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Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats

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A B S T R A C T

Cryptic species are similar in morphology, and make interesting subjects for relating morphological differentiation to ecological resource partitioning. Can species that are morphologically almost identical occupy different ecological niches, and hence potentially need distinct conservation planning? The discovery that the most widespread bat in Europe – the pipistrelle – comprised two cryptic species (*Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*) that emit echolocation calls at different frequencies provides a remarkable model system for investigating links between morphology, echolocation call design and resource partitioning. We investigated resource partitioning between the two cryptic species of sympatric pipistrelle bats by radio tracking breeding females. Habitat selection was investigated by using compositional analysis. *P. pygmaeus* selected riparian habitats over all other habitat types in its core foraging areas, whereas *P. pipistrellus*, although preferring deciduous woodland overall, was more of a generalist, spreading its foraging time in a wider range of habitats. Although morphologically very similar, the cryptic species show quite different patterns of habitat use. Our findings suggest that large-scale differences in habitat preferences can occur between sympatric bat species that are virtually identical in flight morphology; hence morphological differences may be a weak indication of ecological differences between taxa. Conservation planning needs to take account of these differences to meet policy and legal obligations associated with these protected cryptic species.

1. Introduction

Cryptic species are defined as species 'the diagnosable features of which are not easily perceived' (Mayr, 1977). Because humans perceive their world largely by vision, most cryptic species are usually defined in relation to our visual performance (Jones, 1997). Cryptic species are similar in morphology, and these similarities make them ideal taxa for relating morphological differences to ecological resource partitioning. If cryptic species are morphologically similar, and if morphology determines resource use, how then do cryptic species partition resources?

Cryptic species are widespread in bats (Jones, 1997; Jones and Barlow, 2004). Sometimes cryptic bat species are similar

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in terms of both flight morphology and echolocation calls, although in many cases morphologically similar species emit different frequencies of echolocation calls (Jones and Barlow, 2004). The discovery that the most widespread bat in Europe – the pipistrelle – comprised two cryptic species *Pipistrellus pipistrellus* (Schreber, 1774) and *Pipistrellus pygmaeus* (Leach, 1825) that emit echolocation calls at different frequencies (Jones and van Parijs, 1993; Barratt et al., 1997) provides a remarkable model system for investigating links between morphology, echolocation call design and resource partitioning. Although these bats are extremely similar in their flight morphology (Jones and van Parijs, 1993; Barlow and Jones, 1999), they echolocate with call frequencies close to either 45 kHz (*P. pipistrellus*) or 55 kHz (*P. pygmaeus*). Flight morphology is often linked closely with flight performance (e.g. speed and manoeuvrability) and habitat use in bats (Norberg and Rayner, 1987), so species with similar wing shapes are expected to exploit foraging habitats in similar ways. The differences in call frequency between the two species are now thought to facilitate intraspecific communication, rather than allowing the bats to specialise on different size classes of prey as determined by wavelength-dependent target strengths from prey of different sizes (Jones and Barlow, 2004).

The loss or modification of semi-natural habitats and pesticide use associated with agricultural intensification are considered to be primary factors for the reduction of many European bat populations since the 1940s (Stebbings, 1988; Ransome, 1990; Hutson, 1993; Walsh and Harris, 1996a,b; Schober and Grimmberger, 1997). The accurate description of habitat requirements for bats is therefore a key part of their conservation management (Walsh and Harris, 1996a). Bat detector surveys of the two cryptic pipistrelle species suggest that *P. pipistrellus* is a generalist, whereas *P. pygmaeus* is more of a specialist, spending most of its time foraging in riparian habitats (Vaughan et al., 1997; Russ and Montgomery, 2002). *P. pipistrellus* also mainly eats dipteran flies in the families Psychodidae, Anisopodidae and Muscidae, whereas *P. pygmaeus* eats mainly flies with aquatic larvae in the families Chironomidae and Ceratopogonidae (Barlow, 1997).

Studies on resource partitioning of these pipistrelle species thus far have used acoustic monitoring to determine habitat use. No study has investigated habitat use in relation to availability. We previously used radio tracking to successfully determine how these species range away from their maternity sites (Davidson-Watts and Jones, 2006). Our objective here is to investigate habitat preferences by using radio tracking to determine whether the two cryptic pipistrelles select different habitat types. For this we use a novel application of compositional analysis comparing cluster polygons of localizations with habitat available in individual home ranges. Based on dietary studies (Barlow, 1997), we hypothesise that *P. pygmaeus* will be more selective of riparian habitats, while *P. pipistrellus* will spread its flying time more evenly over a range of different habitat types. We relate any differences in habitat selection to morphology and echolocation call design. We are interested in whether protected species that are morphologically almost identical need similar or different conservation planning during a critical period of their life cycle: the breeding period. Maternity roosts are sites of prime conservation concern, and effective habitat management around maternity roosts is vital for protecting key foraging areas of bats.

If resource partitioning exists between the cryptic pipistrelles, separate conservation and monitoring strategies may be necessary for each species, both of which are protected by law in Britain and in the European Union (Wildlife and Countryside Act, 1981 (as amended) and the EC Habitats Directive 1992 (Annex IV)).

2. Methods

2.1. *Study area and habitat mapping*

Study areas were defined on the basis of colony home ranges. *Pipistrellus pipistrellus* was studied at two areas in the Avon Valley, on the Hampshire/Wiltshire county border, England, UK. Study area A was based around the villages of Downton, Redlynch and Charlton all Saints (50°59′N, 1°43′W – maximum elevation 109 m). Data from 12 *P. pipistrellus* were obtained at this study area during May and June (pregnancy) 2001 and 2002. Study area B was based around the village of Breamore, approximately 3 km south of study area A (50°57′N, 1°46′W – maximum elevation 93 m). Data from 12 *P. pipistrellus* were obtained at this study area during July and August 2003 (lactation). There was no overlap in the colony home ranges of study areas A and B because *P. pipistrellus* moved roost between pregnancy and lactation.

The study of *P. pygmaeus* was also conducted in the Avon Valley and based around the villages of Hyde, Bickton and North Gorley (50°54′N, 1°46′W – maximum elevation 83 m). Data were obtained from 25 *P. pygmaeus* in this study area during May, June, July and August (i.e. during pregnancy and lactation) in 2001 and 2002. The *P. pygmaeus* study area is approximately 5 km south of *P. pipistrellus* study area B, and is termed study area C. In total, bats used a total of 45 different roost sites within the study area (see Section 3).

The study areas for both species were dominated by the broad floodplain of the River Avon (The Avon Valley) and comprise mainly hay meadows and pastures, with some arable land dissected by drainage ditches and streams that derive from the main river which is frequently subject to winter flooding. As a result, there is a high proportion of unimproved grasslands and other semi-natural habitats such as reed beds, riparian woodlands with fens on river terraces, making this an area of high ecological importance (English Nature, 1998). Enclosing the broad valley and also forming parts of the study areas was a range of land use/habitat types. These included, intensively managed agricultural land, semi-improved and unimproved acidic and calcareous grassland, woodland and a variety of human settlements from single houses to villages.

For study areas B and C habitat data were extracted from databases of the Hampshire Biodiversity Information Centre (HBIC), which provided digitised Phase 1 habitat survey (Nature Conservancy Council, 2004) data. HBIC habitat data were based on field surveys undertaken from 1979 to 2002 and analysis of aerial photographs in 1996/1997 and 2000. Habitat