)	0.4% (4)	-	-	-

Table 3: Percentage presence of dipteran sub-orders at three elevations and two habitat types along the river Wharfe in August 2000. Figures in brackets represent actual numbers of that sub-order caught in samples.

Elevation	Habitat type	Nematocera	Brachycera	Cyclorrhapha
Hubberholme	1	76.1% (233)	23.5% (72)	0.3% (1)
Hubberholme	3	98.9% (2,136)	0.9% (20)	0.2% (4)
Kettlewell	1	95.2% (555)	3.4% (20)	1.4% (8)
Kettlewell	3	96.4% (612)	2.8% (18)	0.8% (5)
Burnsall	1	93.5% (975)	6.2% (65)	0.3% (3)
Burnsall	3	92.1% (872)	7.7% (73)	0.2% (2)

FIGURE LEGENDS

Figure 1: Map of study locations in Yorkshire Dales National Park (YNDP).

Figure 2: Schematic showing paired habitat structure of study locations at mid altitude of the river Wharfe, UK.

Figure 3: Boxplot of monthly pooled 24-hr Tinytalk logger temperatures along the river Wharfe in 2000 from low (Burnsall) to high (Hubberholme) elevations. Box represents interquartile range and horizontal line is median. Circles are potential outliers. Note: data for Burnsall in May 2000 are absent due to logger being stolen.

Figure 4: Boxplot of aerial insect numbers throughout the night from one hour before sunset till one hour after dawn at three elevations at habitat one (smooth water, trees both sides a-c and g-j) and habitat three (smooth water no trees d-f and j-l) categories. Sampling interval every $\frac{1}{2}$ hr for first $2\frac{1}{2}$ hrs and last $2\frac{1}{2}$ hrs with 1 hr interval in the middle of the night. Vertical solid lines represent sunset and sunrise respectively. Sunset/rise changes throughout the month are corrected for and standard times used for convenience. Note: three outliers are indicated by arrows and their value in parts b, c and j.

Figure 5: Boxplot of the numbers of bat passes present at the two different habitat types: habitat one, smooth water trees both sides and habitat three, smooth water no trees at three elevations. Data for May

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and August 2000

Figure 6: Boxplot of the May 2000 *M. daubentonii* and *P. pipistrellus* detection throughout the night from one hour before sunset until one hour after dawn at three elevations at the smooth water, trees both sides (habitat one a-f) and smooth water no trees (habitat three g-l) categories. Data pooled for six nights per elevation. Vertical solid lines represent sunset and sunrise respectively. Sunset/rise changes throughout the month are corrected for and standard sampling times on the x-axis used for convenience. Note: y-axis scales differ.

Figure 7: Boxplot of the August 2000 *M. daubentonii* and *P. pipistrellus* detection throughout the night from one hour before sunset until one hour after dawn at three elevations at the smooth water, trees both sides (habitat one a-f) and smooth water no trees (habitat three g-l) categories. Data pooled for six nights per elevation. Vertical solid lines represent sunset and sunrise respectively. Sunset/rise changes throughout the month are corrected for and standard sampling times on the x-axis used for convenience. Note: y-axis scales differ

Figure 8: Boxplot of the May 2000 *M. daubentonii* and *P. pipistrellus* Feeding Buzz Ratios (FBRs) throughhout the night from one hour before sunset till one hour after dawn at three elevations at the smooth water, trees both sides (habitat one a-f) and smooth water no trees (habitat three g-l) categories. Data pooled for six nights per elevation. Vertical solid lines represent sunset and sunrise respectively. Sunset/rise changes throughout the month are corrected for and standard sampling times on the x-axis used for convenience. Note: one outlier is indicated by the arrow in (l).

Figure 9: Boxplot of the August 2000 *M. daubentonii* and *P. pipistrellus* Feeding Buzz Ratios (FBRs) throughout the night from one hour before sunset till one hour after dawn at three elevations at the smooth water, trees both sides (habitat one a-f) and smooth water no trees (habitat three g-l) categories. Data pooled for six nights per elevation. Vertical solid lines represent sunset and sunrise respectively. Sunset/rise changes throughout the month are corrected for and standard sampling times on the x-axis used for convenience.

DATA ACCESSIBILITY

Data will be made available on Dryad if accepted.

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COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

Victoria Todd: data collection, and interpretation, manuscript preparation

Laura Williamson: manuscript preparation

Dean Waters: manuscript preparation

A) May 2000 habitat 1

B) May 2000 habitat 3

C) August 2000 habitat 1

D) August 2000 habitat 3