Summer habitat associations of bats between riparian landscapes and within riparian areas

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Abstract The present study examines those features which promote bat feeding in agricultural riparian areas and the riparian habitat associations of individual species. Activity of Nathusius' pipistrelle (*Pipistrellus nathusii*), common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*Pipistrellus pygmaeus*), Leisler's bat (*Nyctalus leisleri*), and *Myotis* species (*Myotis* sp.) were recorded, and their habitat associations both “between” and “within” riparian areas were analyzed. General feeding activity was associated with reduced agricultural intensity, riparian hedgerow provision, and habitat diversity. Significant habitat associations for *P. pipistrellus* were observed only within riparian areas. *Myotis* species and *P. pygmaeus* were significantly related to indices of landscape structure and riparian hedgerow across spatial scales. *Myotis* species were also related to lower levels of riffle flow at both scales of analysis. The importance of these variables changed significantly, however, between analysis scales. The multi-scale investigation of species–habitat associations demonstrated the necessity to consider habitat and landscape characteristics across spatial scales to derive appropriate conservation plans.

Keywords Riparian · Agriculture · Conservation · Habitat associations · Bats

Introduction

Many populations of bat species continue to decline across Britain and continental Europe (BCT 2006). Sixteen species of bat occur in the Britain Isles and all are protected by national and European Union legislation. The foraging habitats associated with a species reflects both species foraging strategies, such as gleaning from surfaces or aerial hawking and also the quality of the forage habitat in providing sufficient insect prey (Fenton 1990; Bogdanowicz et al. 1999). All bat species found in the Britain Isles are known to forage in agricultural landscapes (Wickramasinghe et al. 2003). Within the study area of Northern Ireland, agriculture constitutes 75.7% of total land area, with permanent grassland representing 81.6% of agricultural land use (Eurostat 2008). The predominance of agricultural land increases the importance of marginal agricultural areas and remnant natural habitats for wild species.

Agricultural intensification has occurred at the expense of biodiversity (Mickleburgh et al. 2002). The impact of such intensification on biodiversity has been noted across many different species groups including bats (Wickramasinghe et al. 2003). Identification of effective methods for maintaining biodiversity in agricultural landscapes is an urgent conservation issue, requiring collaboration between policy makers, land managers, and researchers (Ormerod et al. 2003).

Linear landscape features such as river corridors and hedgerows are utilized as forage habitats and are important as dispersal corridors (Walsh and Harris 1996). Rivers are landscape features which are relatively resistant to changes in agricultural practices and small scale land use change, in contrast to hedgerows and other features. They can, however, become degraded from their natural state by agricultural processes. Thus, while riparian habitats and indeed water quality may become degraded, they often

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provide the only remnants of semi-natural vegetation in agricultural landscapes (Marshall 2004).

Eight species of bats occur in Northern Ireland, namely, Nathusius' pipistrelle (*Pipistrellus nathusii*), common pipistrelle (*Pipistrellus pipistrellus*), soprano pipistrelle (*Pipistrellus pygmaeus*), Leisler's bat (*Nyctalus leisleri*), whiskered bat (*Myotis mystacinus*), Natterer's bat (*Myotis nattereri*), Daubenton's bat (*Myotis daubentonii*), and brown long-eared (*Plecotus auritus*). Of these *P. pygmaeus* and *P. auritus* are priority species in the UK Biodiversity Action Plan (Anonymous 1995). Only *M. mystacinus* and *M. nattereri* are not listed as being of international importance in the Irish Red Data Book (Whilde 1993). Aquatic habitats potentially provide abundant sources of insects making ideal foraging habitats for insectivorous bats (Warren et al. 2000). These areas are particularly associated with the activity of Daubenton's bat (*M. daubentonii*), and previous research has shown that this species is affected by the abundance and character of the aquatic habitats, for example, avoiding turbulent river surfaces (Rydell et al. 1999; Dietz et al. 2006). However, it is becoming increasingly apparent that *P. pygmaeus* is also associated with aquatic habitats (Vaughan et al. 1997; Grindal et al. 1999; Russ and Montgomery 2002; Russo and Jones 2003; Wickramasinghe et al. 2003; Sattler et al. 2007). Thus while riparian areas are recognized as important for some bat species, few studies assess the specific aspects of the riparian habitat, which promote the occurrence of individual species.

This study is focused on assessing the features of riparian areas in agricultural landscapes, which are important for promoting bat feeding activity. It is expected that feeding activity shall be negatively related to increased agriculture intensity surrounding riparian areas and also to greater diversity of the riparian habitat itself. Additionally, the habitat associations of species between and within riparian areas are assessed. Analysis of habitat associations is carried out at two scales, between rivers and within rivers. The between-river analysis includes environmental variables from both the riparian and adjacent agricultural areas, while the within-river analysis only examines associations of the immediate riparian area.

Analyses based on spatial scale orientated methods make it possible to identify species responses to changing environments and the processes that lead to species diversity and compositional changes in communities (Willis and Whittaker 2002). The study identifies both the characteristics of rivers and the fine scale characteristics, at a field level, with which bat species are associated. It is expected that aquatic specialist species such as *M. daubentonii* will be more closely associated with the immediate riparian habitat and river character at both analysis scales and to a lesser extent to broad riparian and

larger-scale habitat variables. Conversely *P. pygmaeus*, although increasingly being found to be associated with aquatic habitats, will be more closely associated with the riparian habitat and character of the surrounding broader landscape due to its aerial hawking foraging strategy. Such contrasts are important in constructing successful conservation plans.

Materials and methods

Bat community survey

Fifty, hydrologically independent rivers were surveyed for bat activity and species composition. The rivers were selected from the Environment Agency's River Habitat Survey database across all seven major basins with number of rivers stratified by basin size (Environment Agency 2002). All were situated in agricultural landscapes at altitudes below 150 m with an average channel depth of less than 1 m. Two sampling locations were identified at each river within an area of the dominant riparian vegetation as identified through habitat mapping. The locations were easily accessible by road or track but located further than 50 m from development. Locations were 1.2–1.6 km apart. A corridor of length 1.8 km was mapped, centered on a point equidistant between the two survey locations. The width of the corridor was 0.2 km, which ensured inclusion of the first adjacent habitat patch at all locations (Fig. 1).

The survey was conducted between June 2005 and August 2005 when foraging activity and energy demand in bats is at a peak (Speakman and Thomas 2003; Encarnacao et al. 2006). Sampling commenced 45 min after sunset (Jones and Rydell 1994). Ultrasound surveying was restricted to a period of 2 h to coincide with the general peak in bat feeding activity, which occurs at this time (Hayes 1997). The survey was carried out using a Pettersson D-240x detector to record bat species echolocation calls. At both locations on each river, bat calls were monitored for a total of 5 min with two 150-s sampling periods, one facing upstream and a second facing downstream.

Calls were recorded on a stereo cassette. While a longer sampling period, or repeated visits, may allow a full census of the community, the sampling strategy used does provide a snapshot of the community at each site and more importantly provides a measure of the relative occurrence of individual species (Keating and Cherry 2004). The minimum air temperature during the survey period and time after sunset at survey start were recorded. Surveying was not carried out during adverse weather conditions such as rain and strong wind. Time-expanded calls were obtained using the detector's automatic trigger. All bat activity was recorded using

Fig. 1 Map showing locations of rivers surveyed for bat species composition and bat activity. *a* An example of two river corridors of area 1.8×0.2 km from which habitat variables were extracted and bat

species presence was analyzed. *b* An example of the paired points (50-m radius) on each river at which bat presence was recorded and compared to explore within-site habitat selection

the heterodyne function with the detector tuned to 50 kHz. This allowed feeding activity of *Myotis* sp. and *Pipistrelle* sp. to be captured, but not *N. leisleri* nor *P. auritus*, as *N. leisleri* will not be recorded at this frequency and *P. auritus* will not be detected due to their low call intensity.

To allow species identification, sonograms were obtained from the field recordings using BatSound (Pettersson Elektronik AB), with a sampling rate of 44.1 kHz, a Hanning window and a fast Fourier transform (FFT) of size 512 for sonograms, and a FFT of size 1,024 for power spectrum. Diagnostic measures were taken from one randomly selected unique call from each sonogram of recorded calls at each point to identify species. These measures were compared to known species-specific call parameters (Table 1; Russ 1999). It is difficult, however, to identify bats with frequency modulated (FM) calls to species level (Vaughan et al. 1997; Parsons and Jones 2000). In the sampling region only *Myotis* sp. produce FM calls, which cannot be confidently attributed to individual species. Therefore, these sonograms were unresolved to species level and left grouped as *Myotis* sp. (*Myotis daubentonii*, *M. nattereri*, and *M. mystacinus*). *Pipistrellus* sp. and *N. leisleri* produce echolocation calls with a constant frequency portion. The frequency of maximum energy can be used to identify species (Table 1; Russ 1999). Bat activity, measured as the number of feeding buzzes per minute, was obtained from the continuously recorded heterodyne calls (Griffin et al. 1960). These cannot be attributed to a single species and, as stated above, are only likely to represent the feeding activity of *Myotis* sp. and *Pipistrelle* sp.

Analysis of bat feeding activity and habitat associations

A general linear model was applied to identify those riparian habitat characteristics, which affect feeding rate. The habitat variables used were derived from digitized land cover maps compiled from phase 1 habitat surveys (JNCC 2000). The variables were chosen to reflect the degree of agricultural intensification and provision of semi-natural habitat. All variables were standardized to have a mean of 0 and a standard deviation of 1, to allow for comparison of beta values. Variables were transformed to fit normal distributions. A summary of the variables and transformations used is presented in Table 2.

Generalized linear models (GLZ) were derived independently for each bat species between rivers with species occurrence as the binary dependent. A species was defined as present if it was recorded at either of the two locations at each river. Habitat variables from the $1.8 \text{ km} \times 0.2 \text{ km}$ river corridor maps were used to explore between-river habitat associations (Table 2). To examine fine-scale, within-river habitat associations, species-specific GLZs were derived using differenced variables from the paired surveys on each river using habitat variables taken from an area of 50-m radius around each location (Table 2). An area of radius 50 m was selected to represent the immediate riparian habitat, but not extending beyond the first agricultural field. Differenced variables for both the environmental data and presence data were calculated and a GLZ was applied. The binary dependent was coded (0), indicating no difference in occurrence at both points, and (1), indicating a species occurred at one point but not at the second (Compton et al.

Table 1 The frequency of occurrence of bat species recorded at 50 riparian sites

Species	Frequency of maximum energy (kHz) (Russ 1999)	Not recorded	Single location	Both locations
<i>P. pipistrellus</i>	46.5 (40.8–49.5)	15	23	12
<i>P. pygmaeus</i>	55.5 (48.8–61.6)	10	27	13
<i>P. nathusii</i>	40.7 (36.0–44.1)	48	2	0
<i>N. leisleri</i>	26.9 (21.1–36.6)	11	26	13
<i>Myotis</i> sp.	NA	9	24	17

Two locations were surveyed at each river. Therefore species could be; not recorded, only recorded at a single location, or recorded at both locations

2002). Using these differenced variables, logistic regression was used to assess whether the differences in occurrence at paired points resulted from differences in the environmental variables, rather than the probability of a species occurring, an important distinction which must be recognized for the valid interpretation of the GLZ (Keating and Cherry 2004).

All potential models, based on all possible variable combinations, were constructed in each analysis (Gibson et al. 2004). The models were compared using the Akaike information criteria (AIC). Where no single model was observed to dominate, a model averaging procedure was used to obtain parameter estimates (Burnham and Anderson 2002). Hierarchical partitioning was employed as a technique to identify the independent and joint effects of each variable, allowing explanatory variables to be ranked based on their independent effect (MacNally 2000). The independent effect of each parameter is associated with the increase

in model fit associated with each predictor variable, estimated by averaging its additional explanatory power in all models in which it occurs (MacNally 2000). Using a randomization procedure it is possible to determine which variables have a significant independent effect, based on “Z scores,” calculated as [observed mean (1,000 randomizations)]/SD (1,000 randomizations) with a 0.95 confidence limits ($Z=1.65$; Walsh and Mac Nally 2003).

The validity of the parameter coefficients of a model was assessed using unconditional standard errors (Gibson et al. 2004). Additional confidence was provided by agreement in the results of hierarchical partitioning and the ranking of variables by their summed variable specific Akaike weights (AIC_w ; Stephens et al. 2005; McAlpine et al. 2006). The ability of each model to accurately predict the presence of a species was evaluated using receiver operator characteristic (ROC) curves and using the area under the curve (AUC) as

Table 2 A summary of explanatory variables used in the analysis of bat feeding activity (F), between-river habitat association (H), and within riparian area associations(S)

Variables	Description	Transformation	Analysis
High-intensity farming	Percentage of riparian area (1.8×0.2 km) with improved grassland cover (JNCC 2000)	Arcsine(square root(y))	F/H
Low-intensity farming	Percentage of riparian area (1.8×0.2 km) with semi-improved grassland cover (JNCC 2000)	Arcsine(square root(y))	F
Scrub	Percentage of riparian area (1.8×0.2 km) with scrub cover (JNCC 2000)	Arcsine(square root(y))	F/H
Hedgerow length	Hedgerow length in riparian area: 1.8 km $\times$ 0.2 km (F and H) and within 50 m radius (S)	Log ($y+1$)	F/H/S
Habitat patch number	The number of distinct habitat patches in the riparian area (1.8×0.2 km)	NA	F/H
Patch evenness	A measure of the relative area of different patch types in the riparian area: 1.8 km $\times$ 0.2 km (F and H)/ 50 m radius (S) (McGarigal and Marks 1995)	NA	F/H/S
Riparian diversity	A measure of the riparian boundary diversity: interspersed and juxtaposition index at a class level of the riparian area: 1.8 km (F and H)/ 100 m (S) river course (McGarigal and Marks 1995)	NA	F/H/S
Habitat diversity	A measure of spatial diversity: interspersed and juxtaposition index of the riparian corridor (1.8×0.2 km; McGarigal and Marks 1995)	NA	F
River width	Average river width (m) over 1.8 km river length ($n=10$)	NA	H
Natural land cover	Percentage area of all land cover classes not under agricultural management (JNCC 2000) in a 50 -m radius around each survey point	Arcsine(square root(y))	S
Riffle area	Percentage of stream with riffle surface flow over 1.8 km river length (H) and 100 m (S) river course	NA	H/S

a measure of the predictive capability (Fielding and Bell 1997).

Results

Species occurrence

Four species and one species group were recorded during the survey (Table 1). *P. nathusii* was omitted from analyses as this species was present at only two rivers and is known to be only locally distributed in Ireland (Russ et al. 1999).

Bat activity

The numbers of feeding attempts per minute were summed for the locations surveyed on each river (Griffin et al. 1960). There was no significant effect of minimum air temperature or time after sunset on feeding buzz rate ($F=0.061$; $df=1,48$; $p=0.807$) and ($F=0.01$; $df=1,48$; $p=0.922$), respectively. No single model relating bat feeding with habitat parameters had significantly greater explanatory power among all constructed models of bat feeding activity ($n=255$). The model parameters derived by multimodel inference are presented in Table 3. Feeding rate was positively related with hedgerow length, low-intensity farming, scrub, and riparian diversity, but negatively related with high-intensity farming. Habitat diversity, habitat patch number, and patch evenness had an inconsistent effect. The results of model averaging and hierarchical partitioning concur, supporting the results of the modeling procedure.

Habitat associations of riparian bat species

The presence of *N. leisleri*, *Myotis* sp., *P. pygmaeus*, and *P. pipistrellus* were modeled independently with environmen-

tal variables (Table 2). In all cases, a number of models had similar AIC scores, with nine models of *N. leisleri*, four models of *Myotis* sp., eight models of *P. pygmaeus*, and nine models of *P. pipistrellus* falling within 2 AIC units of the best model, equating to a 78%, 91%, 67%, and 88% confidence model set for each species, respectively. The averaged regression coefficients for occurrence of *N. leisleri* suggested that the derived parameter estimates had poor explanatory power and inconsistent effect (Table 4). The survey start time ($F=1.139$; $df=1,48$; $p=0.291$) and minimum temperature ($F=0.024$; $df=1,48$; $p=0.876$) were not significant variables describing the presence of *N. leisleri*. Similarly, the models for *P. pipistrellus* suggested that there was little confidence in the model parameters as a true reflection of habitat associations for this species (Table 4). The survey start time ($F=0.171$; $df=1,48$; $p=0.681$) and minimum temperature ($F=0.220$; $df=1,48$; $p=0.641$) were not significant factors in determining the presence of this species.

In contrast, models of between-river selection by *Myotis* sp. and *P. pygmaeus* showed that habitat variables had consistent and independent effect (Table 4). *P. pygmaeus* was significantly positively associated with habitat patch number and the patch evenness. The AUC of the ROC curve for the averaged model for the presence of *P. pygmaeus* indicated that the model could correctly predict the presence of *P. pygmaeus* in 68% of cases. *Myotis* sp. also had a positive association with both the habitat patch number and with patch evenness but a negative association with riffle area. The AUC of the ROC curve analysis indicate that the model could correctly discriminate between *Myotis* sp. presence and absence in 86% of cases. In both these models the ranking of parameters in order of importance by parameter coefficients, independent contribution, and AIC ω followed a similar pattern (Table 4). Neither time of survey start nor minimum temperature for *Myotis* sp. ($F=0.686$; $df=1,48$; $p=0.412$) and ($F=3.035$; $df=1,48$; $p=0.089$), respectively, or *P.*

Table 3 Results of hierarchical partitioning analyses and model averaging for feeding attempts

Parameter	Independent variation explained (%)	Coefficient	Unconditional standard error ($\pm$)	Variable Akaike weight (AIC ω)
High-intensity farming	9.89 ^a	−0.057	0.017	0.687
Low-intensity farming	18.68 ^a	0.098	0.043	0.978
Scrub	15.31 ^a	0.067	0.012	0.788
Hedgerow length	33.27 ^a	0.123	0.021	0.982
Habitat patch number	8.62	0.016	0.012	0.273
Patch evenness	4.19	−0.002	0.045	0.108
Riparian diversity	6.51 ^a	0.041	0.011	0.321
Habitat diversity	3.8	−0.002	0.012	0.087

The independent percentage contribution of each variable was determined by hierarchical partitioning (MacNally 2000). Statistical significance (^a) was determined using Z-scores, calculated as [observed-mean (1000 randomizations)]/SD (1000 randomizations) based on upper 0.95 confidence limit ($Z=1.65$). Model-averaged regression coefficients and unconditional standard errors and Akaike variables weights (AIC ω) are also presented

pygmaeus ($F=1.783$; $df=1,48$; $p=0.188$) and ($F=5.323$; $df=1,48$; $p=0.025$), respectively, were significant factors determining the presence at rivers.

For models of habitat selection within rivers, *N. leisleri* again showed no consistent relationship with any variables (Table 5). However, *P. pipistrellus*, *P. pygmaeus*, and *Myotis* sp. were consistently related to a number of variables (Table 5). *Myotis* sp. selected positively for hedgerow length, natural land cover, and habitat patch number but was negatively associated with riffle area. The

AUC of the ROC plot for the derived averaged model of *Myotis* sp. indicated that the model could correctly predict the “difference” in occurrence of *Myotis* sp. in 79% of cases. Both *P. pipistrellus* and *P. pygmaeus* were significantly positively associated with the natural land cover, riparian diversity, and the hedgerow length. Both species also had significant but different relationships with patch evenness; *P. pygmaeus* was positively related and *P. pipistrellus* was negatively related to this variable. The AUC for the ROC curve of the final models indicated that

Table 4 Results of hierarchical partitioning analyses and model averaging for species presence between riparian areas

	Between riparian areas occurrence				
	Variance explained (%)	Z score	Coefficient	Unconditional SE	AIC ω
<i>N. leisleri</i>					
River width	3.31	0.12	0.34	0.97	0.093
Riffle area	5.12	0.22	−0.32	0.67	0.087
Habitat patch number	7.28	0.30	−2.17	0.87	0.312
Hedgerow length	19.1	1.11	0.07	0.33	0.397
High-intensity farming	19.8	1.18	−0.08	0.09	0.441
Patch evenness	21.2	0.52	6.70	3.67	0.412
Scrub	24.3	0.44	−0.09	0.07	0.521
<i>Myotis</i> sp.					
Scrub	1.20	0.44	0.24	0.30	0.191
Hedgerow length	1.21	0.45	1.23	2.12	0.112
High-intensity farming	1.36	0.56	−0.67	0.89	0.197
River width	3.43	1.21	0.67	0.78	0.211
Habitat patch number	18.85	2.17 ^a	0.27	0.04	0.319
Patch evenness	29.51	3.26 ^a	9.71	3.41	0.799
Riffle area	44.44	5.52 ^a	−0.08	0.03	0.934
<i>P. pygmaeus</i>					
Riffle area	0.01	0.04	0.24	0.67	0.098
Hedgerow length	0.34	0.12	−0.45	0.98	0.073
River width	0.36	0.07	−0.08	0.06	0.097
High-intensity farming	10.65	0.03	−0.03	0.04	0.135
Scrub	12.34	1.23	0.22	0.98	0.168
Habitat patch number	36.2	2.11 ^a	4.14	1.23	0.479
Patch evenness	40.1	2.39 ^a	2.77	0.96	0.513
<i>P. pipistrellus</i>					
Riffle area	0.23	0.01	−0.06	0.12	0.112
River width	1.34	0.76	0.03	0.19	0.089
Hedgerow length	2.11	−0.73	0.34	0.45	0.145
High-intensity farming	9.43	−0.33	−0.06	0.09	0.321
Habitat patch number	17.64	−0.36	0.03	0.05	0.245
Scrub	33.49	0.65	−0.02	0.17	0.487
Patch evenness	35.76	0.71	0.23	0.14	0.412

The independent percentage contribution of each variable was determined through hierarchical partitioning (MacNally 2000). Statistical significance (^a) was determined using Z-scores, calculated as [observed-mean (1000 randomizations)]/SD (1000 randomizations) based on upper 0.95 confidence limit ($Z=1.65$). Model averaged regression coefficients, unconditional standard errors and Akaike variables weights (AIC ω) are also presented

they could correctly predict the difference in occurrence of *P. pipistrellus* in 70% of cases and *P. pygmaeus* in 68% of cases.

Discussion

The work demonstrates the wealth of information that can be gained from detector studies, which are both relatively inexpensive and require limited experience to conduct. Detector studies do, however, have limitations which can only be overcome through techniques which allow accurate enumeration, aging, and sexing of bats, factors which are known to affect behavior within species (Encarnacao et al. 2005; Dietz et al. 2006; Dietz and Kalko 2006). While it was shown that the time of survey was not a significant factor determining the species presence, it was not possible, in this work, to include roost location information in the analysis. The presence of a species in an area may be limited by the availability of suitable roosting sites, and the arrival of a species at a foraging site may be affected by distance from roosts (Dietz et al. 2006).

The present study identifies important habitat associations of the riparian bat community. While the application of a paired regression is a widely used technique in experimental approaches, it is rarely used in modeling species occurrence and for identifying habitat requirements (Moran and Jefferies 2001; Compton et al. 2002). Paired logistic regression is a powerful technique, allowing control for both known and unknown confounding factors, maximizing the yield of field survey data (Compton et al. 2002). Bat feeding activity and the presence of bat species both within rivers and between rivers were significantly linked to the land cover and riparian landscape character. In particular, the presence of myotis bats was associated with both land cover variables and the riverine physical environment. Differences in the models of habitat associations between riparian areas and within riparian areas for *Myotis* sp. and *P. pipistrellus* demonstrate a clear need to consider issues of spatial scale when examining species habitat associations. If either model was considered alone, inaccurate habitat associations may be inferred.

Walsh and Harris (1996) recorded low feeding activity of bats over areas of intensive agriculture and related these to lower levels of insect abundance. Wickramasinghe et al. (2003) compared bat feeding rate and insect numbers in organic and conventional farming and found that for many species, feeding rate was higher on organic farms, and agricultural intensification had a profound impact on nocturnal insect communities. The present study agrees with these studies showing that the feeding activity of bat species was positively associated with lower levels of agricultural intensity, the provision of natural land cover,

and riparian hedgerow abundance, elements which reflect increased structural habitat complexity and diversity of the riparian boundary (Table 3). Together these investigations indicate that farmland management strategies, the presence of low-intensity agriculture, and remnant natural vegetation can have significant impacts not only on the presence of invertebrate species but also on higher trophic levels.

The habitat association of *N. leisleri*, *P. pipistrellus*, *P. pygmaeus*, and *Myotis* sp. showed some contrasting patterns of habitat use, and not all species were observed to be closely associated with the selected environmental variables at both scales of analysis. *Myotis* sp. and *P. pygmaeus* had a significant association with riparian areas with higher levels of habitat diversity, as characterized by a greater number of landscape patches and an even provision of different patch types (Table 4). The use of ultrasound detectors in isolation does not permit the identification of individual species of the myotis bats. It is likely, however, that the majority of individuals were *M. daubentonii*, given the known habitat relationships of the *Myotis* sp. (Racey 1998; Russ and Montgomery 2002) and the relative frequency with which it is recorded as the second most commonly occurring bats species in Ireland (O'Sullivan 1994). Clearly, however, as highlighted by the case of the *P. pipistrellus* and *P. pygmaeus*, which, despite having considerably different echolocation calls and potentially significantly different habitat relationships (Sattler et al. 2007), were until recently considered a single species, further species-specific studies of the habitat relationships within *Myotis* sp. group are required.

The strong aquatic associations of *P. pygmaeus* and *M. daubentonii* are thought to relate to water bodies providing an ideal source of food, with many insects having aquatic larval stages (Russ and Montgomery 2002). *P. pygmaeus* feed on insects such as Chironomidae and Ceratopogonidae (Barlow 1997), and *M. daubentonii* often feeds by trawling insects from the surface of water bodies (Norberg and Rayner 1987; Kalko and Schnitzler 1989). In addition to the broad landscape level associations of *Myotis* sp., the present study also supports the finding that this group of bats avoids areas with a turbulent water surface (Rydell et al. 1999). The turbulent nature of riffle areas is thought to impair the ability of *M. daubentonii* to detect and capture prey (Rydell et al. 1999). Riffle areas are one component of the structural river unit, contrasting with other flow features such as pools and glides. Pools and glides, in contrast to riffles, are characterized by calm, smooth surface flow (Leopold et al. 1964). The identification of the associations with habitat character and the physical nature of a river shows conservation management plans of *Myotis* sp. in riparian areas must consider both hydromorphological character rehabilitation and land use change (Warren et al. 2000).

The use of paired regression analysis indicated significant patterns of within-river selection by *Myotis* sp. and *Pipistrellus* sp. (Table 5). No significant relationships were observed, however, for *N. leisleri*. Shiel and Fairley (1998) also found no overall habitat preference for *N. leisleri* except for street lights. Shiel et al. (1999) reported this species foraging over grassland and water and avoiding pasture. Russ and Montgomery (2002) suggested that a lack of detected habitat association in this species may be related to survey methodology, as *N. leisleri* forages at heights up to 120 m (Russ and Montgomery 2002) and have long-range echolocation systems (Rydell 1992).

No significant associations between rivers were observed in the incidence of *P. pipistrellus* but the results suggest that this species selects particular areas within

riverine areas. Within-riverine habitat selection for *P. pipistrellus* was similar to that of *P. pygmaeus* with both species selecting riverine areas characterized by a greater area of natural land use, a diverse riparian boundary, and greater amounts of hedgerow. These variables indicate rivers within landscapes with greater amounts of land cover diversity and structure, providing ideal habitat for invertebrate prey and, therefore, foraging opportunity. These two species, however, showed a contrasting relationship with the evenness of the habitat cover. The negative relationship of *P. pipistrellus* with habitat patch evenness may reflect an ability to forage in relatively small suitable areas in otherwise unfavorable habitats, whereas *P. pygmaeus* selects larger areas of suitable habitat to forage in riparian zones.

Table 5 Results of hierarchical partitioning analyses and model averaging for species presence within riparian sites

	Within riparian area occurrence				
	Variance explained (%)	Z score	Coefficient	Unconditional SE	AIC ω
<i>N. leisleri</i>					
River width	2.34	0.01	0.03	1.12	0.061
Riffle area	2.37	0.01	−0.04	0.76	0.082
Patch evenness	5.04	0.02	−1.12	1.14	0.126
Natural land cover	6.73	−0.08	0.04	0.08	0.119
Habitat diversity	36.63	1.06	0.03	0.03	0.362
Hedgerow length	46.89	1.41	−0.76	0.59	0.339
<i>Myotis</i> sp.					
Patch evenness	1.23	0.78	0.05	0.11	0.119
River width	3.33	1.34	0.24	0.78	0.304
Habitat diversity	8.31	2.45 ^a	0.15	0.04	0.543
Natural land cover	12.02	7.64 ^a	1.62	0.64	0.454
Riffle area	25.41	9.81 ^a	−0.06	0.02	0.867
Hedgerow length	49.7	11.43 ^a	0.83	0.37	0.912
<i>P. pygmaeus</i>					
Riffle area	3.21	1.12	−0.07	0.24	0.011
River width	4.17	1.41	−0.12	0.15	0.012
Natural land cover	4.32	2.34 ^a	0.02	<0.01	0.015
Habitat diversity	5.43	4.55 ^a	0.03	0.01	0.045
Patch evenness	19.84	6.24 ^a	−0.06	<0.01	0.216
Hedgerow length	63.03	9.01 ^a	0.83	0.02	0.765
<i>P. pipistrellus</i>					
Riffle area	3.21	1.15	0.45	0.45	0.098
River width	5.49	1.59	0.44	0.44	0.112
Natural land cover	11.36	7.82 ^a	0.05	0.05	0.467
Patch evenness	21.56	6.78 ^a	0.45	0.45	0.469
Habitat diversity	24.67	3.89 ^a	0.02	0.02	0.721
Hedgerow length	33.71	6.80 ^a	0.14	0.14	0.846

The independent percentage contribution of each variable was determined by hierarchical partitioning (MacNally 2000). Statistical significance (^a) was determined using Z-scores, calculated as [observed-mean (1000 randomizations)]/SD (1000 randomizations) based on upper 0.95 confidence limit (Z=1.65). Model averaged regression coefficients, unconditional standard errors and Akaike variables weights (AIC ω) are also presented

P. pygmaeus is increasingly being considered as a species with a strong association to aquatic habitats (Vaughan et al. 1997), while *P. pipistrellus* is regarded as a generalist in terms of both habitat and diet (Barlow 1997; Vaughan et al. 1997; Russ and Montgomery 2002; Wickramasinghe et al. 2003; Davidson-Watts and Jones 2006). However, in some cases *P. pipistrellus* also select foraging sites associated with aquatic habitats (Glendell and Vaughan 2002). In the present study, which examined specifically riparian habitats, the two species had significantly different levels of habitat association (Table 4). *P. pipistrellus* was not associated with any of the broad riverine landscape variables, in contrast to strong associations of *P. pygmaeus*, supporting the increasingly apparent differences in the ecology and conservation requirements of these two morphologically similar species (Nicholls and Racey 2006; Sattler et al. 2007). The lack of broad habitat association for *P. pipistrellus*, but positive selection within riverine corridors for diverse habitat areas, suggests that this species has only limited association with riverine areas, but that when it occurs it may select specific habitats. Within the study region the species may be highly selective of small areas of optimal habitat, a pattern which is lost when only a broad scale is examined.

As expected *Myotis* sp. had a negative relationship with the area of riffle flow within and between rivers (Table 4). The *Myotis* sp., as with *Pipistrellus* sp., selected areas within the riverine landscapes, which were characterized by higher levels of habitat diversity and greater amounts of natural land cover (Table 5). However, comparison of the models for *Myotis* sp. between and within riparian areas demonstrated that while the amount of riparian hedgerow may be a significant factor in the selection of feeding areas by *Myotis* sp., this variable is not significant in determining at which rivers these bats occur. The contrast of these two models demonstrates clearly how analysis of species habitat associations and, therefore, conservation measures must address issues of spatial scale by addressing fine scale habitat management within the context of the surrounding landscape.

Each species analyzed in the present study had disparate affiliations with a range of habitat elements. This increases understanding of the relative importance of different riverine variables and the requirements to manage habitats and the wider landscape for the conservation of bat communities. The conservation of *Myotis* sp. and *Pipistrellus* sp. in agricultural riparian zones requires maintenance of bank side vegetation, natural land cover, and habitat diversity. The area of calm surface flow within a stream may also be important for the *Myotis* sp., but this may simply reflect an association with a river structure with a natural pattern of changing flow types (Leopold et al. 1964). The frequency and abundance of riffle areas is

determined by many processes within fluvial systems, and these areas represent a key component of river structure (Leopold et al. 1964). Additionally, while *M. daubentonii* may prefer to forage over calm surface areas, the preferred habitats of many invertebrate species, which they feed on, are riffle areas (Brown and Brussock 1991). Maintenance and restoration of these natural flow regimes is also considered to be important for other species, such as endangered salmonid populations (Stanford et al. 1998). Activities such as dredging and straightening of water courses, which may impact on hydromorphological diversity, should be avoided, or managed carefully, to avoid adversely impacting on riparian communities (Warren et al. 2000). This research highlights the requirements of bat species, particularly *Pipistrellus* sp. and *Myotis* sp., in riparian landscapes and habitats. Further work is required, however, to further elucidate the individual species requirements of *Myotis* sp.

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