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Behavioural context of multi-scale species distribution models assessed by radio-tracking

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Abstract

Incorporating ecological processes and animal behaviour into Species Distribution Models (SDMs) is difficult. In species with a central resting or breeding place, there can be conflict between the environmental requirements of the 'central place' and foraging habitat. We apply a multi-scale SDM to examine habitat trade-offs between the central place, roost sites, and foraging habitat in *Myotis nattereri*. We validate these derived associations using habitat selection from behavioural observations of radio-tracked bats. A Generalised Linear Model (GLM) of roost occurrence using land cover variables with mixed spatial scales indicated roost occurrence was positively associated with woodland on a fine scale and pasture on a broad scale. Habitat selection of radio-tracked bats mirrored the SDM with bats selecting for woodland in the immediate vicinity of individual roosts but avoiding this habitat in foraging areas, whilst pasture was significantly positively selected for in foraging areas. Using habitat selection derived from radio-tracking enables a multi-scale SDM to be interpreted in a behavioural context. We suggest that the multi-scale SDM of *M. nattereri* describes a trade-off between the central place and foraging habitat. Multi-scale methods provide a greater understanding of the ecological processes which determine where species occur and allow integration of behavioural processes into SDMs. The findings have implications when assessing the resource use of a species at a single point in time. Doing so could lead to misinterpretation of habitat requirements as these can change within a short time period depending on specific behaviour, particularly if detectability changes depending on behaviour.

Zusammenfassung

Es ist schwierig die ökologischen Prozesse und das Verhalten von Tieren in Modellen der Artverbreitung (species distribution model: SDM) zu berücksichtigen. Bei Arten, die einen zentralen Ruhe- oder Brutplatz haben, kann es einen Konflikt zwischen den Umweltanforderungen an diesen zentralen Platz und dem Nahrungshabitat geben. Wir wenden ein SDM auf multiplen Skalen an, um die "trade offs" in Bezug auf das Habitat zwischen dem zentralen Ort, den Rastplätzen und dem Nahrungshabitat bei *Myotis natteri* zu untersuchen. Wir validieren die abgeleiteten Beziehungen

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indem wir die Habitatselektion auswerten, die wir durch Verhaltensbeobachtungen an besenderten Fledermäusen feststellen. Ein generalisiertes lineares Modell (GLM) der Rastvorkommen, das die Variablen der Flächenanteile auf gemischten räumlichen Skalen auswertet, war auf der feinen Skala mit Waldvorkommen und auf der großen Skala mit Weidelandvorkommen positiv assoziiert. Die Habitatselektion der besenderten Fledermäuse spiegelte das SDM wider, da die Fledermäuse Waldvorkommen in der unmittelbaren Umgebung der individuellen Rastplätze wählten, dieses Habitat jedoch in den Nahrungsgebieten mieden, und Weideflächen bei den Nahrungsgebieten signifikant positiv ausgewählt wurden. Die Verwendung der Habitatselektion aufgrund der Telemetrie ermöglicht es, ein SDM auf multiplen Skalen in einem Verhaltenskontext zu analysieren. Wir schlagen vor, dass das SDM auf multiplen Skalen für *M. natteri* einen "trade off" zwischen dem zentralen Platz und den Nahrungshabitaten beschreibt. Multiskala-Methoden ermöglichen ein besseres Verständnis der ökologischen Prozesse, die bestimmen wo Arten auftreten, und erlauben es, Verhaltensprozesse in ein SDM zu integrieren. Die Ergebnisse haben Auswirkungen, wenn abgeschätzt wird, welche Ressourcen eine Art zu einem Zeitpunkt nutzt. Bei dieser Vorgehensweise können Fehlinterpretationen in Bezug auf die Habitatansprüche auftreten, da diese innerhalb einer kurzen Zeitperiode vom spezifischen Verhalten abhängen, besonders wenn sich die Erfassbarkeit mit dem Verhalten verändert.

Keywords: Central place forager; Habitat selection; Multi-scale modelling; *Myotis nattereri*; Radio telemetry; Species Distribution Modelling (SDM)

Introduction

Species distribution models (SDMs) offer an alternative to direct mapping, allowing the prediction of species' current, future and past distributions (Guisan & Zimmermann 2000; Thomas, Cameron, Green, Bakkenes, & Beaumont 2004). SDMs are used to assess a species' conservation status (Cabeza, Araújo, Wilson, Thomas, & Cowley 2004; Thomas et al. 2004), describe and predict changes in species' distribution in response to environmental change (e.g. Lundy, Montgomery, & Russ 2010), identify sites for reintroductions (e.g. Wilson & Roberts 2010), and define priority conservation areas (e.g. Fiorella, Cameron, Sechrest, Winfree, & Kremen 2010). For a comprehensive review of current issues and applications of mapping species distributions see Franklin (2009). The predictions of SDMs are based on correlations with environmental variables. The suitability of an area is not solely related to the availability of habitat but to the context of the surrounding landscape habitat structure, size and shape (Virkkala 1991; Jokimäki & Huhta 1996; Bennett, Radford, & Haslem 2006). Species respond to heterogeneous landscapes at multiple scales which combine to determine presence and population processes (e.g. Fryxell et al. 2005). Using a multi-scale approach allows the immediate habitat to be placed in the context of the surrounding landscape (Wiens 1989; Jokimäki & Huhta 1996). Multi-scale methods can identify species-specific relationships with aspects of habitat spatial scale (McAlpine, Rhodes, Callaghan, Bowen, & Lunney 2006; Lundy & Montgomery 2010).

Central place foragers utilise a defined location, which provides suitable conditions to rest or protect juveniles and make repeated trips to foraging areas. A central place is selected to minimise the energetic cost of travel to foraging areas (Rosenberg & McKelvey 1999). The character of a central place and foraging area may contrast in some species. Species distribution can also change significantly during the life cycle in response to changed resource requirements (Law & Dickman 1998). Jaberg and Guisan (2001) demonstrated a seasonal contrast in the habitat associations and predicted that the distribution of the Greater mouse-eared bat (*Myotis myotis*) in Switzerland would shift from low elevation during summer to higher elevation with structured vegetation cover outside the breeding period.

Defining the geographical ranges in bats is difficult due to their nocturnal behaviour (Walsh & Harris 1996; Vaughan, Jones, & Harris 1997) and, hence, SDMs are particularly useful for examining the ecology of bat species (Jaberg & Guisan 2001; Rebelo & Jones 2010). Roosts are crucial in bat ecology and distribution (Kunz & Lumsden 2003; Findley 1993), with different species having specific roost requirements (Marnell & Presetnik 2010). Roosts are considered 'central places' particularly during the maternity period (Daniel, Korine, & Pinshow 2008). Roost choice is associated with thermal conditions (Lourenço & Palmeirim 2004; Smith & Racey 2005) and predator avoidance (Jones & Rydell 1994). Whilst SDMs allow predictions of occurrence across a landscape, behavioural observations contribute to understanding habitat selection of bat species (Fenton 1997; Bontadina, Schofield, & Naef-Daenzer 2002). Radio-tracking individual bats elucidate behavioural patterns such as roost switching, foraging habitat selection and home ranges (Fenton 1997; Bontadina et al. 2002; Russo, Cistrone, Jones, & Mazzoleni 2004). In contrast to predictive modelling, radio-tracking is applied on a smaller scale, assessing habitat selection of a small proportion of a population.

Myotis nattereri is a foraging generalist, hunting in a variety of habitats utilising gleaning and aerial hawking (Arlettaz 1996; Siemers, Kaipf, & Schnitzler 1999; Siemers & Swift 2006; Smith & Racey 2008). However, it emerges from roosts later than other species. This is considered as predator avoidance behaviour related to the slow flight of *M. nattereri* (Jones & Rydell 1994). We develop a multi-scale SDM (McAlpine et al. 2006) to examine habitat associations of *M. nattereri* maternity roosts at a landscape scale. We