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Diet and feeding ecology of the wintering shorebird assemblage in the Bijagós archipelago, Guinea-Bissau

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ABSTRACT

Detailed data on shorebird feeding ecology is mostly lacking for tropical wintering sites, limiting our understanding of trophic interactions among shorebird species and their prey. Using dropping analysis and video recordings we compared the diet of eight shorebird species wintering in the Bijagós archipelago, Guinea-Bissau, one of the most important but also least known coastal sites for shorebirds in Africa. We also calculated niche width and foraging niche overlap among these eight species.

Whimbrel, grey plover and redshank fed mainly on fiddler crabs, confirming previous observations made in the Bijagós. A large proportion of the diet of bar-tailed godwit, curlew sandpiper, sanderling and ringed plover was composed of polychaetes, particularly *Nereis* and *Glycera*, and also *Marphysa* in the case of larger shorebirds. Red knots fed mainly on the bivalve *Dosinia isocardia*. All species showed narrow trophic niches, but particularly so whimbrel, red knot, grey plover and redshank. Niche overlap among shorebird species was mostly insignificant, with the exception of species that fed mainly on fiddler crab.

Low levels of niche overlap suggest that shorebirds are able to partition the available food resources in the Bijagós despite the reported low macrobenthic densities in the area. In fact, observational data for bar-tailed godwit suggests resource partitioning even occurs within species, with dietary differences among sexes.

1. Introduction

Outside their breeding season, migratory shorebirds rely on a limited number of key wintering and staging sites (Delany et al., 2009), mostly located on coastal wetlands, where they take advantage of abundant intertidal stocks of macroinvertebrates to maintain themselves and fuel up for subsequent migratory periods (van de Kam et al., 2004; Piersma, 2012). Shorebirds are important predators in these habitats, and can have a critical structuring effect on intertidal benthic communities (e.g. Wootton, 1997), while being themselves strongly affected by changes in the abundance of their prey (e.g. Piersma et al., 1993a; Quaintenne et al., 2014).

High densities of shorebirds found at wintering and staging sites reflect both the abundance of their benthic prey (e.g. Piersma, 2012) and their ability to partition trophic resources (Bocher et al., 2014). This resource partitioning is possible due to the considerable morphological, behavioural and perceptual variation among (Lifjeld, 1984; Piersma et al., 1998; Piersma, 2011) and within shorebird species (Nebel, 2005; Duijns et al., 2014), which results in different habitat and prey preferences. This allows for dietary segregation among species (e.g. Lourenço et al., 2016) and in some cases among sexes (e.g. Catry et al., 2012) or age classes of a given species (e.g. Goss-Custard and Durrel, 1987) by either consuming different prey species or different size classes of the same prey. Still, community-wide studies on shorebird trophic ecology are scarce (but see Bocher et al., 2014; Lourenço et al., 2016, Catry et al., 2016), limiting our understanding of how competition and diet overlap affect resource use by different species.

The macrobenthic community in shorebird tropical wintering sites tends to exhibit lower biomass and higher diversity than in both northern and southern temperate sites (Piersma et al., 1993b; Ricciardi and Bourget, 1999). This reduced prey biomass can be predicted to lead to increased overlap in shorebird diets (Kober and Bairlein, 2009), but the increased prey diversity may allow different species to explore different trophic sources, allowing for low levels of diet overlap (e.g. Lourenço et al., 2016).

Understanding the trophic links between shorebirds and their prey, and among different shorebird species, is critical to assess effects of ongoing changes and emerging anthropogenic pressures at wintering sites, such as habitat loss and degradation, disturbance, introduced species and the multiple effects of climate change (e.g. Piersma and Lindström, 2004; Harley et al., 2006; Sutherland et al., 2012). Such understanding is particularly relevant from a conservation point of

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view, as many shorebird populations worldwide are currently facing sharp declines (Stroud et al., 2006; van Roomen et al., 2015).

Located off the West African coast, the Bijagós archipelago, in Guinea-Bissau, is one of the most important wintering areas for shorebirds migrating along the East Atlantic Flyway (EAF), and the second most important shorebird wintering area along the coasts of Africa, just behind the Banc d'Arguin, Mauritania (Delany et al., 2009). In the Bijagós, maximum counts reach 700,000 shorebirds, which represent roughly 10% of all shorebirds migrating along the EAF, estimated at ca.7 million birds (Salvig et al., 1994; Delany et al., 2009). Wintering sites in tropical Africa are good examples of how the availability of ecological data on shorebirds is unevenly spread over the flyway. Shorebird trophic ecology has been studied in considerable detail at the north and south temperate ends of the flyway, in Europe (e.g. Goss-Custard et al., 1977; Perez-Hurtado et al., 1997; van de Kam et al., 2004), and in southern Africa (e.g. Kalejta, 1993; Turpie and Hockey, 1993), but this type of information is still very limited for tropical areas of Africa such as the Bijagós. In fact, to our knowledge there is a single study that focused on shorebird trophic ecology in the Bijagós (Zwarts, 1985), which emphasized the importance of fiddler crabs *Uca tangeri* as an important shorebird prey.

Thirty years ago, macrobenthic biomass in the Bijagós was reported to be comparatively low (Zwarts, 1985), which was in line with low shorebird densities observed in the area (Zwarts, 1988; Salvig et al., 1994). Recent surveys support evidence for low macrobenthic biomass, with average values of 5.2 g AFDW.m^{-2} (Lourenço et al. unpub. data) which are among the lowest reported for soft intertidal substrates anywhere in the world (Piersma et al., 1993b; Ricciardi and Bourget, 1999) while for some shorebird species wintering numbers appear to have declined (van Roomen et al., 2015). Still, low food availability may be predicted to lead to increased competition within and among shorebird species

Here we gathered detailed data on the diet and foraging behaviour of the eight most abundant wintering shorebirds in Guinea Bissau: curlew sandpiper (most recent estimate: 130,000 individuals), bar-tailed godwit (130,000 inds.), red knot (45,000 inds.), sanderling (35,000 inds.), whimbrel (34,000 inds.), ringed plover (27,000 inds.), redshank (22,000 inds.) and grey plover (15,500 inds; van Roomen et al., 2015). These were derived from the analysis of droppings and also from video footage of foraging birds, and enabled us to estimate trophic niche and degree of niche overlap within the shorebird assemblage. We then tested the hypothesis that low prey densities imply strongly overlapping dietary niches, or whether these birds are rather able to avoid competition by partitioning the available resources (with minimum overlap) as observed for a narrower range of shorebird species at the Banc d'Arguin.

2. Methods

2.1. Study area

The Bijagós archipelago lies off the coast of Guinea-Bissau (11°12′N, 15°53′W) and comprises 88 islands and islets. The intertidal area comprises over 140,000 ha mostly dominated by large areas soft sediment beds interspaced with smaller areas of sandy sediments, often bordered by significant extension of mangrove (Pennober, 1999; Campredon and Catry, 2017). Field work took place in the islands of Bubaque (at Escadinhas, Bubaque, Bijante and Bruce) and Canhabaque (Inorei and nearby islet of Porcos; Fig. 1) in January–February 2014 and February 2015. Most of the sampling was carried out in the most common muddy intertidal habitats, but we also surveyed some of the less widespread sandy intertidal areas, to examine its use by foraging sanderlings *Calidris alba*. Different species were not sampled in the same proportions in different study sites, rather reflecting their relative abundance at each site. To some extent, this could drive dietary differences among species; however, these spatial differences among shorebird species are also likely to be caused by their dietary preferences, e.g. red knot only occurred in areas where small bivalves, their preferred prey, where available.

2.2. Macroinvertebrate collection and biomass content

We randomly collected sediment cores (86.6 cm^2, approximately 20 cm deep) at the same sites were bird faeces were sampled. These cores were sieved through 1 mm and 0.5 mm meshes to collect the macroinvertebrate species in order to build a reference collection and to calculate regression equations relating total structural size and biomass of individuals of different species with the size of their hard structures (shell hinges from bivalves, claws from crabs and mandibles from polychaetes). These equations were then used to estimate size and mass of prey from hard structures found in bird droppings (Table 1). Macroinvertebrates were stored in 70% ethanol immediately after collection and later identified to the lowest possible taxonomic level. We measured the size of specimens (measurement varied among taxa, see Table 1 for more details) as well as the size of the corresponding hard structures potentially found in bird droppings to the nearest 0.1 mm. In order to convert prey size into biomass (measured as mg of ash free dry mass, hereafter AFDM), we measured AFDM for individuals of known size (following the methods described in Lourenço et al., 2016) and used these data to calculate regression equations (Table 1). For a few prey it was not possible to estimate sizes based on structures found in droppings, either because these structures do not correlate with size, or because individuals in our samples did not show sufficient variation in size to calculate a reliable regression. In these cases, we calculated the average biomass of individuals obtained in the field, and assumed this value for individuals consumed by shorebirds (Table 1).

2.3. Diet composition and niche overlap of shorebirds

Shorebird diets were determined through the analysis of droppings. Droppings were collected by following (usually mono-specific) flocks during the out-going tide, or identifying faeces by their shape and size, by the footprints found on the sediment, or by observing individual birds producing droppings. We obtained a total of 353 droppings from eight shorebird species, 304 of which were later found to contain identifiable prey remains (see Tables 2 and 3 for specific sample sizes).

Droppings were analysed under a magnification of 10–400 ×, and prey remains were identified to the lowest possible taxonomic level by comparison with invertebrates collected in the field and based on available bibliography (Day, 1967; Manning and Holthuis, 1981; von Cosel, 1989; Oliver and von Cosel, 1992). All identifiable prey remains were counted and measured to the nearest 0.1 mm. The number of bivalves, aciculated polychaetes (Polychaeta: Subclass Aciculata) and crabs was estimated by pairing shell hinges, mandibles or claws of similar size (Lourenço, 2007), respectively, while individual gastropod shells and other crustacean exoskeletons could be directly counted as they were mostly found whole. Sedentary polychaetes (Polychaeta: Subclass Sedentaria) were identified by the presence of characteristic chaetae, mainly thoracic hooks, which vary among different polychaete families. Since each individual has many hundreds of chaetae and their number varies with the size of the animal, it is very difficult to estimate the number of individuals consumed based on chaetae. One study estimated 84–154 thoracic hooks per individual *Scoloplos armiger* in a faecal sample (Scheiffarth, 2001) so we used as a rule of thumb that each 100 chaetae represented a single individual. In practice, very few faecal samples ($n = 4$) had over 100 chaetae of a particular polychaete family.

The importance of each prey type on shorebird diet is presented both as frequency of occurrence (i.e. the proportion of droppings containing a given prey taxon), and numerical frequency (i.e. the number of each prey taxon in one dropping relative to all prey in the same dropping). Additionally, we estimated the size and biomass content of