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Modelling small-scale foraging habitat use in breeding Eurasian oystercatchers (*Haematopus ostralegus*) in relation to prey distribution and environmental predictors

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ABSTRACT

Detailed knowledge of species distributions at a fine spatial scale is an essential prerequisite for the understanding of ecosystems. However, relating species distributions to environmental variables is difficult, and distribution patterns of mobile benthic top predators can only be estimated at a rough spatial scale using visual cues. This is particularly problematic in systems with strong environmental gradients, such as intertidal habitats. Monitoring predators using GPS tags allows collecting precise spatial data over wide areas and during night time. We collected fine-scale data on prey abundance and quality, sediment composition, inundation time of tidal flats, and foraging distances from nest sites to develop a predictive distribution model for oystercatchers (*Haematopus ostralegus*) in the Wadden Sea, Germany. This shorebird species was able to identify the patches with high biomass and abundance of its endobenthic prey at a very fine spatial scale. Modelling suggested that prey abundance and biomass were essential for predicting oystercatcher occurrence: the probability of encountering a foraging oystercatcher was higher than expected in areas with >100 cockles per m^2 and areas with 80 g ash-free dry weight per m^2. Our modelling approach also showed that habitat use by oystercatchers was very strongly dependent on abiotic factors, i.e., oystercatchers preferred muddy and low-lying tidal flats with short exposure times close to their breeding sites. Oystercatchers only used patches >4 km away from their breeding territories if such patches were particularly prey-rich. This study demonstrates the importance of fine-scale models of predators and environmental predictors in patchy environments. These results have two conclusions with important management implications: (1) fine-scale models of distribution data for predators can provide a valuable indicator of the location of important sites worthy of protection; and (2) abiotic predictors alone are suitable to identify potential valuable feeding sites for oystercatchers without the need for time-consuming collection of prey-base data, even in a coastal zone with strong gradients.

1. Introduction

A comprehensive understanding of ecosystems requires detailed knowledge of species distributions and habitat choices at a fine spatial scale which is also essential for the management of ecosystems (e.g., Barbosa et al., 2010). Higher spatial resolutions of species and environmental data allow more precise predictions of species distribution patterns (e.g., McPherson et al., 2006; Gastón and García-Viñas, 2010). Numerous studies have investigated the relationships between habitat use by shorebirds and different environmental variables, particularly prey distribution and quality (e.g., Sutherland, 1982a; Goss-Custard et al., 1991; Colwell and Landrum, 1993; Yates et al., 1993; Meire, 1996; Granadeiro et al., 2004; van Gils et al., 2006; van Colen et al., 2014). However, it is important to consider the effects of the spatial scale of the study, particularly when relating prey abundance and biomass to predator abundance. Although data on abiotic environmental parameters may be available at relatively fine spatial scales, it is difficult to obtain high-resolution data on space use by birds particularly over wide areas and during night time (see overview in Colwell and Landrum, 1993), leading to potential spatial mismatches between visual

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observations of predators and environmental data, such as prey-species distribution. This is particularly problematic in highly-structured ecosystems where environmental conditions may show strong gradients over a very fine spatial scale. The intertidal of the Wadden Sea is such an example of a highly structured ecosystem, as for instance different levels of elevation, inundation time, sediment and species composition may alter within a range of a few hundred metres (e.g., van Gils et al., 2006; Kraan et al., 2009, 2010).

Most studies aiming to relate habitat use by shorebirds to prey distribution in the intertidal zone on a relatively small spatial scale have used visual observations (e.g., Goss-Custard, 1977a,b; Sutherland, 1982b; Meire, 1996). However, these are limited to daylight hours and to sites close to the observer. Furthermore, even using a small-scale study design and sampling prey organisms at specific foraging locations where the birds have been observed visually may be biased, because it can be difficult to sample the precise foraging spot of an observed individual over a wider range particularly in visually unstructured landscapes. However, this is crucial within patchy ecosystems such as intertidal habitats. Although the use of telemetry devices such as radio tags allows for higher temporal resolution, the spatial deviation is still usually within a range of hundreds of metres (e.g., Exo et al., 1996; van Gils et al., 2006). In contrast, the deviation of GPS devices is within a few metres. Furthermore, data can be collected throughout the day and night, leading to highly accurate spatial-presence data (Schwemmer and Garthe, 2011; Shamoun-Baranes et al., 2012).

Applying this comparatively new methodology to shorebirds, this study aimed to relate habitat use by oystercatchers (*Haematopus ostralegus*), a numerous benthivorous top predator in the World Heritage Site of the German Wadden Sea (e.g., Koffijberg et al., 2013), to environmental predictors at two different spatial scales (Fig. 1).

Prey distribution has already been shown to influence the distribution of oystercatchers on comparatively coarse spatial scales (e.g., Sutherland, 1982b; Meire, 1996). Sediment composition and exposure time of tidal flats are known to affect benthic biomass and abundance, as well as the distribution patterns of the shorebirds themselves (e.g., Ens et al., 1993; Yates et al., 1993; van Colen et al., 2014). Distance from the nest site limits the foraging range of oystercatchers during the breeding period (Ens et al., 1992; Schwemmer and Garthe, 2011). In detail we tested the following hypotheses:

(1) Oystercatchers would optimise their intake rate by selecting patches with high prey biomass and abundance, following the functional response theory (Goss-Custard et al., 2006).
(2) Oystercatcher numbers would increase with increasing inundation times and with increasing mud contents, as these abiotic factors are known to reflect productivity and thus prey availability and quality (e.g., Sutherland, 1982a,c).
(3) Finally, oystercatcher numbers would increase in areas close to the breeding site in order to save energy (Schwemmer and Garthe, 2011).

The first hypothesis was tested on two different spatial scales. For the fine-scale approach (range of metres) the most important foraging locations for oystercatchers were identified by GPS data, and the abundance and quality (i.e., biomass) of potential prey items within these sites were compared with areas in the close vicinity that had not been used by oystercatchers (Fig. 1). To account for different spatial scales, we tested the first and the other hypotheses (again) using a larger-scale approach within the range of several hundred metres. We therefore used sediment data, exposure time of tidal flats, and distance of oystercatchers to their nests as additional abiotic predictors, together with availability and quality of the most important prey types (Fig. 1), to shed light on the distribution of oystercatchers across larger areas close to major breeding sites in the Wadden Sea using generalised additive models (GAM; Fig. 1) For an overview of studies using GAM to model species distributions, see Guisan et al. (2002) and Hastie and Tibshirani (1990).

2. Materials and methods

2.1. Study area

The study was conducted on two islands in the northern (Hallig Oland, May–July 2009) and southern (Spiekeroog, May–August 2010) German Wadden Sea, respectively. Hallig Oland is a small island (total area, 2 km^2) located ca. 3 km off the mainland coast and connected to the mainland by a small railway track (Fig. 2;

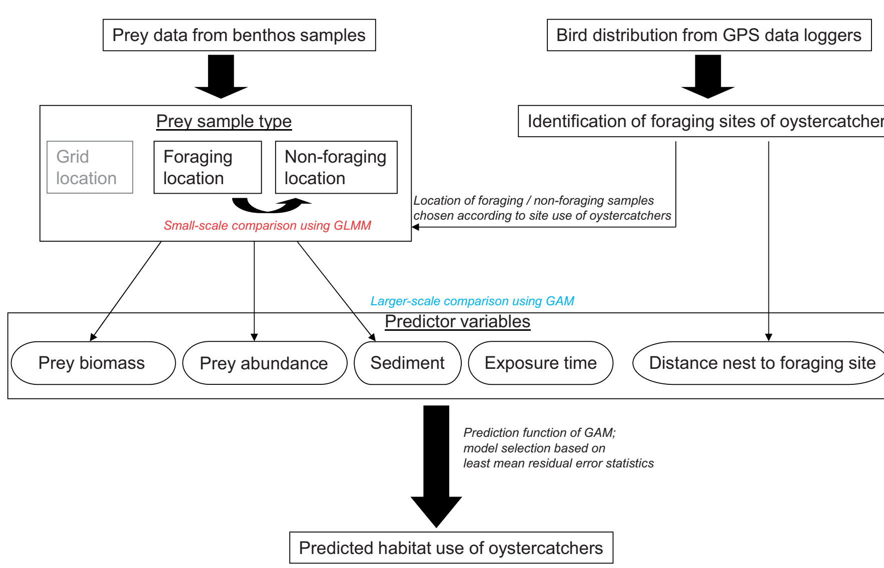

Fig. 1. Flowchart of modelling design: (1) small-scale comparison of prey abundance and biomass between foraging and non-foraging locations of oystercatchers, and (2) larger-scale model, using five different predictors for bird distribution.