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Original Investigation

The spatial ecology of the whiskered bat (*Myotis mystacinus*) at the western extreme of its range provides evidence of regional adaptation

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ABSTRACT

Although widespread, the ecology of the whiskered bat, *Myotis mystacinus* in Europe remains poorly understood. Ireland is positioned at the most western extreme of this species' range. To ascertain the ecology of *M. mystacinus* at its geographic range extreme, the roosting behaviour, home range and habitat use of females in a maternity roost in Ireland was investigated by radio-tracking. *M. mystacinus* were active in a diversity of habitats: namely, mixed woodland, riparian vegetation, arable land and rough grassland. However, only mixed woodland and riparian habitats were selected as core foraging areas. This is in contrast to a previous study from Britain where only pasture was utilised but is in agreement with data from Slovakia, where woodland was also selected, whilst riparian areas were also utilised by this species in Germany. A high degree of overlap in the foraging areas of individuals was observed. A total of seven roosts were utilised by tracked bats and roost switching behaviour was observed. We discuss our contrasting results in respect to range limitations, regional variability in landscape structure and the composition of bat communities. The present results have implications for the conservation of *M. mystacinus* within Ireland and other parts of its range, highlighting the need for range wide ecological studies. Regional variability in the ecology of bats related to landscape factors is an important consideration for bat conservation and therefore must be incorporated into future management plans.

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Introduction

Human activities have had a major impact on the landscape in the temperate zone (Vitousek et al. 1997). For example, agricultural intensification has removed important foraging habitats whilst pesticides have reduced populations of insects (Aebischer 1991). Woodland habitats are also vulnerable to human activities due to insensitive harvesting practices (Patriquin and Barclay 2003) and conversion to commercial forestry, or clearance for agriculture (Peterken 1996). Species' ecology can vary across the extent of their range in response to changing environmental conditions and variation in community species richness and composition (Oliver et al. 2009). At the range edge, where environmental conditions can be at the extreme of a species' tolerable limits, populations tend to be at a lower density making them more vulnerable to factors effecting decline or possible extinction (Andrewartha and Birch 1954;

Brown 1984; Thomas et al. 1999; Bridle and Vines 2007; Carroll 2007). Hence, the suitability of typical habitat used by a species may decrease on the margins of its range due to diminished productivity or changing climate (Jump and Woodward 2003). This may lead a species to switch its habitat preferences to habitats that they would not be typically associated with (Lesica and Allendorf 1995). Island populations may also show different ecological traits to continental populations, due to restricted area of preferred habitat and/or reduced species richness, or absence of particular competitors, leading to local adaptation and ecological release in the absence of competition (Cox and Moore 1985; Bolnick et al. 2010).

Ireland represents the extreme north western range limit of bats in Europe. Ireland's bat fauna is dominated by species adapted to foraging in edge and open environments, whilst woodland specialists, such as *M. bechsteini* (Bechstein's bat) and *Barbastella barbastellus* (Barbastelle bat) are absent and *Rhinolophus hipposideros* (lesser horseshoe bat) is restricted to the south western areas (Kelleher 2004; Harris and Yalden 2008). Therefore, Ireland offers an ideal context to investigate the possible effects these factors have on the ecology of bat species present there.

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Myotis mystacinus (whiskered bat) is a small myotis bat that is widely distributed across Europe and northern Africa (Mitchell-Jones et al. 1999; Benda et al. 2004). In Western Europe, it forms part of a species complex, including two other morphologically similar species; *M. brandtii* (Brandt's bat), and *M. alcaethoe* (Alcaethoe's bat) whilst, further east, it is replaced by *M. aurascens* (Steppe whiskered) (Dietz et al. 2009). In Ireland, *M. mystacinus* is widespread but localised (Boston et al. 2010). Records of the morphologically similar *M. brandtii* are extremely rare (Boston et al. 2010) and *M. alcaethoe* has not yet been found.

Morphological features suggest *M. mystacinus* is an aerial forager and an edge space aerial/trawling forager (Fenton and Bogdanowicz 2002; Siemers and Schnitzler 2004). The diet of *M. mystacinus* includes day-flying insect taxa which indicate gleaning behaviour (Taake 1992). In western Europe summer roosts of *M. mystacinus* have been found in buildings, bat boxes and trees (Marnell and Presetnik 2010). Roosts are vital for the survival of individual bats and conservation of populations, being utilised for shelter, mating, raising young, hibernation and predator avoidance (Kunz and Lumsden 2003). The degree of roost switching behaviour exhibited by *M. mystacinus* is unknown (Kunz and Lumsden 2003).

Highly contrasting habitat associations have been described for *M. mystacinus*, in different localities spanning the extent of its European range; Taake (1984), for example, found an association with agricultural landscapes and riparian habitats surrounding roosts in Germany, whilst Kanuch et al. (2008) suggested that it is a woodland generalist with no association with any particular forest type in Slovakia. In Britain, in contrast to continental studies, *M. mystacinus* select pasture with hedgerows in southern England (Berge 2007). Little is known about the habitat associations of *M. mystacinus* in Ireland.

Here we investigate the roosting ecology, range behaviour and habitat use of maternity roosting *M. mystacinus* in an area of agricultural grassland and woodland mosaic, typical of lowland Ireland. We investigate if the ecology of *M. mystacinus* in Ireland differs from populations in Britain and continental Europe and discuss whether variation in the ecology of this species in Ireland is due to geographical isolation, variation in landscape or composition of the bat fauna of islands in comparison to continental populations.

Material and methods

Traditional methods of habitat assessment, such as walked transects using bat detectors are unsuitable for *M. mystacinus*, due to the difficulty of separating myotis species using sonogram analysis (Vaughan et al. 1997b). Assessing habitat use using capture records within habitats does not allow an unbiased assessment of habitat selection. Radio telemetry offers a relatively unbiased method for assessing habitat use in *M. mystacinus* as it is not affected by prior assumptions on habitat use and questions of species identification (Kenward 2001).

Study site

A radio telemetry study was conducted between the 15th of May and 08th July 2009 at a maternity roost of *M. mystacinus*, in County Cork, Ireland (51°85N, 08°89W, alt: 82 m; labelled A in Fig. 1). Previous emergence counts at this roost estimated the number of individuals present to be 30–40 (Buckley 2004). The roost was in the attic of an occupied, detached house (over 100 years old), located between a timber joist and a brick chimney. The surrounding landscape was predominantly improved pasture with hedgerows and tree lines and some areas of broadleaved, mixed and coniferous woodland (Fig. 1), typical of the lowland agricultural landscape that covers around 66% of the land area of Ireland (EPA 2008).

Capture and tracking of bats

Bats were captured during evening emergence using harp traps inside the attic of the study roost on three separate occasions and at the exit points of a second roost (identified during the tracking) on two occasions (labelled C in Fig. 1). Body mass and forearm length were recorded and no bat less than 5 g was tagged (Cochran 1980). 'Pip4' transmitters (0.3 g) (Biotrack, Dorset, United Kingdom, www.biotrack.co.uk) were used to tag bats. The fur was trimmed between the scapulae and transmitters attached using surgical cement (Skin-Bond, Montreal Ostomy). All procedures were conducted under license from the National Parks and Wildlife Service (License number: 13/2009). Bats were tracked, typically for five nights in the pre-partum and post-partum period (Table 1). Both trapping and tracking were avoided when bats were in late stages of pregnancy or likely to be carrying dependent young.

Up to five bats were tracked at the same time using Sika receivers (Biotrack Ltd) and Yagi antennae (Biotrack Ltd) (Table 1). Bat locations were established by triangulation with 2–4 simultaneous fixes taken between dusk emergence and dawn return. Fixes were taken every 15 min during the first hour after emergence and also for the final hour before dawn return. At all other times, fixes were taken every 30 min. These time intervals were chosen to avoid autocorrelation of fixes. Bat positions were calculated from simultaneous fixes using the triangulation program, Locate (Nams 2005). The daytime roosting locations of all bats were ascertained by tracking on foot. Triangulation error from fixed positions for Pip4 transmitters was assessed as 30.4 m (s.e. ± 4.3 m), at a distance of 1.5 km from transmitters (Lundy et al. 2012).

Analysis of spatial ecology

The home range of each bat was estimated using the Minimum Convex Polygon (MCP) for all locations, and the core foraging area was estimated as the 50% contour line of a kernel estimation using the program Hawth Tools (Beyer 2004), an extension for ArcMap 9.3 (www.esri.com). Kernel analysis was applied with locations weighted by time intervals between fixes. The smoothing factor, which determined the smoothness of the kernel shape, was calculated from the likelihood cross validation value (CVh) as it has been found to be much less variable and a better fit for data with a sample size of location points of less than 50 than the more commonly used least squares cross validation value (LSCVh) (Horne and Garton 2006). Likelihood cross validation values were calculated for each bat using the program Animal Space Use 1.3 Beta (Horne and Garton 2009). Differences in home range size and total distance travelled pre and post partum, were tested using a Mann–Whitney *U* test (Mann and Whitney 1947). To test whether the amount of home range overlap between individuals was greater than the amount of core area overlap between individuals, a Wilcoxon Paired-samples test (Wilcoxon 1945) was conducted.

The habitat composition of the study area was determined from a circular area which encompassed the outermost 95% kernel contour of all individuals, this being the furthest distance that bats could travel in any direction. Habitats in the study area were mapped from aerial photographs (Ordnance Survey Ireland), using ArcMap (www.esri.com) and were divided into twelve discrete habitats based on Fossitt (2000) and Smith & Racey (2008). Habitat use was investigated on two levels: (1) Home range selection assessing which habitats were utilised within the home ranges compared to the entire study area. (2) Foraging area selection in which habitats utilised in the core foraging area were compared to the home range.

The proportion of used to available habitat was calculated from the surface area of the habitat polygons. Habitat selection was analysed using selection ratios (\hat{w}_i) providing a measure of

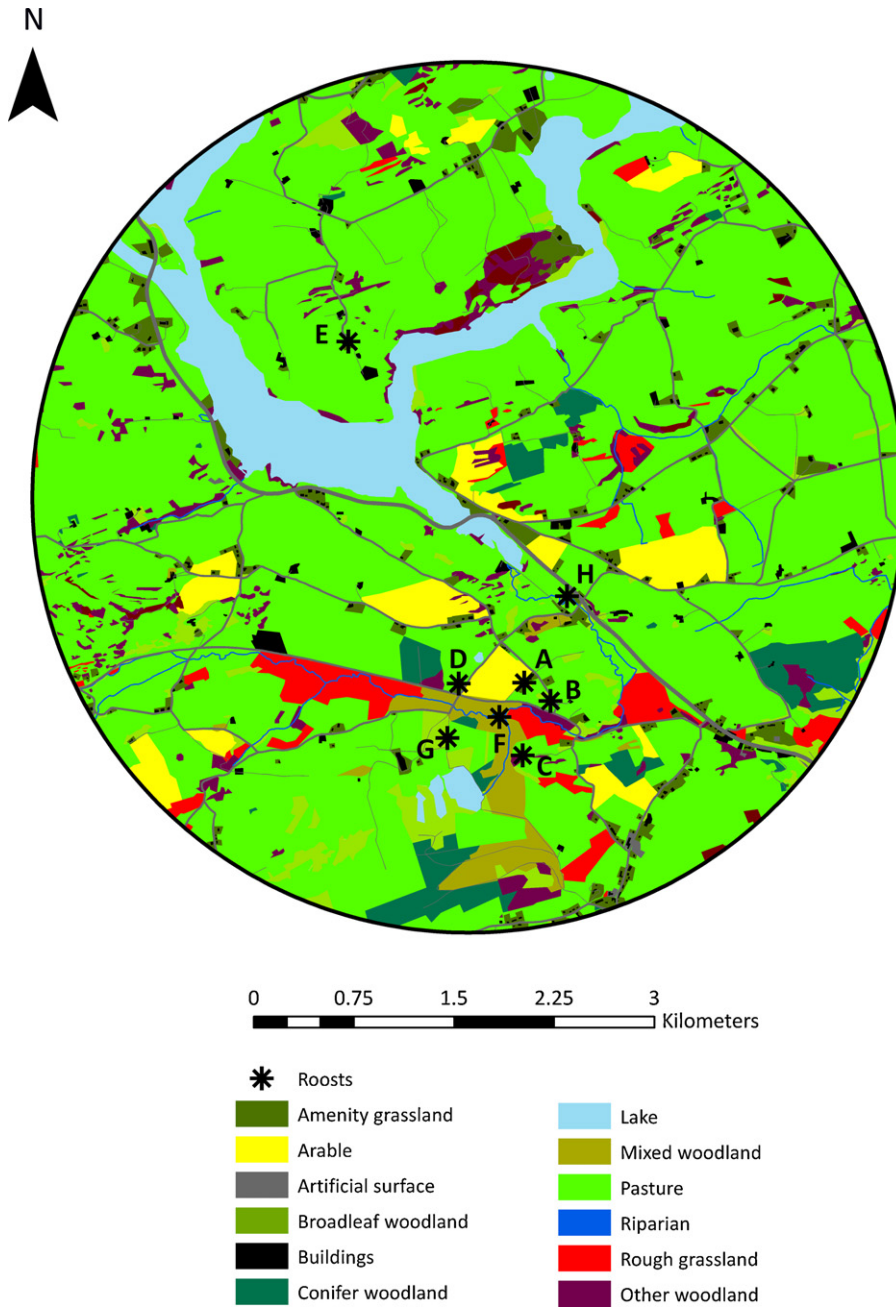


Fig. 1. The principal habitat types in the study area available to *M. mystacinus*. Roosts locations are marked with an asterisk.

Table 1
Tracking data of the 13 bats studied.

Bat code	Date of capture	Weight (g)	Nights tracked	Pre/Post partum	Home range (MCP, ha)	Foraging area (50% kernel, ha)	Number of roosts used
01	15/05/2009	5.5	5	Pre	94.5	28.7	2
02	15/05/2009	5	5	Pre	131.2	18	2
03	15/05/2009	4.9	5	Pre	164.5	14.5	2
04	23/05/2009	5.5	5	Pre	71.2	5.8	2
05	26/06/2009	5.5	5	Post	201.9	43.9	2
06	26/06/2009	5	5	Post	376.9	69.5	2
07	26/06/2009	5	5	Post	412.2	110.1	2
08	26/06/2009	5	4	Post	160.6	55.9	2
09	26/06/2009	5	4	Post	788.1	293.8	4
10	04/07/2009	5.5	5	Post	115.4	29.8	1
11	04/07/2009	5.5	5	Post	84.5	42	1
12	04/07/2009	5	5	Post	264	33	2
13	04/07/2009	5	5	Post	97	18.2	1

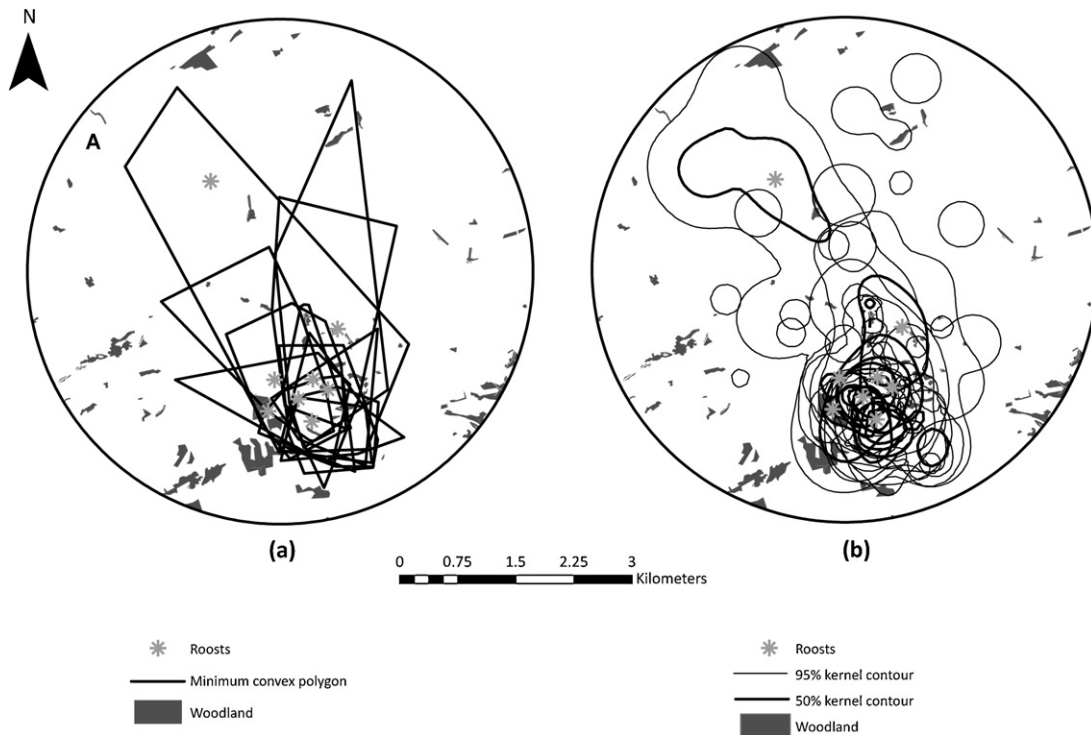


Fig. 2. (a) The home range (Minimum convex polygon); and (b) the core foraging area (50% kernel contour) and 95% kernel contour for each *M. mystacinus* individual. Woodland blocks are marked in grey.

selection/avoidance for discrete habitat types (Manly et al. 2002). If the \hat{w}_i of a habitat is >1 , there is positive selection for that habitat; and, if <1 , the habitat is avoided. Confidence intervals were estimated for \hat{w}_i using the z statistic. Habitat analysis was applied using the package “Adehabitat” (Calenge 2006) in R (R Development Core Team 2009).

Results

Eighteen bats were tagged (17 females and one male). However, sufficient data (four or five tracking nights as recommended by Smith and Racey (2005a)) for analysis were only collected for 13 bats (all female). Four bats were tracked pre-partum and nine post-partum (Table 1).

Mean home range area (MCP) for all tagged individuals was 227.8 ha (s.e. ± 55.6). Home range area for individual bats ranged from 71.2 ha to 788 ha (Table 1). Mean core area (50% kernel contour) was 58.7 ha (s.e. ± 21.06), ranging from 5.8 ha to 293.8 ha (Table 1). The mean home range size pre-partum was 115.35 ha (s.e. ± 20.5), whilst the mean home range size post partum was 277.8 ha (s.e. ± 92.6). This difference was not significant (Mann–Whitney $U=8, n1=4, n2=9, P>0.05$). The mean Euclidean distance between the most frequently used day roosts and the centre of core foraging

areas by individuals was 0.7 km (s.e. ± 0.2). The mean total distance travelled by bats each night was 5.01 km (s.e. ± 0.39). The mean total distance travelled pre-partum was 3.9 km (s.e. ± 0.52), whilst the mean total distance travelled post-partum was longer at 5.1 km (s.e. ± 0.43) but this difference was also not significant (Mann Whitney $U=6, n1=4, n2=8, P>0.05$). The average percentage overlap of home ranges (48% (s.e. ± 2.05)) was significantly greater than the average percentage overlap between core foraging areas (38% (s.e. ± 2.49) (Fig. 2)) ($P<0.05$).

Habitat use

The available area utilised by bats encompassed 33.2 km² (Fig. 1). Pasture was the dominant habitat in the surrounding area making up over 60% of land cover. Cover by all woodland classes summed to less than 7.5% (Fig. 3). The test of overall home range selection (MCPs v available area) was significant ($P<0.05$). Mixed woodland, riparian areas, arable land and rough grassland were selected positively (Fig. 3). The test for overall foraging area selection (core areas v MCPs) was significant ($P<0.05$), with mixed woodland and riparian areas selected (Fig. 3). Pasture, amenity grassland and lake were avoided at both selection levels.

Table 2
Details of roosts utilised by *M. mystacinus* in this study.

Roost	Type	Construction material	Roof material	Age (yrs)	Number of bats using roost
Roost A ^a	Dwelling house	Stone	Natural slate	100+	9 ^a
Roost B	Dwelling house	Concrete	Artificial slate	<10	2
Roost C ^a	Shed	Concrete	Corrugated iron	30+	10 ^a
Roost D	Dwelling house	Brick	Artificial slate	30+	1
Roost E	Dwelling house	Stone	Natural slate	100+	1
Roost F	Beech tree	Not applicable	Not applicable	100+	2
Roost G	Beech tree	Not applicable	Not applicable	100+	1
Roost H	Sycamore tree	Not applicable	Not applicable	100+	1

^a Roost at which bats were captured for tracking study.

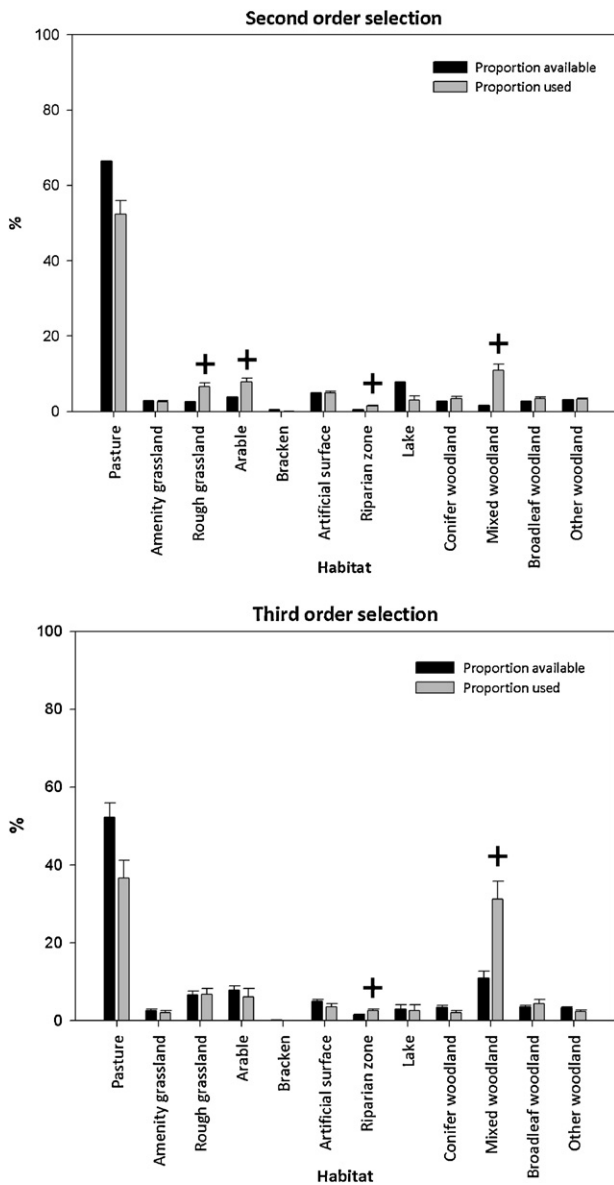


Fig. 3. Selectivity indexes (\hat{w}_i) with standard errors (S.E.) for second order (MCPs v Available area) and third order (core area v MCPs) habitat selection as described in Manly et al. (2002). Habitats that were selected by *M. mystacinus* are marked by a cross.

Roost use

M. mystacinus utilised a variety of structures for roosting in this study (Fig. S1). Buildings ranged from a 100 year old house with natural stone walls and a natural slate roof to a farm shed with concrete walls and a corrugated roof. All tree roosts were mature broadleaved species, *Fagus sylvatica* (Beech) or *Acer pseudo-platanus* (Sycamore). Individual *M. mystacinus* were not faithful to single roosts but utilised a network of seven daytime roosts, comprising four dwelling houses, one agricultural building and two trees (Table 2 and Fig. 1). Bats generally returned to their daytime roosts during the night. An additional tree roost (G, Fig. 1) was used as a night roost by a single bat. On average, female bats used 1.8 (s.e. ± 0.2) roosts over a tracking session (5 days). Bats were observed directly during the day in roost A (between rafters) and roost C (between the corrugated iron roof and interior bitumen lining).

Discussion

In continental Europe, *M. mystacinus* has been described as both a forest species (Kanuch et al. 2008) and a species of open, lowland agricultural landscapes (Taake 1984). Taake (1984) described an association between *M. mystacinus* with open landscapes but also an association with rivers. In Britain, Berge (2007) identified semi-improved and improved grassland as the most important habitat for this species. Here, we show that *M. mystacinus* in Ireland, an island population at the north west limit of its range, selectively favoured mixed woodland and riparian habitats both with respect to home range and foraging area selection. Arable areas and rough grassland were also selected at the home range level. The present study found that intensively managed grassland was avoided. The wing morphology of *M. mystacinus* suggests adaptation for foraging in cluttered spaces as opposed to more open environments (Jones 1991; Siemers and Schnitzler 2004). Hence, the present study and that of Kanuch et al. (2008) are more in keeping with the presumed primary adaptations for feeding in this species than those suggesting preference for open areas of grassland (Taake 1984; Berge 2007). These differences, however, are independent of proximity to edge of range.

M. nattereri also displays regional differences in habitat use, foraging principally over pasture in Ireland (Lundy et al. 2012) but in broadleaf riparian woodland in England (Smith and Racey 2008), in pine plantations and waterbodies in Scotland (Mortimer 2006) and meadows and orchards in Switzerland (Arlettaz 1996). Regional variation in habitat use have also been observed in the European woodland avifauna, where some bird species which are confined to the forest interior in Eastern Europe have been shown to occupy a broader range of habitats in both the British Isles and mainland Western Europe and species utilisation of broadleaf and conifer woodland can differ across regions (Fuller 2002). This has been attributed to a number of factors, including climate, habitat structure, habitat complementarity, intra and inter specific competition, adaptation to local conditions, environmental stability and landscape history (Fuller 2002) and some of these factors may also explain habitat variability in bats.

Competitive release of a species due to the absence of an ecological competitor has been recorded on some island populations of bats. *Lasius cinereus semotus* (the Hawaiian hoary bat) has undergone a 45% reduction in body size, altered its' wing morphology, enabling it to forage in both open and closed environments and increased its' jaw gape to consume hard-bodied insects (Jacobs 1996). Similarly, *Nyctalus azoreum* (the Azorean noctule) is able to forage diurnally, possibly due to a lack of competition from birds (Moore 1975). As *M. brandtii* is known to forage in forested environments in Britain and continental Europe (Ekman and De Jong 1996; Berge 2007), the difference in habitat use between *M. mystacinus* in Ireland and other regions of Europe may be due to the scarcity or absence of *M. brandtii* (Boston et al. 2010) or other woodland specialist species in Ireland, enabling *M. mystacinus* to select woodland habitats in the absence of competition. Regional differences in landscape composition, particularly in relation to forest and freshwater, and prey distribution could also potentially explain the utilisation of different habitats by *M. mystacinus* in different regions. These local adaptations can have evolutionary consequences as they can lead to population structuring based on local phenotypic and genetic change due to differential selective pressure (Holt 1987).

During this study, individual bats were observed foraging over and adjacent to a woodland stream, but other stands of broadleaved trees were not utilised. This may indicate that the riparian component of woodland is more important to *M. mystacinus* than tree species composition. Riparian areas have been shown to be important as a foraging habitat for bats (Vaughan et al. 1997a;

Russ and Montgomery 2002; Downs and Racey 2006). Walsh and Harris (1996) found that bat abundance in Britain was positively correlated to the availability of woodland, riparian and lacustrine habitats. Grindal et al. (1999) found significantly higher bat activity and also captured more female bats in riparian forest stands in southern British Columbia. The abundance of emerging aquatic insects in riparian woodlands was shown to be one of the most important factors affecting the distribution of foraging bats in riparian deciduous woodland in Japan (Fukui et al. 2006). Forest streams also provide suitable foraging environments for bats as they create larger gaps between trees facilitating commuting and hunting by bats along structural edges (Seidman and Zabel 2001) as well as providing shelter for insects. This may be important to bat species that have slow manoeuvrable flight like *M. mystacinus*, which may also be vulnerable to predation (Warren et al. 2000; Lundy and Montgomery 2009).

Our radio tracking results revealed a large amount of overlap in home ranges and core foraging areas between individuals as similarly described in *Pipistrellus* spp. (Nicholls and Racey, 2006). In contrast, Dietz and Pir (2009) showed individual *M. bechsteinii* to have little or no overlap in core foraging areas. As survival and reproduction are often food limited, the abundance and predictability of food resources in time and space are likely to be important factors influencing spatial organisation (McLoughlin et al. 2000). Carpenter and MacMillen (1976) theorised that territoriality in a species breaks down at an upper and lower threshold of resource abundance due to putative costs and benefits of defending a feeding territory. As Ireland lies at the north western edge of the range of *M. mystacinus* (Dietz et al., 2009), it may be more constrained by the availability of suitable habitat, particularly for female bats which require more productive habitats, to rear young successfully (Encarnação et al. 2005). This may lead to a breakdown in territoriality as observed in the present study. Alternatively, as insect availability is highly aggregated (Taylor 1963), suitable habitat patches may have a super abundance of potential prey for bats negating the need for territoriality between individuals. Similarly, as insect abundance varies over time (Fukui et al. 2006), a colony could switch between territorial and non-territorial foraging depending on immediate resource abundance.

Female *M. mystacinus* were not roost faithful, using more than one roost during the breeding period. Although roost switching is generally associated with species that utilise roosts, such as trees (Lewis 1995), where environmental conditions can frequently change, this behaviour also occurs in species that use more permanent structures, such as buildings. *M. nattereri* (Natterer's bat), for example, uses a network of roosts within the foraging range of a colony and frequently moves between them (Smith and Racey 2005b). In Ireland, however, *M. nattereri* has been shown to be roost faithful (Lundy et al. 2012). Lewis (1995) proposed that roost switching in bats is due to individuals needing to be close to their core foraging areas. This appears to be the most likely scenario in the present study as bats roosted in close proximity to their core foraging areas and roosts were occupied by relatively small numbers of bats. Berge (2007) found a similar pattern of roost switching and short commuting distance for *M. mystacinus* with the average maximum distance travelled being 0.81 km. Although buildings (both occupied and unoccupied) were utilised as roosts by *M. mystacinus* in both the current Irish study and the British study, tree roosts, which were utilised in the Irish study, were not utilised by *M. mystacinus* in the British study (Berge 2007).

Conclusions and conservation implications

This study highlights the different ecological relationships that can occur within a species across its range. This variation amongst

bat populations seems to be related to local or regional factors rather than proximity to the edge of the species range. Consequently, where regional adaptations occur, reliance on information from remote studies to develop detailed conservation plans for a particular region is inappropriate. The use of a diverse range of buildings in both age and structure, as displayed by *M. mystacinus*, indicates that this species is adaptable in its roosting behaviour. However, this roost switching behaviour also implies that protection of a single roost may not be sufficient to ensure long-term population survival. A protected area should include a number of suitable roost sites. The retention of stands of mature deciduous trees could potentially benefit *M. mystacinus* through the long term provision of natural roosting sites.

Protection of riparian woodland in the immediate vicinity (within 0.5–1 km) of roosts should also be a conservation priority. Indeed, the establishment and protection of such woodlands in Ireland, may benefit *M. mystacinus* greatly, given the low level of woodland cover there (Gallagher et al. 2001; Perrin et al. 2006). Conversely, clear felling in riparian areas may have negative impacts on *M. mystacinus*. The creation of riparian buffer zones (minimum 30 m) of natural vegetation, particularly native woodland would help to mitigate for this (Broadmeadow and Nisbet 2004; Lloyd et al. 2006).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.mambio.2012.06.007.

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