Foraging activity of bats in four different habitats within Paignton Zoo Environmental Park.

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Summary

1. A reduction in the quality and availability of foraging sites is thought to be one of the main causes of population decline for many British bat species. Developing a thorough understanding of habitat use by foraging bats at the local level is fundamental to the implementation of effective site management practices for supporting bat populations. Currently, there is little known about the foraging activity of bats in Paignton Zoo Environmental Park in Devon.

2. Foraging activity was investigated in four habitat types: deciduous woodland, wetland, semi-improved grassland and unimproved grassland. A bat detector and a point sampling method of data collection were used to compare total levels of foraging activity, species composition and diversity of foraging bats and temporal variation in both, within the first three hours after sunset.

3. Total foraging activity was significantly higher in the wetland and did not differ significantly between the three other habitats. This corresponded with the foraging activity of Pipistrellus pipistrellus which was the dominant species in this study.

4. Bat species diversity was highest in the deciduous woodland and wetland and only Pipistrellus pipistrellus was recorded in the two grassland habitats. Myotis species foraged in the deciduous woodland and wetland. Plecotus species
foraged only in the deciduous woodland and *Pipistrellus pygmaeus* foraged only in the wetland.

5. In the deciduous woodland, wetland and semi-improved grassland, the foraging activity of *Pipistrellus pipistrellus* peaked within the first 45 minutes after sunset. Levels of foraging activity in the wetland remained high at the end of the three hour sampling period.

6. *Synthesis and applications.* The results of this study indicate that the wetland is a key foraging site, particularly for *Pipistrellus pipistrellus* and as such, its maintenance and enhancement should be a conservation priority. Further research is required in order to draw firm conclusions on the relative importance of the deciduous woodland and the species composition and diversity of foraging bats in both of these habitats.

*Key-words:* conservation, feeding, temporal variation, *Pipistrellus, Myotis, Plecotus,* biodiversity, wetland

**Introduction**

As insectivores, British bats play an important ecological role (Altringham 2003). Due to their reliance on a wide variety of habitats and their relatively high sensitivity to habitat degradation, they are considered to be valuable indicators of the health of the countryside (Bat Conservation Trust 2008).

There is strong evidence that the population sizes of many British bat species have declined dramatically in the last 100 years (Harris *et.al.* 1995; Walsh & Harris 1996a). In response to this, the UK Biodiversity Action Plan (2007) now lists seven of the 16 bat species native to Britain as priority species. All bats and their roosts are
protected by UK legislation (Wildlife and Countryside Act, 1981; Conservation (Natural Habitats, &c.) Regulations, 1994). Foraging habitats, however, are rarely protected (Glendell & Vaughan 2002). A reduction in the quality and availability of foraging sites is thought to be one of the main causes of population decline for many bat species (Walsh, Harris & Hutson 1995; Bat Conservation Trust 2008). The key elements of this are believed to be the loss or modification of natural and semi-natural habitats, due to agricultural intensification and urbanisation (Altringham 2003; Wickramasinghe et.al. 2003).

Landscape modification has lead to habitat fragmentation, restricting the ability of bats to utilize valuable foraging sites, within range of the roost (Harris et.al. 1995; Walsh & Harris 1995; Verboom & Huitema 1997). A reduction in the number and connectivity of hedgerows and tree lines (Entwistle et.al. 2001; Devon Biodiversity Partnership 2005) limits the range of available foraging sites even further for most bat species, which are reluctant to cross open spaces. These linear features are known to serve as important sheltered commuting routes between roosting and foraging sites and as additional foraging sites themselves (Verboom & Huitema 1997; Verboom & Spoelstra 1999). The remaining natural and semi-natural areas may represent ‘islands’ of favourable habitat that are critical in sustaining local bat populations (Glendell & Vaughan 2002).

Studies of bat foraging activity have identified deciduous woodland and habitats associated with water as those most frequently selected by foraging bats (Racey & Swift 1985; Walsh Harris & Hutson 1995; Vaughan, Jones & Harris 1997a; Russ & Montgomery 2002; Smith & Racey 2008). The distribution of both of these habitat types has declined dramatically in recent years (Harris et.al. 1995; Entwistle et.al. 2001)

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The critical importance of fresh water habitats for bats is well documented (Racey 1998). *Myotis daubentonii* and *Pipistrellus pygmaeus* in particular are believed to be heavily reliant on riparian habitats and are highly faithful to specific foraging sites (Davidson-Watts, Walls & Jones 2006; Davidson-Watts & Jones 2006; Kapfer *et.al.* 2008; Akasaka, Nakano & Nakamura 2009). The preservation and improvement of these habitats should be central to bat conservation (Vaughan, Jones & Harris 1996; Vaughan, Jones & Harris 1997a; Racey 1998; Russ & Montgomery 2002).

Although research into the foraging activity of bats has increased in recent years, there is still limited information on the distribution and foraging habitat requirements of individual bat species (Harris *et.al.* 1995; Altringham 2003, Richardson 2000). The common pipistrelle, which is the most widespread bat in Europe, has recently been discovered to represent two cryptic species; now identified as *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* (Barrat *et.al.* 1997). Subsequent research has revealed that the two species have clear differences in their selection of foraging sites, indicating distinct conservation needs (Davidson-Watts, Walls & Jones 2006). There is also a paucity of information on the distribution and foraging habitat requirements of bats in the *Myotis* and *Plecotus* genera, due to the difficulties in detecting and differentiating between these species (Harris *et.al.* 1995; Walsh, Harris & Hutson 1995; Russ 1999; Richardson 2000; Altringham 2003).

It is important that further information is obtained so that the status and conservation requirements of bats on a national level can be fully understood. Additionally, developing a thorough understanding of the use of habitats by foraging bats on a local scale is vital so that key foraging sites can be identified and protected. This should include gathering information on the foraging activity of individual species so that site management plans can be developed that are species specific and effective.

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in maintaining and enhancing the suitability of these foraging sites for bats (Bat Conservation Trust 2008).

There is currently little known about the intensity or distribution of foraging activity within Paignton Zoo Environmental Park in Devon. The purpose of this study was to gather baseline data on the foraging activity of bats within this site and to identify priorities for further research. Specifically, foraging activity was investigated in four different habitat types, to compare total levels of foraging activity, the species composition and diversity of foraging bats and temporal variation in both, within the first three hours after sunset.

Method

STUDY SITE

Paignton Zoo Environmental Park is managed by the Whitley Wildlife Conservation Trust and is located within Torbay in South Devon (SX878595), considered to be a prime biodiversity area (Devon Biodiversity Partnership 2005). The site is a mosaic landscape of deciduous woodland, botanical gardens, scrub, grassland, artificial water bodies, buildings, concrete paths, disused limestone quarries and caves, providing a wide variety of potential foraging and roosting opportunities for bats.

Summer roosting sites in Devon have been confirmed for 13 of the 16 bat species native to Britain, however records are still limited (Richardson 2000). The following species/genera were detected in Paignton Zoo during the study: *Eptesicus serotinus*, *Nyctalus noctula*, *Rhinolophus ferrumequinum*, *Rhinolophus hipposideros* (commuting passes only); *Barbastella barbastellus* (one single commuting pass in
the woodland); *Pipistrellus pipistrellus, Pipistrellus pygmaeus, Myotis species,* *Plecotus* species (commuting and foraging passes).

Four habitat types were investigated in this study: deciduous woodland, wetland, semi-improved grassland and unimproved grassland (fig.1).

**Deciduous woodland:** This area is situated within a steep limestone valley and is composed of semi-natural ancient woodland and hazel *Corylus avellana* coppice with standards (Torbay Biodiversity Steering Group 2006). The dominant tree species within the study area are ash *Fraxinus excelsior*, beech *Fagus sylvatica*, oak *Quercus sp.*, field maple *Acer campestre* and elm *Ulmus sp.* These include a number of veteran trees with a high potential for bat roosts. Due to the large size of the woodland it was only possible to survey a small proportion of the habitat. Sampling took place on a clear-cut, circular nature trail at the north-western end of the valley.

**Wetland:** This habitat consists of an artificially constructed lake and two outdoor ape enclosures, bordered by a series of moats. These are supplied by an ephemeral stream that runs southward through the zoo and then through the woodland valley. The area is part of a botanical garden with a high diversity of predominantly native and some exotic plant species. Almost all areas are bordered by mature trees and sub-canopy vegetation, of which the most common species are willow *Salix sp.* and alder *Alnus glutinosa*. The sub-canopy and ground level vegetation increase in density around the ape enclosures, which are adjacent to the woodland, creating a sheltered environment with a diverse structure.

**Semi-improved grassland:** The selected area consists of the zebra, leckwe and anoa enclosures, all of which are grazed regularly. Some areas are bordered by tree
lines and hedgerows. It was not possible to gain access to these enclosures so instead sampling took place on adjacent concrete paths, with the detector pointed towards the grassland.

**Unimproved grassland:** The fourth habitat was an area of unimproved calcareous grassland, bordered predominantly by immature trees and encroaching scrub. Typical plant species at this site include wild marjoram *Origanum vulgare*, spurge laurel *Daphne laureola*, bugle *Ajuga reptans*, autumn ladies tresses *Spiranthes spiralis*, autumn squill *Scilla autumnalis* and carline thistle *Carlina vulgaris*. Recent surveys have recorded an extremely high abundance and diversity of invertebrates, most notably *Lepidopteran* species. The site is situated on top of a limestone plateau, at the highest altitude in the zoo and is frequently exposed to strong winds.

**DATA COLLECTION**

Bat activity was sampled using a Batbox Duet detector (Batbox Ltd. West Sussex, England), which has a frequency division facility to ensure that the full frequency range for all British bat species is sampled. When an echolocation call was heard, the detector was pointed towards the bat to gain the clearest signal. Simultaneous recordings were made using an EDIROL R-09 recorder (Roland Corporation, UK), connected to the detector in stereo mode, for later analysis. Field observations and information obtained from the detector’s heterodyne function were also noted to aid species identification.

A point sampling method was used instead of a walked transect, for ease of recording and to reduce the likelihood of a sampling bias due to varying levels of bat activity and patchy terrain (Russ & Montgomery 2002). Within each of the four habitats, five sample areas were chosen randomly and marked on a map. These
were spaced a minimum of fifty meters apart to prevent an overlap in the bat detector range for most species. Due to the large number of inaccessible areas in the zoo, each actual sample point was then selected as the closest accessible point to the marking on the map (Wickramasinghe et al. 2003). In the two grassland habitats, the selected sample points were in close proximity to linear features, as bats were likely to avoid open spaces (Verboom & Huitema 1997; fig.1).

Fig. 1. Aerial photograph of Paignton Zoo Environmental Park, displaying the sample points within the 4 habitats: deciduous woodland (points 1,2,3,4 and 5), wetlands (points 6,7,8,9 and 10), semi-improved grasslands (points 11,12,13,14 and 15), unimproved grassland (points 16,17,18,19 and 20).

20 nights of data were collected between the 4th of June and the 28th of July. By this period, all species are believed to have made the transition between hibernacula and

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summer roosts (Altringham 2003). Sampling took place between 0-180 minutes after sunset (Hayes 2000) and one five minute recording was made at each sample point, each night. Errors introduced through sampling over 20 nights were likely to be low because variation in bat activity is considered to be greater within a night than between nights (Hayes 2000). As a precaution, a balanced rota was designed so that no habitat was sampled at the same time on two consecutive nights and within each habitat, the order in which the points were sampled was also rotated. This provided a total of 100 minutes of recordings, evenly spaced across the three hour sampling period, at each sample point, for the analysis.

Sampling did not take place on nights with precipitation or lightning because these conditions are known to reduce bat activity (Grindal et.al. 1992) and heavy rain would have damaged the sensitive equipment. Temperature readings were taken every 30 minutes and the survey was abandoned if the temperature dropped below 10°C because insects become less active below this temperature (Rydell, Entwistle & Racey. 1996; Wickramasinghe et.al. 2003). Due to the short time scale of this study and the location of the zoo, it was not possible to avoid sampling on nights with high wind speeds.

SPECIES IDENTIFICATION

The recorded echolocation calls were analysed using computer software (BatSound v.3.3, Pettersson Elektronik AB, Uppsala, Sweden), which transforms the sound into spectrograms, oscillograms and power spectra. All spectrograms were set to a 256 fast fourier transform with a Hanning window to ensure that the analysis was consistent.
Species identifications were made based on a combination of quantitative call parameters (frequency of maximum energy, minimum frequency, pulse duration inter-pulse interval) and qualitative information (pulse curvature and slope on the spectrogram, tonal quality and observations made in the field). These were interpreted with reference to Vaughan, Jones & Harris (1997b) and Russ (1999). An attempt at species identification was not made on any echolocation sequence of less than three pulses (Betts 1998) or on calls of low amplitude (Russ 1999).

There is considerable overlap between the echolocation call parameters for many British bat species (Parsons & Jones 2000). Echolocation calls can also vary intraspecifically, between different habitats, due to the influence of acoustic clutter and foraging strategy (Webster & Michael 1960; Arlettaz, Jones & Racey 2001; Jones & Holderied 2007). Consequently it was not possible to consistently distinguish all species by frequency division recordings of their echolocation calls alone (Vaughan, Jones & Harris 1996). The calls made by Myotis species and Plecotus species were identified to genus level only. Pipistrellus calls with a frequency of maximum energy greater than 42kHz but less than 49kHz were classified as *P.pipistrellus* and those greater than 52kHz as *P.pygmaeus*. A small proportion of bats produced echolocation calls with a frequency of maximum energy equal to or between 49 and 52 kHz. These were classified as unidentified *Pipistrellus sp.* (Vaughan, Jones & Harris 1997b, table 1). *Nyctalus noctula* (noctule), *Eptesicus serotinus* (serotine), *Barbastella barbastellus* (barbastelle), *Rhinolophus ferrumequinum* (greater horseshoe) and *Rhinolophus hipposideros* (lesser horseshoe) were identified to species level.
Table 1. Taxonomic groupings used and the identification criteria.

<table>
<thead>
<tr>
<th>Species/ genus name</th>
<th>Criteria/ species represented</th>
<th>Common names</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myotis sp.</td>
<td><em>Myotis daubentonii</em></td>
<td>Daubentons's bat</td>
</tr>
<tr>
<td></td>
<td><em>Myotis nattereri</em></td>
<td>Natterer's bat</td>
</tr>
<tr>
<td></td>
<td><em>Myotis mystacinus</em></td>
<td>Whiskered bat</td>
</tr>
<tr>
<td></td>
<td><em>Myotis bechsteinii</em></td>
<td>Bechstein's bat</td>
</tr>
<tr>
<td></td>
<td><em>Myotis brandtii</em></td>
<td>Brandt's bat</td>
</tr>
<tr>
<td>Plecotus sp.</td>
<td><em>Plecotus auritus</em></td>
<td>Brown long-eared bat *</td>
</tr>
<tr>
<td></td>
<td><em>Plecotus austriacus</em></td>
<td>Grey long-eared bat</td>
</tr>
<tr>
<td>Pipistrellus pipistrellus</td>
<td>Pipistrellus calls:</td>
<td>Common pipistrelle</td>
</tr>
<tr>
<td></td>
<td>42kHz &lt; FmaxE &lt; 49kHz</td>
<td></td>
</tr>
<tr>
<td>Pipistrellus pygmaeus</td>
<td>Pipistrellus calls:</td>
<td>Soprano pipistrelle</td>
</tr>
<tr>
<td></td>
<td>52kHz &lt; FmaxE</td>
<td></td>
</tr>
<tr>
<td>Pipistrellus sp.</td>
<td>Pipistrellus calls:</td>
<td>Unidentified pipistrelle</td>
</tr>
<tr>
<td></td>
<td>49kHz ≤ FmaxE ≤ 52kHz</td>
<td></td>
</tr>
</tbody>
</table>

*In this study area, *P. auritus* is believed to be more common than *P. austriacus* (Richardson 2000).

ANALYSIS

Only foraging activity was investigated in this study and so recordings of commuting passes were not included in the analysis. Bats were categorized as foraging based on field observations of their flight pattern and behaviour (taking into account interspecific differences) and analysis of echolocation call pattern and pulse structure (appendix 1). On the rare occasions when the activity could not be confidently identified, the recording was not included in the analysis.

Total foraging activity was quantified by dividing the recordings into 15 second intervals and counting the number of intervals in which foraging bats were present. It is not possible to quantify bat abundance by acoustic methods and so this measure provided an estimate of relative use of the habitat by foraging bats, rather than relative abundance (Hayes 2000). When a bat detects and approaches an insect...
target, the repetition rate of its echolocation pulses increases and a distinctive
terminal feeding buzz is produced (Griffin, Webster & Michael 1960). The number of
feeding buzzes detected was used as a relative measure of feeding activity (Griffin,
Webster & Michael 1960; Vaughan, Jones & Harris 1996). A buzz ratio (number of
feeding buzzes / number of 15 second intervals with foraging bats present) was
calculated and used as an indicator of foraging effort (Vaughan, Jones & Harris
1996).

The foraging activity of each individual species was also quantified using the same
15 second interval count method. These counts were made separately so as to
prevent any influence of species diversity on the results for total bat activity. Feeding
buzz counts could not be species specific and so were not used to measure species
composition and diversity.

STATISTICS

The data in this study were not normally distributed and so non-parametric statistical
methods were applied, using SPSS version 17.0 (SPSS Inc. Chicago, Illinois).
Kruskal-Wallis tests were carried out to identify significant differences in bat
presence, number of feeding buzzes and buzz ratios between the four habitats.
Mann-Whitney tests were used to make individual comparisons between habitats
and Bonferroni adjustments were employed for multiple tests of the same variable.
Species diversity was measured using the Shannon-Weiner Diversity Index. The
unidentified ‘Pipistrellus sp.’ records were not included in the species diversity
calculations because this category did not represent a separate species or genera.
Results

FORAGING ACTIVITY

There was a significant difference in how intensively each habitat was used by foraging bats, with the wetland habitat selected above all others ($H=12.281$, df=3, $p<0.01$, fig. 2). The number of feeding buzzes was also significantly higher in the wetland ($H=11.469$, df=3, $p<0.01$, fig. 3). No significant difference was found between the deciduous woodland, semi-improved grassland and unimproved grassland for either feeding buzzes or intensive use (Mann-Whitney, $p>0.05$).

\[ \text{Fig. 2. Mean levels of relative habitat use by foraging bats. Each bar represents the mean number of 15 second intervals in which foraging bats were present over 100 minutes (out of a possible total of 400). Error bars represent the S.E. mean for the five sample points in each habitat.} \]

\[ \text{Fig. 3. Mean number of feeding buzzes recorded in each habitat over 100 minutes. Error bars represent S.E. mean for the five sample points in each habitat.} \]

In the wetlands, 50.6% of the 15 second intervals with bats present contained more than one bat (table 2). More than one bat was present in 16.5% of intervals in the
semi-improved grassland. In the deciduous woodland and unimproved grassland, the proportions were relatively low at 5.5% and 4.8% respectively.

Table 2. The proportion of 15 second intervals with foraging bats present, that contained more than one bat.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Proportion (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous woodland</td>
<td>5.5</td>
</tr>
<tr>
<td>Wetlands</td>
<td>50.6</td>
</tr>
<tr>
<td>Semi-improved grasslands</td>
<td>16.5</td>
</tr>
<tr>
<td>Unimproved grasslands</td>
<td>4.8</td>
</tr>
</tbody>
</table>

No significant difference was found between the buzz ratios for the deciduous woodland, semi-improved grassland and unimproved grassland (Mann-Whitney, p>0.05). The buzz ratio in the wetlands however, was significantly higher (H=9.971, df=3, p<0.05, fig. 4).

Fig. 4. Mean buzz ratio for each habitat (number of feeding buzzes/ number of 15 second intervals with foraging bats present). Low scores indicate a higher foraging effort. Error bars represent S.E. mean for the five sample points in each habitat.

Fig. 5. Total levels of relative habitat use for each species. Each bar represents the total number of 15 second intervals in which foraging bats were present, for the entire study (out of a possible total of 2000 intervals). Data labels above bars show the species diversity index for each habitat (H).
SPECIES COMPOSITION AND DIVERSITY

Species composition and diversity varied between habitats (fig. 5). *P.pipistrellus* was the most common species foraging in the deciduous woodland and wetland, and the only species detected in the semi-improved and unimproved grasslands. *Myotis* species foraged in both the deciduous woodland and wetland, *P.pygmaeus* foraged only in the wetland and *Plecotus* species were recorded foraging only in the deciduous woodland. Species diversity was highest in the deciduous woodland *(H=0.9)* and was slightly lower in the wetland *(H=0.84)* due to the dominance of *P.pipistrellus*. Unidentified *Pipistrellus* calls were only recorded in the deciduous woodland and wetland. In these habitats the levels of acoustic clutter were higher, causing pipistrelles to modulate their echolocation calls, thus making species identification more difficult.

*P.pipistrellus*, significantly selected the wetland habitat *(H=9.970, df=3, p<0.05, fig. 5)* and showed no significant difference in use of the other three habitats (Mann-Whitney, *p>0.05*). The high levels of foraging activity in the wetlands were also influenced, to a lesser extent, by the activity of the *Myotis* species. This taxonomic group significantly selected wetland over deciduous woodland *(U= 2, z= -2.193, p<0.05, fig. 5)*.

TEMPORAL VARIATION

**Total foraging activity:** Foraging activity in the deciduous woodland peaked within the first 30 minutes after sunset and then gradually declined over the three hour sampling period (Fig. 6a). In the semi-improved grassland, foraging activity peaked between 30-45 minutes after sunset and then declined more rapidly (fig. 6c). Very little foraging activity was
observed in this habitat beyond 90 minutes after sunset. A similar early peak in the number of feeding buzzes was observed in the wetland from 30 minutes after sunset (fig 6b). No corresponding peak in time interval counts was found in this habitat. Foraging activity in the wetlands remained high at the end of the three hour sampling
period. In the unimproved grassland, foraging activity remained low throughout the three hours and no clear pattern in temporal variation could be identified (fig. 6d).

**Individual species:** In the deciduous woodland, semi-improved grassland and unimproved grassland, *P.pipistrellus* foraged most intensively within the first 60 minutes after sunset and was the only species to show this pattern (fig. 7). *Myotis* species began foraging from 18 minutes after sunset onwards and levels of foraging activity remained relatively constant throughout the three hour period. *P.pygmaeus* was recorded foraging from 72 minutes after sunset onwards and *Plecotus* species were recorded foraging from 81 minutes after sunset onwards.

Fig. 7. Changes in relative habitat use over time for each species. Each coloured square represents the mean number of 15 second intervals in which foraging bats were present in a five minute recording (out of a possible total of 20 intervals). Means were calculated from all of the five sample points in each of the habitats in which the species was present.
Discussion

TOTAL FORAGING ACTIVITY

The results of this study indicate that foraging activity is considerably higher in the wetlands, in comparison with the deciduous woodland, semi-improved grassland and unimproved grassland. It is not possible to draw firm conclusions as to the quality of a foraging site, based solely on the levels of bat activity (Hayes 2000). However, assuming that bats exhibit optimal foraging behaviour (Barnard 2004), by selecting habitats where the foraging efficiency is highest, it is likely that the high levels of foraging activity can be attributed to a higher abundance of insect prey (Hayes 2000).

Many studies have demonstrated a positive correlation between bat activity levels and insect abundance (Racey & Swift 1985; Rautenbach, Fenton & Whiting 1996; Hayes 1997; Verboom & Spoelstra 1999; Wickramasinghe et al. 2004). Freshwater habitats are known to have high insect densities since many species have aquatic larval stages (Vaughan, Jones & Harris 1996; Akasaka, Nakano & Nakamura 2009). The presence of bank-side vegetation with a high botanical and structural diversity in the wetland site is also likely to be associated with a high insect abundance and diversity (Warren et al. 2000; Haddad et al. 2001). This relationship is thought to be the main reason why bat foraging activity is generally found to be higher in freshwater habitats bordered by trees and low level vegetation (Warren et al. 2000; Ciechanowski 2002; Russ & Montgomery 2002). Additionally, bordering trees provide bats with shelter from wind and predation (Verboom & Spoelstra 1999) and are believed to aid them in navigation (Jones & Holderied 2007). The maintenance and enhancement of these features, along with water quality, is likely to be a key
factor in maintaining the high levels of foraging activity at this site (Vaughan, Jones & Harris 1996; Warren et al. 2000).

A lower botanical diversity and corresponding insect diversity is likely to have reduced the profitability of the semi-improved grasslands as a foraging site (Haddad et al. 2001; Wickramasinghe et al. 2004). When foraging, most bat species avoid open areas, in favour of vertical landscape elements, where insect densities are generally higher (Lewis & Dibley 1970; Verboom & Spoelstra 1999; Russ & Montgomery 2002).

In the unimproved grasslands, biodiversity is known to be high for both plants and insects, however it is not known whether the insect species present are those favoured by foraging bats. Many studies have provided evidence that this habitat type, originally thought to be highly suitable for many bat species, is actually avoided (Racey & Swift 1985; Walsh & Harris 1996a,b; Russ & Montgomery 2002). The main reason for this is thought to be lack of shelter, particularly at elevated sites (Walsh & Harris 1996a; Russ & Montgomery 2002). Strong winds are also known to have a negative effect on bat activity; impairing echolocation, thermoregulation and flight (Verboom & Spoelstra 1999). Activity in the unimproved grassland area investigated during this study was highly concentrated around one sample point (appendix 2). This area appeared to be considerably more sheltered from the wind, however further study on the effect of wind speed in this habitat would be required to confirm this relationship.

Despite a comparatively high number of bat species in the deciduous woodland, foraging levels were low. Structurally diverse woodland habitats are often associated with a high abundance and diversity of bats due to a larger food supply and range of
foraging conditions (Grindal & Brigham 1999; Patriquin & Barclay 2003; Hein, Castleberry & Miller 2009). However, in this site the steep sides of the valley, open path and coppice areas all create gaps in the canopy which may act as a deterrent to many bat species which forage preferentially in mature, closed canopy areas (Ford et al. 2005; Russo, Cistrone & Jones 2007). When the degree of canopy closure above is low, areas of dense sub-canopy coppice re-growth, with a high degree of structural clutter, are often avoided by bats, even when potential insect availability is high. In these conditions, constraints on flight and echolocation ability are believed to make foraging a more energetically costly exercise (Brigham et al. 1997; Adams, Law & French 2009). An additional possibility is that bats are foraging less in the deciduous woodland because the adjacent wetland habitat offers a more profitable foraging area.

When interpreting results it is important to take into consideration the limitations of acoustic methods for estimating bat activity (Hayes 2000; Gannon, Sherwin & Haymond 2003). As it is not possible to quantify bat abundance using a bat detector (Hayes 2000), the estimates of habitat use were based on the assumption that only one bat was present at a time. As shown in table 2, the proportion of time intervals with more than one present was a great deal higher in the wetlands and consequently, the results for relative use of this habitat were a considerable underestimate. Relative levels of habitat use in the semi-improved grassland were also underestimated, however it should be noted that no more than two bats were ever observed foraging at the same time here, whereas in the wetlands there were frequently more than three.

The high buzz ratio in the wetland habitat could suggest that the effort required for prey capture here was low in relation to the other habitats. However, this result...
should be interpreted with caution. As large numbers of bats were present in this habitat, it is likely that a high buzz ratio would relate more to bat abundance than to foraging effort. Furthermore, there is a possibility that in this busy foraging site, foraging effort was sometimes higher due to competition with other bats. No significant difference in the buzz ratios for the deciduous woodland, semi-improved grassland and unimproved grassland could indicate that foraging effort in these habitats was similar and this may relate a similar abundance of suitable prey species (Vaughan, Jones & Harris 1996). However, due to the previously stated reasons, the actual buzz ratio in the semi-improved grasslands is likely to have been slightly lower.

Most studies of habitat use consider a two dimensional distribution of bat activity (Gannon, Sherwin & Haymond 2003). However, Adams, Law and French (2009) found that foraging activity in woodland can be grossly underestimated when acoustic sampling takes place at ground level only. Additionally, radio-tracking studies often reveal large areas of deciduous woodland to be much more intensively used than indicated by acoustic studies. This is thought to be due to an effect of concentration, whereby bats have more freedom to forage over a wider area, rather than their activity being concentrated within range of the bat detector (Celuch & Zahn 2008). This could have implications for the present study, given the large size of the woodland in relation to the other habitats. Furthermore, given the small proportion of the deciduous woodland surveyed and the fact that foraging activity can vary dramatically within a woodland area (Gannon, Sherwin & Haymond 2003; Ford et.al. 2005), it can not be assumed that the results were representative of the rest of the woodland valley. A more detailed survey of the deciduous woodland, encompassing
a wider area, could provide more conclusive information on the level of and degree of variation in foraging activity in this habitat.

The full area of the unimproved grassland was sampled thus the results of this study are likely to be representative of the habitat during that time period. In the semi-improved grassland, the far end of the enclosures could not be surveyed, although given the relatively homogenous structure of this habitat and the fact that bats were rarely observed foraging out of range of the detector, it is unlikely that the activity was underestimated to a significant degree. In the wetlands, the five sample points were distributed across the majority of the habitat, however there was a great deal of variation in the levels of foraging activity at each sample point (appendix 2). It could be of benefit to survey this habitat in more detail to identify the main habitat characteristics that are influencing foraging activity.

SPECIES COMPOSITION AND DIVERSITY

The correlation between *P. pipistrellus* activity and total foraging activity (all species combined) indicates that this was the species responsible for the pattern of differential habitat use recorded in this study. Additionally, the extremely high levels of *P. pipistrellus* activity recorded in the wetlands, in relation to the other species present, suggests that total foraging activity in this habitat was mainly due to the foraging preference of one species, rather than to a high species diversity.

*P. pipistrellus* is known to be a generalist forager (Russ & Montgomery 2002; Davidson-Watts, Walls & Jones 2006), with a wing morphology and echolocation call structure both well adapted to foraging in a wide range of habitats (Altringham 2003; Jones & Holderied 2007). The distribution of foraging activity demonstrates that the species is well suited to the heterogenous landscape of the zoo and can take
advantage of insect abundances in most areas. Previous studies have shown a preference of *P. pipistrellus* for deciduous woodland edge and freshwater habitats (Racey & Swift 1985; Walsh & Harris 1996a; Kanuch *et al.* 2008). Considering that the zoo wetlands are adjacent to the deciduous woodland, this area may be a highly suitable foraging site.

The activity of the other species/ species groups corresponds with the majority of literature on their foraging behaviour. *Myotis* species usually select woodland and riparian habitats (Altringham 2003; Wickramasinghe *et al.* 2003; Kanuch *et al.* 2008; Smith & Racey 2008), *Plecotus* species forage most frequently in woodland (Altringham 2003) and *P. pygmaeus* has a clear preference for riparian habitats (Russ & Montgomery 2002; Davidson-Watts, Walls & Jones 2006; Davidson-Watts & Jones 2006). In this case, it could be suggested that species diversity is mainly influenced by the foraging preferences of each individual species, although insect densities almost certainly play a part.

Whilst this study provides an indication of the species diversity within the 4 habitats, a distinction between the deciduous woodland and wetland cannot be made without identification of the individual *Myotis* and *Plecotus* species. Collectively, the *Myotis* species foraged more in the wetland, however whether this result was due to a larger number of species or an individual species preference is unclear. One possible explanation is that *M. daubentonii* was regularly observed foraging in the wetlands. This species can be confidently identified in the field as the only bat to forage within one meter of the water surface (Russ 1999; Altringham 2003). The presence or absence of *M. daubentonii* in the woodland could not be confirmed, however this species is known to forage predominantly over water (Akasaka, Nakano & Nakamura 2009) and to be the dominant *Myotis* species in many studies of riparian habitats.
(Warren et al. 2000; Ciechanowski 2002). Mist netting and harp trapping studies in the deciduous woodland and wetland could provide confirmation of the species present in these habitats.

In deciduous woodland, species number has been found to be positively related to area (de Jong 1995). Throughout the research, Rhinolophus hipposideros was occasionally observed commuting from a known roost, through the woodland sampling area and into further areas of the woodland valley. A single commuting pass was also recorded in the same area from Barbastella barbastellus at 30 minutes after sunset. Given that both species are known to forage preferentially in deciduous woodland (Sierro 1999; Bontadina, Schofield & Naef-Daenzer 2006) and that Rhinolophus hipposideros rarely forages more than 1km from the roost (Altringham 2003), there is a strong possibility that they are utilising areas of woodland not covered by this study. This further supports the need for a more extensive survey of the deciduous woodland.

It should be noted that the ability to detect different bat species is not uniform (Hayes 2000). Due to the high amplitude calls produced by Eptesicus serotinus and Nyctalus noctula (Russ 1999), it can be confidently assumed that these species were not foraging within the zoo. In contrast, Plecotus species produce echolocation calls of low amplitude and occasionally forage in silence (Russ 1999; Hayes 2000). Consequently the foraging activity of these bats was almost certainly underestimated.

It must also be considered that species composition and diversity within the zoo as a whole is influenced not only by habitat suitability but by the proximity of roosting sites (Hayes 2000; Gannon, Sherwin & Haymond 2003). P.pygmaeus was recorded in low
numbers and foraged considerably later than the average emergence times documented for this species (Jones & Rydell 1994; Davison-Watts & Jones 2006). As *P.pygmaeus* is not thought to be adversely affected by interspecific competition, especially when prey densities are high (Racey & Swift 1985; Altringham 2003) and is known to travel longer distances than *P.pipistrellus* to specific foraging sites (Davidson-Watts & Jones 2006), the most likely explanation is that it is not roosting nearby.

**TEMPORAL VARIATION**

Foraging activity in the wetland, deciduous woodland and semi-improved grassland peaked soon after sunset and this was mainly due to the activity of *P.pipistrellus*. No corresponding peak was recorded for time interval counts in the wetlands, however this is likely to be due to the limitations in assessing bat abundance which were discussed earlier. These results correspond with previous studies of temporal variation in bat activity (Kunz 1973; Jones & Rydell 1994; Rydell, Entwistle & Racey 1996; Hayes 1997; Duverge *et al.* 2000; Lee & McCracken 2004).

Most small aerial insect species, particularly *Diptera*, show a peak abundance at around dusk and this is the most likely explanation for the early peak in *P.pipistrellus* activity (Rydell, Entwistle & Racey 1996, Hayes 1997). Although no peak in foraging activity was observed for the *Myotis* group, it should be noted that foraging activity began considerably earlier than the documented average emergence times for these species (Jones & Rydell 1994). As many *Myotis* species also forage on small aerial insects, it stands to reason that some individuals are also taking advantage of the early peak in prey abundance (Rydell, Entwistle & Racey 1996).
Most bat species face a critical conflict between early emergence from the roost before food supplies decrease and increased risk of predation from raptorial birds (Jones & Rydell 1994; Rydell, Entwistle & Racey 1996; Duverge et al. 2000). Increasing canopy cover and the connectivity of tree lines has been recommended as a mitigation to enable bats to exploit these early prey densities, without increased predation risk (Duverge et al. 2000; Russo, Cistrone & Jones 2007). A higher degree of shelter in the deciduous woodland may explain why the peak in foraging activity was earliest in this habitat.

Foraging activity remained high in the wetlands by the end of the three hour sampling period, indicating a very high, prolonged insect abundance, supporting a large number of bats. It is likely that this activity pattern also corresponds to a high insect species diversity, as different species would be abundant at different times of the night.

It has been suggested that an early evening activity peak, followed by low levels of activity may indicate that bats are foraging briefly near to the roost, before moving on to more distant, preferred foraging sites (Fenton et al. 1998). In these cases, foraging activity would largely be due to coincidence and convenience. Additionally there is a possibility that bats could be moving from the deciduous woodland and semi-improved grassland to the more profitable wetland habitat when levels of competition with other bats have decreased.

It must also be considered that this study coincided with the breeding period for all British bat species (Altringham 2003). During late pregnancy and lactation, females commonly begin foraging soon after sunset, due to a higher energetic demand, and then return to the roost early (Duverge et al. 2000; Davidson-Watts & Jones 2006).
In contrast, this possibility would represent a relatively high ecological value of these foraging sites. Further study would be required to confirm any of the above and it is unlikely that these relationships could be demonstrated by acoustic methods alone.

Plecotus species are known to emerge later than most bat species and feed predominantly on moths, which show a peak abundance at around midnight (Jones & Rydell 1994, Rydell, Entwistle & Racey 1996; Altringham 2003). This corresponds with the timing of activity recorded in the zoo. The results of this study illustrate that when selecting a sampling period, there is a trade-off between sampling during periods of peak foraging activity and introducing a sampling bias due to the varying emergence times of different bat species.

CONCLUSIONS AND PRIORITIES FOR FURTHER STUDY

This study has demonstrated that the foraging activity of bats within Paignton Zoo Environmental Park is not uniformly distributed. This highlights the importance of gathering information on a small scale, so that specific management plans can be developed to provide the appropriate support for local bat populations. High levels of activity in the wetlands indicate that this area is likely to be a key foraging site, particularly for *Pipistrellus pipistrellus*. As such, its maintenance and enhancement should be a conservation priority.

Further research is required in order to draw firm conclusions on the relative importance of the deciduous woodland for foraging bats and species composition and diversity. The following three areas of research are recommended as priorities, based on feasibility and the importance for conservation of the information that would be obtained:
1. A detailed acoustic study of the wetlands, to determine the causes of the high levels of variation in foraging activity in this habitat. Identifying the key habitat characteristics influencing bat activity, by investigating variables such as insect abundance and diversity, botanical diversity, structural variation and wind speed, could provide important information on how the suitability of this area for foraging bats could be further enhanced.

2. A detailed acoustic study of the entire deciduous woodland habitat, to discern to what extent this area is being used as a foraging site. Small scale variation in foraging activity could also be investigated here to ascertain if certain areas are being avoided or selected by foraging bats.

3. Mist net and harp trap surveys of both the wetland and deciduous woodland to confirm which species of *Myotis* and *Plecotus* bats are foraging in these habitats. The results could provide supplementary information on the distribution of these species in Devon and could also be used to develop species specific management plans for Paignton Zoo Environmental Park.

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References


Appendices

Appendix 1. Criteria for identifying foraging and commuting behaviour. Bats were categorized if three or more of the behaviour criteria were met. On the rare occasions when the behaviour could not be categorized, the recording was not included in the analysis. Flight pattern varied both interspecifically and intraspecifically, therefore the criteria used were qualitative. Echolocation call structure was interpreted with reference to Vaughan, Jones & Harris (1997b) and Russ (1999), taking into account the influence of varying levels of acoustic clutter on call parameters.

Commuting Behaviour:

- **Flight pattern**: Fast, directional, flight
  Amount of time spent around sample point is brief

- **Echolocation**: Brief period of time on the recording
  Characteristic or long inter-pulse interval and pulse duration
  Characteristic or low FmaxE for FM-CF bat species*
  Characteristic or extended constant frequency component for FM-CF bat species*

Foraging Behaviour:

- **Flight pattern**: Circling or hovering flight
  Frequent, swift changes in direction and quick darts towards insects
  Continued presence around sample point
  Flying within 1 meter of water surface (Daubenton’s bat only)

- **Echolocation**: Long period of time on the recording
  Presence of feeding buzzes
  Characteristic or short inter-pulse interval and pulse duration
  Characteristic or high FmaxE for FM-CF bat species *
  Characteristic or suppressed constant frequency component for FM-CF bat species *

* FM-CF (frequency modulated-constant frequency) bat species detected during the study were: Pipistrellus pipistrellus, Pipistrellus pygmaeus, Nyctalus noctula and Eptesicus serotinus.
Appendix 2. Total foraging activity at each sample point, in (a) deciduous woodland, (b) wetland, (c) semi-improved grassland and (d) unimproved grassland. Dark blue columns represent the total number of 15 second intervals in which foraging bats were present (habitat use), over 100 minutes (out of a possible total of 400). Red columns represent the total number of feeding buzzes in 100 minutes (feeding activity). Note: habitats have different y axis scales.