Testing for complex drivers of resource utilisation: A case-study of roost dynamics in bats

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Abstract

The extent to which a resource (e.g. nest site, food resource) is available and utilised in the wild is of fundamental importance to the understanding of species' biology, community ecology, and for evidence-based conservation and habitat management. However, dynamics of resource use is challenging to study because it is likely determined by a complex set of (often unknown) factors and their interactions, and because of imperfect and biased detection rates (usually false absences). In this study we test for multiple drivers of summer roosting site occupancy by bats, using a rigorous statistical framework that combines multi-state occupancy models with two-class heterogeneity models. Understanding the utilization of this critical resource is a pre-requisite for any successful conservation management of (often declining) bat populations. We evaluated the importance of several external and internal sources of inter-annual roost occupancy dynamics in a community of three sympatric woodland bat species: weather, roost spatial position, roost intrinsic (unmeasurable) quality, memory effect in roost use, and inter-species dynamics. We identified the existence of two classes of the roost's intrinsic quality, and showed that bats tend to re-occupy previously occupied roosts irrespective of the roost intrinsic quality (memory effect). At the landscape scale, distance from water but not from the woodland edge influenced occupancy dynamics, with roosts closer to water having higher probability of being occupied. We also identified species-specific patterns of roost occupancy, colonisation and extinction, and between-species roost interchange. Our statistically powerful and flexible modelling approach can distinguish between multiple drivers of resource occupancy: measurable factors (environmental conditions and resource traits), unmeasurable (hidden or unknown) factors, previous use of the resource (memory effect) and community-level interactions. As such, it can be used to identify important areas for species (or communities), as well as to test evolutionary and ecological hypotheses concerning resource utilisation.

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Introduction

The extent and the dynamics of resource use are fundamental to understanding ecological patterns and processes, and to the evidence-base that underpins conservation (Guillera-

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Arroita et al. 2014; Sutherland et al. 2014). Resource use, often referred to as resource occupancy, can broadly be viewed as the probability of an entity occurring in/using a predefined type of a unit (Chambert et al. 2015) and has been used to study wildlife epidemiology, invasion biology, meta-population dynamics, and community ecology (Gimenez et al. 2014). Monitoring and understanding the dynamics of species distribution and patterns of resource use is also crucial to inform management of wild populations, especially in the face of human-induced biodiversity loss and environmental change (Carvalho et al. 2015). The basis of such attempts relies on defining accurate and unbiased variation in resource use, influential extrinsic (e.g. environmental) and intrinsic (inherent to the resource itself) factors, and the way a resource is partitioned within the wider community of species utilising it.

Despite its pivotal importance, estimating occupancy of a resource and its extrinsic and intrinsic drivers is challenging. Imperfect and often biased detection rates (usually false absences) reduce the accuracy of occupancy estimates and can lead to misleading interpretations (Knape & de Valpine 2012; Peron et al. 2013; Guillera-Arroita et al. 2014). The problem is exacerbated if detection bias is species- or population-specific, and/or temporally variable within the population. Further errors may arise when the resource use is heterogeneous, but the sources of heterogeneity are unknown and unaccounted for (Peron et al. 2010; Gopalaswamy et al. 2015). This heterogeneity is usually attributed to some measurable traits. However, the complexity of, and interaction amongst many potential sources of heterogeneity, as well as the possibility that an important trait (or traits) was not taken into account can lead to misidentification or omission of important differences in resource attractiveness. This 'hidden' heterogeneity, thus, remains poorly studied.

Summer diurnal roosts are a crucial resource for the majority of bat species, providing shelter and protection from predators and environmental extremes. Roost occupancy patterns also influence disease dynamics, parasite loads, social interactions, and reproductive strategies (Barclay & Kurta 2007; Encarnação, 2012). Understanding the roost occupancy dynamics in woodlands, as a primary foraging and roosting habitat for many bat species, plays an important role in conservation of declining bat populations in highly human-impacted landscapes (Psyllakis & Brigham 2006). The total number of roost sites available to, or utilised by, a given population of bats is usually unknown and difficult to estimate. When the same roosts are utilised by more than one species the importance of a particular roost for a given species requires an understanding of the wider context of roost availability and occupancy patterns exhibited by both that species and other sympatric species.

In this study we use long-term data on summer day roosts utilised by three sympatric bat species to increase understanding of bat roosting community ecology and to formulate a general and flexible framework for studying heterogeneous rates of resource use and the memory effect in resource use under imperfect and biased detection rates. Specifically, in our study system we tested if:

i) roost attractiveness to bats depends on the distance from water and woodland edge (reflecting the species' feeding ecology), and/or hidden heterogeneity in roost quality (intrinsic quality);

ii) boxes used as roosts in year t are more likely to be reoccupied in year $t + 1$ regardless of their intrinsic quality (a memory effect);

iii) between-year variation in box occupancy rates depends on weather conditions: average temperatures, cumulative rainfall, and number of cold dawns;

iv) species show different patterns of box use, including the likelihood of colonising 'unoccupied' boxes, and rates of roost interchange between species.

We formulate a framework that combines occupancy models (which estimate occupancy while accounting for false absences) with two-class mixture models (which allow for the incorporation of unknown sources of heterogeneity, Gimenez & Choquet 2010). This approach is thus valuable beyond our study system, offering a statistically robust and flexible framework to determine factors influencing heterogeneous and dynamic use of resources in wild populations: resource quality (measured and unmeasured/hidden), external factors, memory effect (repeated use of the same resource) and communities of species using the resource (Fig. 1).

Materials and methods

Ethical statement

All bat species found in the UK are European Protected Species (EPS) and their roosts are protected from disturbance. All survey work carried out by bat researchers at Wytham has been undertaken in accordance with Natural England project licence 2014/SCI/0399 and preceding licences.

Studied species

Myotis daubentonii Kuhl (abbreviated to Md), *Myotis nattereri* Kuhl (abbreviated to Mn), and *Plecotus auritus* L. (abbreviated to Pla), are medium-sized (7–13 g) insectivorous vespertilionid bats common and widespread across the UK and NW Europe. All three species roost in tree cavities, especially in deciduous woodland habitats, and occupy a variety of man-made structures (Altringham 2003). *M. daubentonii* specialises in foraging over calm water, with a high proportion of foraging activity concentrated at waterbodies (Kapfer et al. 2008). Niches of *M. nattereri* and *P. auritus* partially overlap as both species forage within woodland and a variety of other habitats (Entwistle, Racey, Speakman, 1996; Smith & Racey 2008) and capture prey by gleaning non-volant arthropods (Swift & Racey 2002).