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Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey

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ABSTRACT

Agricultural expansion has led to the widespread destruction of habitats and the creation of fragmented landscapes. Woodland has been severely affected by habitat loss; remaining woodland is often highly fragmented and degraded, immersed in an agricultural matrix. Woodland is one of the most important habitats for bats because it offers roosting and feeding opportunities for many species. A number of agri-environment schemes aim to increase the amount and quality of woodland on agricultural land; however, little is known about how woodland character relates to bat abundance/activity and recommendations for woodland creation and management for foraging bats are scarce. We studied temperate bat communities and examined bat foraging activity and relative abundance (and insect prey availability) in 34 woodland fragments in agricultural landscapes using two complementary methods (acoustic monitoring and trapping assisted by an acoustic lure). We evaluated the relative importance of woodland vegetation character, patch configuration and surrounding landscape in order to assess the importance of local- vs. landscape-scale woodland management to bat populations. Bat abundance and activity were influenced by both local and landscape-level attributes. At the local scale, woodland vegetation character appeared more important than patch configuration. High activity levels of aerial hawkers (e.g. *Pipistrellus* species) were related to low tree densities and an open understory, while gleaning species (e.g. *Myotis* bats) showed the opposite trend. Areas of cluttered vegetation were associated with high insect (mostly Diptera) abundance and could act as sources of prey for certain bat species. Bats' responses to the surrounding landscape depended on species mobility. For relatively low mobility species (e.g. *Pipistrellus pygmaeus*), local woodland character was more important than the landscape context, whereas the opposite was observed for higher mobility species (e.g. *Pipistrellus pipistrellus* and *Myotis* bats). Higher bat activity levels were observed in small and isolated woodland fragments, and in sparsely wooded landscapes. This may reflect a more intensive use of woodland in landscapes where this habitat is scarce, where woodland creation should be prioritised. Woodland management and creation schemes should encourage habitat heterogeneity to fulfil the requirements of different bat species.

1. Introduction

Agricultural expansion has led to the widespread destruction of habitats and the creation of fragmented landscapes. Forest systems have been severely affected by habitat loss and their cover has been reduced by ca. 50% worldwide in the last three centuries (Groom et al., 2006). Remaining woodlands are often highly fragmented and degraded, consisting of a large number of relatively small and isolated patches immersed in an agricultural matrix. Vegetation structure and spatial configuration are usually altered in fragmented woodlands, which can affect biological communities by e.g. creating dispersal barriers and edge effects (Groom et al., 2006). Although species responses to habitat fragmentation are variable (depending on life-history traits such as specialisation and mobility; Groom et al., 2006), this process is regarded by many as one of the greatest threats to biological diversity (e.g. Fahrig, 2003).

Woodland is one of the most biologically diverse systems on Earth and one of the most important habitats for bats because it offers roosting and feeding opportunities for many species (Lacki et al., 2007). Therefore, worldwide deforestation has resulted in many bat species suffering severe population declines (Mickleburgh et al., 2002). Woodland vegetation structure is of great importance in determining habitat quality and availability for bats. Although the concept of 'quality' depends on the specific requirements of a particular species, in general, mature hardwood forest stands with high availability of large diameter snags,

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dense canopy cover and reduced clutter (e.g. low tree density and understory cover) are often associated with high bat activity levels because they provide roosting and foraging opportunities for bats (Lacki et al., 2007).

The configuration and extent of a woodland patch can also have a strong influence on bat communities. Island biogeography theory (IBT; MacArthur and Wilson, 1967) suggests that the number of species inhabiting an island depends on its size and isolation. Its conceptual framework has been extended from real islands to terrestrial ecosystems in order to understand the effects of habitat loss and fragmentation on biodiversity. Patterns of bat species richness on real islands are consistent with those predicted by IBT (i.e. positively related to area and negatively related to isolation; Frick et al., 2008). In terrestrial ecosystems, however, large woodland patches do not necessarily support more species or larger populations of bats than small patches (Law et al., 1999; Estrada and Coates-Estrada, 2002). Relatively small woodland fragments may provide roosting opportunities and support populations of many bat species, especially if they are located relatively close to other fragments and have a high structural diversity (Estrada and Coates-Estrada, 2002; Meyer and Kalko, 2008; Boughey et al., 2011). However, the response of bats to woodland fragmentation can vary between species. Fast-flying species adapted to forage in uncluttered environments are relatively tolerant to habitat fragmentation, and may show higher abundance and activity levels in small and isolated fragments (Estrada-Villegas et al., 2010) or in sparsely wooded landscapes (Klingbeil and Willig, 2009). In contrast, slow-flying and highly manoeuvrable species are usually more sensitive to habitat isolation and show positive associations with woodland availability (Law et al., 1999; Meyer and Kalko, 2008). Roosting ecology and edge-affinity have also been identified as good predictors of bat species' sensitivity to habitat fragmentation; 'woodland interior' species (often tree-roosting bats) are negatively affected by fragmentation, as opposed to species which show affinity for woodland edges (often roosting in human-made structures; e.g. Meyer et al., 2008). Many bat species are highly mobile; therefore, it is likely that they will be influenced not just by the local character of a woodland patch, but also by the surrounding landscape at relatively large spatial scales (e.g. within 5 km; Klingbeil and Willig, 2009).

As a consequence of long-term deforestation, woodland cover in the United Kingdom (UK) has been drastically reduced. At the beginning of the 20th century woodland comprised a mere ca. 5% of the UK's land area, but programmes of afforestation over the last 50 years have increased this figure to approximately 12% (Mason, 2007). Much of this consists of forestry plantations, which in many cases have low species richness and structural diversity, and which provide fewer roosting and feeding opportunities for bats than ancient semi-natural woodland (Altringham, 2003; but see Mortimer, 2006). The remaining woodland is highly fragmented and consists of a large number of relatively small patches (<100 ha) within agricultural landscapes (Watts, 2006). Currently in the UK, a number of agri-environment schemes (AES; financial incentives used in Europe and North America for farmers to adopt less intensive, environmentally-sensitive agricultural practices) aim to increase the amount and quality of woodland on agricultural land. Despite the importance of woodland habitat for all UK bat species (e.g. Walsh and Harris, 1996; Vaughan et al., 1997), little is known about how woodland character relates to prey availability and bat abundance and diversity (but see Hill and Greenaway, 2008). To date, most studies assessing the effects of woodland character and fragmentation on bats have been conducted in tropical ecosystems and/or predominantly forested areas, and only rarely in farmland-dominated landscapes where the effects of woodland fragmentation are likely to be stronger (Andrén, 1994). As a result, recommendations for the creation and management of farm woodland to improve habitat for wildlife in many temperate countries seldom take the needs of bats and their insect prey into consideration; therefore, management guidelines for bats are scarce, and the ones that exist focus on creating/maintaining roosting opportunities rather than enhancing good foraging habitat (Anonymous, 2005; but see Entwistle et al., 2001). Furthermore, studies that investigate the effect of woodland character at several spatial scales, incorporating local character and surrounding landscape effects on bat populations are few (e.g. Erickson and West, 2003).

Here, we assess the response of a temperate bat community, and their insect prey, within an agricultural landscape to woodland fragmentation at several spatial scales. In particular, we address four specific questions:

1. Does insect prey availability relate to woodland characteristics and, if so, to which specific attributes?
2. Do bat abundance and activity levels relate to woodland vegetation character (e.g. tree density) and patch configuration (size and shape) and, if so, to which specific attributes?
3. Does the surrounding landscape (e.g. proportion of woodland cover) influence bat abundance and activity levels in woodland patches and, if so, to what spatial extent?
4. What is the relative importance of woodland vegetation character, patch configuration and surrounding landscape for bats (i.e. is local management of woodlands sufficient to enhance bat populations or is a landscape-scale management approach important)?

We expect certain bat species to be more strongly affected by woodland fragmentation than others, according to differences in their ecology (Table 1). In addition, we expect the relative importance of woodland vegetation character, patch configuration and surrounding landscape to differ between bat species: lower mobility species should be more influenced by the local habitat (e.g. vegetation character), and by patch isolation, compared to higher mobility species which may be more affected by landscape factors at large spatial scales.

2. Methods

This work was conducted in the same sites and parallel to a study assessing the influence of woodland character on moth assemblages. Therefore, only essential information on site selection and vegetation survey methods is presented here; for further details see Fuentes-Montemayor et al. (2012).

2.1. Site selection and study design

Thirty-four woodland patches of different size (0.1–30 ha) and shape (ranging from compact to complex) within agricultural land in central Scotland, UK (Appendix A) were surveyed for vegetation, nocturnal insects and bats once during the summers of 2009 (June to August, 20 sites) and 2010 (May to July, 14 sites). Woodlands consisting purely of conifer plantations were excluded from the site selection process because they are often composed mainly of exotic tree species and are of comparatively low conservation value to biodiversity (Mason, 2007). Bat surveys and nocturnal insect sampling occurred simultaneously and were only conducted in dry weather, when temperature was $\geq 8\,^{\circ}C$ and wind force $\leq$ Beaufort scale 4.

2.2. Tree vegetation surveys

Surveys were conducted along transects 100 m in length (number of transects per site depended on woodland size) with points