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Seasonal variation in the diet of migratory shorebirds wintering in the Bijagós Archipelago, Guinea-Bissau

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As on intertidal flats across the globe, the migratory shorebirds that spend most of their annual cycle in the Bijagós Archipelago, Guinea-Bissau, feed on macrozoobenthic prey buried in the intertidal soft sediments. Understanding the diet of shorebirds throughout the period of residence in the Bijagós can help to understand the degree of their trophic flexibility. In this study, we first reconstruct the diet of eight migratory shorebirds in the Bijagós, then investigate how their diet changes throughout the three main periods of the non-breeding season (arrival, mid-winter and fuelling periods) and finally explore the intraspecific dietary overlap between the three periods. We found significant changes in the diet of most shorebirds across the three periods, with some smaller species increasing the proportion of polychaetes in their diet in the fuelling period, while larger species increased the proportion of bivalves. The fuelling period showed the lowest overlap values with the other two periods, confirming that during this time most shorebirds considerably changed their diet, which may either reflect changes in prey availability or in prey selection.

Key words: fuelling, macrozoobenthos, biomass, dropping analysis, non-breeding season

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Shorebird populations across the East Atlantic Flyway (EAF) are undergoing rapid declines and for species with wintering populations in both Europe and West Africa, population trends tend to be less favourable in the tropics than in temperate zones (Oudman *et al.* 2020, Henriques *et al.* 2022a, van Roomen *et al.* 2022). Conditions in the breeding areas substantially influence demographic parameters and population trends (Gunnarsson *et al.* 2005, van Gils *et al.* 2016, Rakhimberdiev *et al.* 2018, Alves *et al.* 2019). However, the extent to which conditions in the African wintering areas may contribute towards such declines remains largely unknown (Oudman *et al.* 2020). A detailed understanding of shorebirds' diet and foraging plasticity

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allows the establishment of a fundamental baseline, upon which further feeding ecology and energetic studies can investigate if local food conditions may be constraining some of these populations. For example, local food resources may limit shorebirds' capacity to fuel their return migration in spring (Ens *et al.* 1994, Rakhimberdiev *et al.* 2015). Furthermore, analysing if and how shorebird diet varies through the wintering season can also help to evaluate their capacity to respond to changes in local food availability (Rakhimberdiev *et al.* 2015, Coelho *et al.* 2022).

Although shorebirds are specialized in their prey and known to segregate into dietary niches while foraging on the same habitat (Prater 1981, Mazzochi *et al.* 2022), their diet can vary substantially between sites (Alves *et al.* 2013, Duijns *et al.* 2013, Penning *et al.* 2022), periods (Sánchez *et al.* 2005) and habitats (Masero & Pérez-Hurtado 2001, Alves *et al.* 2010). Understanding the causes and consequences of such dietary range and its variation can help identify how diet may influence individual condition and scale up to affect population level processes. For example, Dunlins *Calidris alpina* foraging in the Tagus estuary show a marked dietary shift from winter to spring, by changing from using a tactile technique feeding upon juvenile bivalves to a visual foraging technique targeting polychaetes, bivalve syphons and shrimps, which resulted in a 65% increase in intake rates (Martins *et al.* 2013). Another example of how dietary choices can scale up to influence survival and population trends is provided by the Red Knot *Calidris canutus*, a bivalve specialist, which in the Banc d'Arguin, Mauritania, consumes a highly available but toxic bivalve species, the lucinid *Loripes lucinalis*. Red Knots are able to adjust their diet to avoid poisoning by that widely available prey, by also consuming non-toxic but less profitable prey, the bivalve *Dosinia isocardia*. However, when these alternative prey are not available in sufficient densities, annual survival rates are lower (van Gils *et al.* 2013).

Along the East Atlantic Flyway, two tropical sites host the majority of the shorebirds during the northern winter: the Banc d'Arguin in Mauritania and the Bijagós Archipelago in Guinea-Bissau (van Roomen *et al.* 2022). While detailed research on movement ecology, predation, diet and food availability of these species has been ongoing on Banc d'Arguin for several decades (Zwarts & Dirksen 1990, Wolff *et al.* 1993, Leyrer *et al.* 2006, Ahmedou Salem *et al.* 2014, Lourenço *et al.* 2016b, El-Hacen *et al.* 2020), much less is currently known for the Bijagós Archipelago, particularly regarding shorebirds' diet (but see: Zwarts 1985, Lourenço *et al.* 2017, 2018, Carneiro *et al.* 2021, Correia *et al.* 2023). This is a clear knowledge gap that needs to be urgently addressed in order to work towards reversing current population trends.

Shorebirds arrive at the Bijagós Archipelago in September/October, coinciding with the end of the local wet season, and remain in the archipelago throughout the local dry season, leaving in April/May (Salvig *et al.* 1997, Coelho *et al.* 2022). During their stay in the Bijagós, shorebirds rely on benthic macroinvertebrates as a source of food and energy, foraging on the extensive intertidal flats when these are exposed during low tide and retiring to beaches or mangroves when these are submerged (Zwarts 1988). Despite an apparent low overall biomass of macroinvertebrates in the mudflats of the Bijagós, and in particular a low harvestable biomass for shorebirds (Zwarts 1985, Lourenço *et al.* 2018, Coelho *et al.* 2022), seasonal predation by shorebirds does not appear to deplete the benthic community (Coelho *et al.* 2022). In fact, macroinvertebrate density increases towards the shorebird's fuelling period (in March/April; Coelho *et al.* 2022), contrary to what is described for the Banc d'Arguin in Mauritania (Ahmedou Salem *et al.* 2014). Despite some earlier studies on the diet of shorebirds in the Bijagós in the middle of the nonbreeding season (Zwarts 1985, Lourenço *et al.* 2017, 2018), spatial and temporal representativeness has been limited and therefore much remains unknown with respect to their diet in this important West African site, currently with no information regarding diet variation throughout the entire season for any shorebird. In this study we use dropping analysis to (1) reconstruct the diet of eight migratory shorebird species in the Bijagós and assess for each of them (2) the seasonal variation in diet (as proportion of prey group and its biomass), as well as (3) the level of dietary overlap across three periods: arrival, midwinter and fuelling. Finally, we discuss if species-specific dietary variation correlates with seasonal variation in shorebird prey abundance (Coelho *et al.* 2022).

METHODS

Study area and sample collection

The Bijagós Archipelago, located off the coast of West-Africa in Guinea-Bissau is composed of 88 islands and is well known for its rich biodiversity and cultural heritage (Campredon & Catry 2017). The climate is tropical and bi-seasonal, with a dry season from November to May followed by an intense wet season characterized by the heavy rains common in the region (Pennober 1999, Campredon & Catry 2017). Tidal

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Flock of Ringed Plovers and Curlew Sandpipers gathering with the incoming tide at Bubaque island, Bijagós Archipelago, Guinea-Bissau (photo APC, January 2019).



Sanderlings feeding in the surf of Bruce beach, Bijagós Archipelago, Guinea-Bissau (photo APC, March 2019).

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amplitude is very high in this continental archipelago, reaching up to 4.5 m in spring tides and exposing up to 450 km^2 of intertidal flats twice a day during low tide (Pennober 1999, Granadeiro *et al.* 2021, Hill *et al.* 2021, Henriques *et al.* 2022b). In this study, data was collected across seven study sites at three islands (Figure 1) in order to capture the variability of this ecosystem. Given wader specific associations with intertidal sub-habitats, no species was sampled in every site in each season (Table S1), and therefore site effect is not investigated here as the sampling regimen was not designed to capture any potential spatial variation.

Eight shorebird species were targeted: Common Ringed Plover *Charadrius hiaticula*, Curlew Sandpiper *Calidris ferruginea*, Sanderling *Calidris alba*, Red Knot *Calidris canutus*, Common Redshank *Tringa totanus*, Grey Plover *Pluvialis squatarola*, Bar-tailed Godwit *Limosa lapponica* and Eurasian Whimbrel *Numenius phaeopus*. Five of the sampled sites were visited monthly from October to May during three consecutive winter seasons (2017–2018, 2018–2019 and 2019–2020), and faeces were collected opportunistically from the mudflats when a mono-specific flock was observed foraging (searching the area for fresh faeces once individuals were observed defecating and/or immediately after the flock left). Additionally, fresh faeces were also collected from single-species keeping cages when birds were captured with mist nets during ringing operations (Alves *et al.* 2021; Table 1). In both cases only intact faeces were collected, hence, those trampled were not retrieved. Collected samples were stored separately in Eppendorf tubes or paper envelopes, labelled according to species and date, and then taken to the laboratory for analysis.

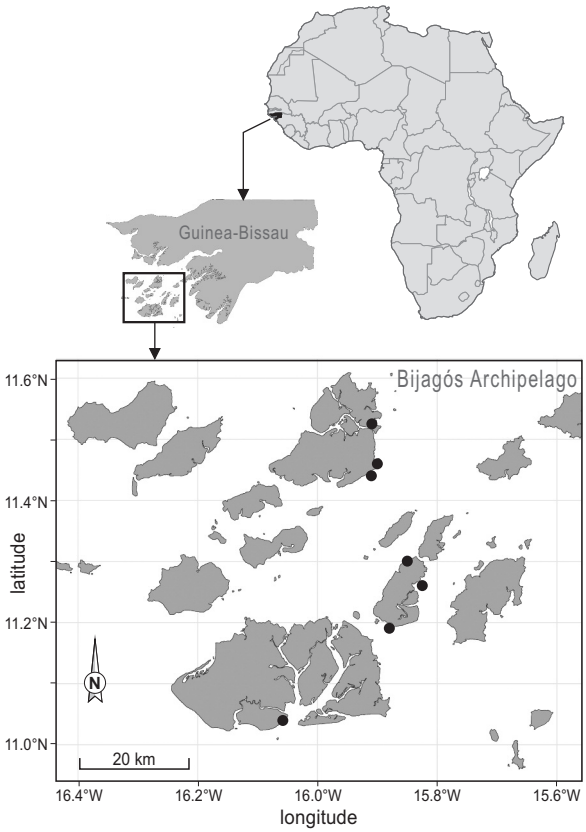


Figure 1. Map of the Bijagós Archipelago, off the west coast of Africa, highlighting the locations of study sites where droppings were collected.

Table 1. Total number of analysed droppings in each month (all winter seasons aggregated), for each shorebird species.

Period	**Month**	*Charadrius hiaticula*	*Calidris ferruginea*	*Calidris alba*	*Calidris canutus*	*Tringa totanus*	*Pluvialis squatarola*	*Limosa Lapponica*	*Numenius phaeopus*	**Total**
Arrival	October	11	5			5	2		17	**40**
	November	4	8		4	10	9	22	3	**60**
Mid-winter	December					1	1		3	**5**
	January	4	1	13		9			6	**33**
	February	33	32	43		8	3	22	14	**155**
Fuelling	March	14	15	13		12	18		4	**76**
	April	4	4					10	6	**24**
	May			7						**7**
	Total	**70**	**65**	**76**	**4**	**45**	**33**	**54**	**53**	**400**

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Diet reconstruction

Diet was reconstructed based on identifiable prey remains found in birds' faeces. Air dried samples were sorted using a 30× magnification stereo microscope (Leica Zoom 2000) and all identifiable prey remains (jaws, pincers, hinges, claws, body whorls or whole intact individuals) were separated from the remaining content. Prey remains from the droppings were identified by comparison with a hard-structure reference collection of individuals collected at the same sampling sites in a previous study (Coelho *et al.* 2022). To build this reference collection, the diagnostic structures of identified, intact prey individuals were manually extracted, labelled and stored separately.

The number of individuals in each sample was attained by matching left and right structures for most prey (pincers for crustaceans, hinges for bivalves and jaws for most polychaetes), while for gastropods the number of individuals was attained by using the number of body whorls found and for *Glycera* sp. polychaetes by dividing the number of similar sized jaws by four, as species of this genera have four jaws (Day 1967, Duijns *et al.* 2013). Identified diagnostic prey remains were measured to the nearest 0.1 mm and the biomass of each ingested individual estimated using previously published regression equations (Lourenço *et al.* 2016b, 2017), that first relate the size of the prey remain with the individual total body length and then to its respective biomass (mg of Ash Free Dry Mass; AFDM). Fish remains were not converted into biomass, as no equation converting remain size to body size was available; however, these never comprised more than 0.03% of the number of prey items of any of the three species where these were found (see below).

Data analysis

We distinguished three periods to decompose the shorebird season in the Bijagós (Table 1): (1) the arrival period (Oct–Nov), corresponding to the progressive arrival of shorebirds in the archipelago (Zwarts 1988, Salvig *et al.* 1997) during the end of the local wet season, after shorebirds have depleted their body stores during the post-breeding migration while simultaneously having to finding the best quality patches in a new environment and complete a full body moult (Conklin *et al.* 2013, Aharon-Rotman *et al.* 2016), (2) the mid-winter period (Dec–Feb), in the beginning of the dry season and when shorebirds are in a relative stasis, and (3) the period of fuelling (Mar–May), which corresponds to the end of the local dry season, when the climate is the driest and freshwater availability is reduced (Campredon & Catry 2017), and when shorebirds increase their food intake in order to store energy for their migratory flight towards the breeding areas (Zwarts & Dirksen 1990, Zwarts *et al.* 1990, Lindström & Piersma 1993).

Intraspecific dietary variation between periods was assessed for each shorebird species by comparing the proportions of individuals and biomass of each main prey group (polychaetes, bivalves, gastropods and crustaceans) found in the droppings. This was done using Generalized Linear Models (GLMs) with a Binomial error structure (or Quasibinomial when encountering overdispersion; Zuur *et al.* 2009). The response variable was a matched pair (i.e. matrix) of successes (number of items of the focal prey group or biomass of the focal prey group) and failures (number of items of the remaining prey groups or biomass of the remaining prey groups), and the explanatory variable was period. GLMs indicating significant differences between periods were followed by pairwise post-hoc Tukey tests. Red Knot was excluded from this analysis as this species was not commonly recorded in the field sites, which limited sample collection to a single period (arrival; Table 1).

In order to quantify the level of intraspecific dietary change between periods, we calculated the Schoener index of overlap using the average proportion of biomass (i.e. mean percentage from all droppings from that species) of each prey group (polychaetes, bivalves, crustaceans and gastropods) in each season (Lourenço *et al.* 2017). A mean Schoener overlap index value (± SD) was obtained through bootstrapping 999 times, using the 'niche.overlap.boot' function from the R package 'spaa' (Gotelli 2000, Zhang 2016). While this index varies between 0 and 1, overlaps were considered low (0–0.39), intermediate (0.4–0.6) or high (0.61–1), with low overlap levels indicating that diet has changed substantially (Grossman 1986, Lourenço *et al.* 2017, Maitra *et al.* 2020). All statistical analyses were conducted using the R environment for statistical programming v. 3.6.1 (R Development Core Team 2011).

RESULTS

Wintering shorebird diet

The overall diet of the eight shorebird species studied was mostly composed of four prey groups (polychaetes, bivalves, crustaceans and gastropods), while three also included a small percentage of fish (Redshank, Bar-tailed Godwit and Whimbrel; Table 2, Figure 2A). The diet of the smaller species was composed mainly of polychaetes, contributing 83% to the diet of Curlew

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Sandpiper, and close to 70% in Sanderling and Ringed Plover. The latter two species also consumed crustaceans (17% and 13%, respectively). Redshank and Bar-tailed Godwit had the most diverse diet, with a larger proportion of crustaceans (around 40%), but also considerable percentages of bivalves and polychaetes (both between 20 and 30%). Grey Plover also had a large proportion of crustaceans in its diet (33%) but the most abundant prey were polychaetes (44%). In the remaining two species, the diets consisted mostly of one prey group alone: 78% bivalves in Red Knots and 76% crustaceans in Whimbrel.

Regarding biomass, the percentages were similar to the number of individuals consumed by the three smaller species (Curlew Sandpiper, Sanderling and Ringed Plover), with polychaete biomass corresponding to between 60 and 70% of the total (Figure 2B). Despite also consuming more individual polychaetes than any other prey, most biomass in the Grey Plovers' diet consisted of crustaceans (c. 60%). This was also the case for Redshank, but not for Bar-tailed Godwit, as most of the biomass in their diet consisted of polychaetes (around 50%). The proportion of biomass for Red Knot and Whimbrel, reflected the proportion of

Table 2. Composition of shorebird diet based on number of individuals found on droppings, expressed as the percentage of each taxon in each shorebird's diet.

Prey group	Prey species	*Charadrius hiaticula*	*Calidris ferruginea*	*Calidris alba*	*Calidris canutus*	*Tringa totanus*	*Pluvialis squatarola*	*Limosa Lapponica*	*Numenius phaeopus*
POLYCHAETE	*Diopatra* sp.	0.01	0.01	NA	NA	0.02	0.03	0.04	0.01
	Eunicidae	0.02	<0.01	0.01	NA	NA	NA	0.03	NA
	Glycera sp.	0.08	0.04	0.22	NA	NA	0.04	0.05	0.01
	Lumbrineridae	NA	<0.01	NA	NA	0.02	0.09	NA	NA
	Marphysa sanguinea	NA	<0.01	NA	NA	0.01	0.11	0.04	NA
	Nereididae	0.55	0.77	0.44	NA	0.17	0.17	0.01	NA
	Polychaete NID	0.01	NA	0.02	NA	NA	NA	0.07	NA
	Total polychaete	**0.67**	**0.83**	**0.69**	**0.00**	**0.20**	**0.44**	**0.23**	**0.02**
BIVALVE	*Arcuatula senhousia*	NA	<0.01	NA	NA	NA	NA	NA	NA
	Austromacoma nymphalis	NA	0.01	0.03	NA	0.26	0.01	0.09	0.01
	Lucinidae	NA	NA	NA	NA	NA	NA	0.06	NA
	Pelecyora isocardia	0.01	0.00	0.01	NA	0.01	0.01	0.02	NA
	Senilia senilis	0.02	NA	0.01	0.11	0.01	NA	0.01	0.01
	Tagelus adansonii	NA	NA	NA	NA	NA	NA	0.01	NA
	Bivalve NID	0.01	0.04	0.01	0.67	0.01	0.04	0.02	0.03
	Total bivalve	**0.04**	**0.05**	**0.05**	**0.78**	**0.29**	**0.06**	**0.20**	**0.05**
GASTROPOD	Cylichnidae	0.03	NA	0.01	NA	0.03	0.11	0.04	NA
	Hyala sp.	NA	NA	0.02	NA	0.06	0.01	0.10	0.03
	Hydrobiidae	0.09	0.07	0.05	0.11	0.01	0.03	NA	0.10
	Skeneidae	NA	<0.01	NA	NA	NA	NA	NA	NA
	Solariella sp.	0.03	<0.01	0.01	0.11	NA	0.02	0.02	NA
	Gastropod NID	0.01	NA	0.01	NA	NA	NA	NA	0.01
	Total gastropod	**0.16**	**0.07**	**0.09**	**0.22**	**0.10**	**0.17**	**0.15**	**0.14**
CRUSTACEAN	*Afruca tangeri*	0.03	0.01	0.04	NA	0.30	0.24	0.10	0.55
	Anthuridae	0.10	0.02	0.12	NA	NA	0.05	0.03	0.01
	Balsscallichirus balssi	NA	0.01	0.01	NA	0.07	0.02	0.23	0.05
	Callinectes marginatus	NA	<0.01	NA	NA	0.01	0.02	0.04	0.14
	shrimpNID	NA	NA	NA	NA	NA	NA	0.02	NA
	Crustracean NID	NA	0.01	NA	NA	NA	0.01	0.01	0.01
	Total crustacean	**0.13**	**0.05**	**0.17**	**0.00**	**0.38**	**0.33**	**0.41**	**0.76**
Fish		**NA**	**NA**	**NA**	**NA**	**0.03**	**NA**	**0.01**	**0.03**

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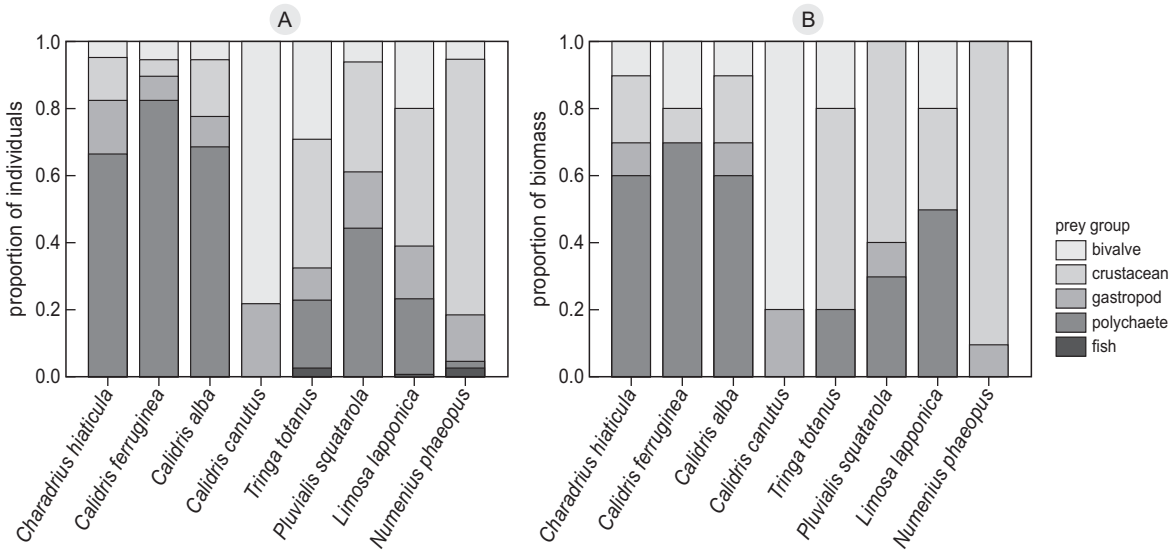


Figure 2. (A) Diet composition of eight shorebird species based on prey remains found in droppings, and (B) the reconstructed biomass (mg AFDM), expressed as the proportion of each prey group (%) on each shorebird's diet.

individual prey in their diet, with 80% and 90% of biomass originating from bivalves and crustaceans respectively.

Seasonal variation of diet

In almost all shorebird species the proportion of prey groups in their diet varied significantly between periods, for at least one of the prey groups (Figures 3 and 4, Table S2). Only Whimbrels did not show significant differences between periods, maintaining a high proportion of crustaceans in their diet throughout the season (Table S3). Two of the smaller species (Ringed Plover and Curlew Sandpiper) had significantly more polychaetes in their diet during fuelling than during arrival, and while this pattern was also noticeable for the biomass values in both species, it was only significant for Curlew Sandpipers (Figure 3, Table S3). Furthermore, both species had lower crustacean biomass in the fuelling period, but the proportion of crustaceans in their diet was only significantly lower for Ringed Plovers, which also had lower proportion of gastropods. Sanderlings did not show any major changes in their diet, except for the proportion of polychaetes that was significantly lower in fuelling compared to mid-winter (Figure 3). None of the smaller species showed variation in the proportion of bivalves, which was very low in their overall diets (less than 5%).

Of the larger shorebirds, both Redshank and Bar-tailed Godwit had a higher proportion of bivalves in their diet during fuelling than mid-winter (mid-winter was also lower than during arrival for Bar-tailed Godwits), and the same occurred regarding biomass, despite not being significant for Redshanks (Figure 4, Table S3). Both these species had lower polychaete biomass in their diet in fuelling, in comparison to the remaining periods, but only Redshanks showed significantly lower proportion of polychaetes in fuelling compared to mid-winter. Grey Plovers showed significant variation only in the proportions of bivalve and gastropod biomass, which was lower during fuelling than during arrival (Figure 4). The proportion of consumed crustaceans (both in individuals and biomass) did not vary between periods for these three larger shorebirds, despite representing a considerable part of their overall diet (more than 30% of both individuals and biomass).

Diet change between periods was considerable for most species, with only two (Curlew Sandpiper and Bar-tailed Godwit) showing intermediate values of diet overlap, both between fuelling and another period (Table 3). Interestingly, half of the analysed shorebird species (Ringed Plover, Curlew Sandpiper and Redshank) showed the lowest overlap, and therefore the largest seasonal change, between the two periods furthest in time: arrival and fuelling. For the remaining larger species, Grey Plover had the lowest overlap, i.e. largest seasonal change, between arrival and mid-winter, whilst for both Bar-tailed Godwit and Whimbrel this was recorded between mid-winter and fuelling.

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Table 3. Mean diet overlap (± SD) between seasons for each shorebird species quantified using Schoener index. Periods on the top row of comparisons were abbreviated as: A (arrival) and W (mid-winter). The pair of periods with the lowest overlap for each species is outlined in bold.

	Charadrius hiaticula		*Calidris ferruginea*		*Calidris alba*		*Tringa totanus*		*Pluvialis squatarola*		*Limosa lapponica*		*Numenius phaeopus*	
	A	W	A	W	A	W	A	W	A	W	A	W	A	W
Mid-winter	0.74 (0.11)	–	0.69 (0.14)	–	–	–	0.82 (0.13)	–	**0.61** (0.16)	–	0.75 (0.14)	–	0.73 (0.26)	–
Fuelling	**0.63** (0.16)	0.68 (0.23)	**0.56** (0.21)	0.80 (0.17)	–	0.77 (0.11)	**0.75** (0.19)	0.82 (0.11)	0.77 (0.13)	0.79 (0.20)	0.67 (0.18)	**0.45** (0.26)	0.99 (0.01)	**0.72** (0.26)

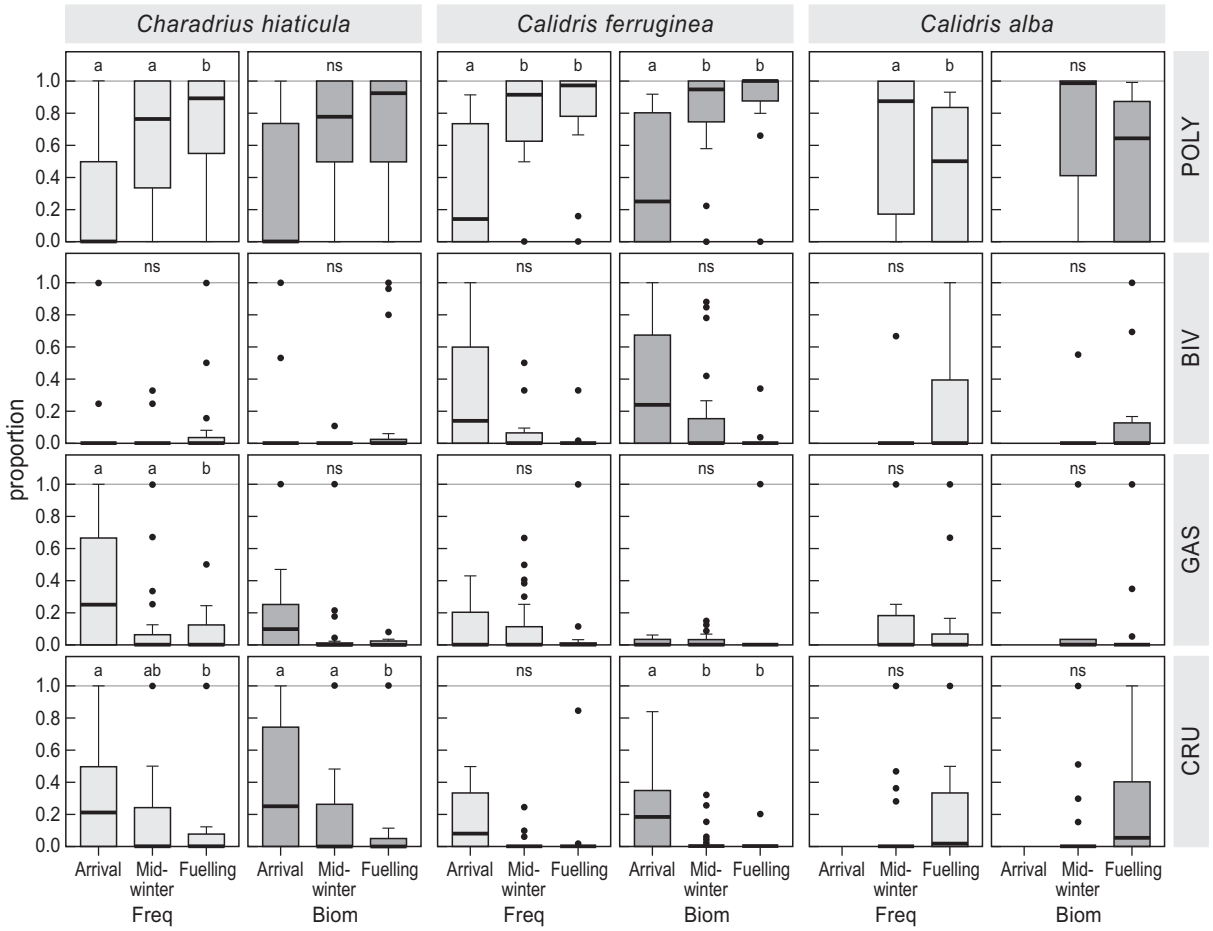


Figure 3. Seasonal variation in diet composition across three periods of the non-breeding season, for the smaller shorebirds (Ringed Plover, Curlew Sandpiper and Sanderling, indicated in the top row), expressed as the proportion of individuals ('Freq', light grey boxplots) and proportion of biomass ('Biom', estimated as mg AFDM, dark grey boxplots) of each given prey group (one per row), as indicated to the left of the plots ('POLY' = polychaetes, 'BIV' = bivalves, 'GAS' = gastropods, 'CRU' = crustaceans). Each species therefore has two columns of plots: 'Freq' and 'Biom'. Letters above each plot indicate significant differences between periods. See Table S2 and S3 for model and pairwise test results and associated *P*-values.

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DISCUSSION

The diet of most shorebirds changed in the course of the non-breeding season in the Bijagós, with several species showing the largest difference between arrival and fuelling periods. It is to be expected that this temporal variation in diet reflects adjustments in response to the more energetically demanding fuelling period, although it could also reflect changes in prey behaviour and therefore harvestability (Zwarts & Dirksen 1990). These results highlight the importance of analysing the temporal aspect of shorebirds' diet throughout the non-breeding season, which is seldom considered in dietary studies, possibly leading to incorrect estimates of energetic trade-offs.

While dropping analysis is a practical tool that allows for a comprehensive study of shorebird diet, there are some potentially relevant prey that may not be detected by this method, specifically those that do not have hard structures excreted in faeces. The main limitations relate to sedentary polychaetes and bivalve syphons, both widely available locally (Coelho *et al.* 2022), and preyed upon by shorebirds in other locations (Moreira 1996, Lourenço *et al.* 2015). While video recordings and DNA metabarcoding may help elucidate the proportion of both these prey items in shorebird diet, the contribution of these resources in terms of biomass is likely to be quite limited. Sedentary polychaetes are less mobile, making them harder to detect for shorebirds, and the size ranges found in the Bijagós for this

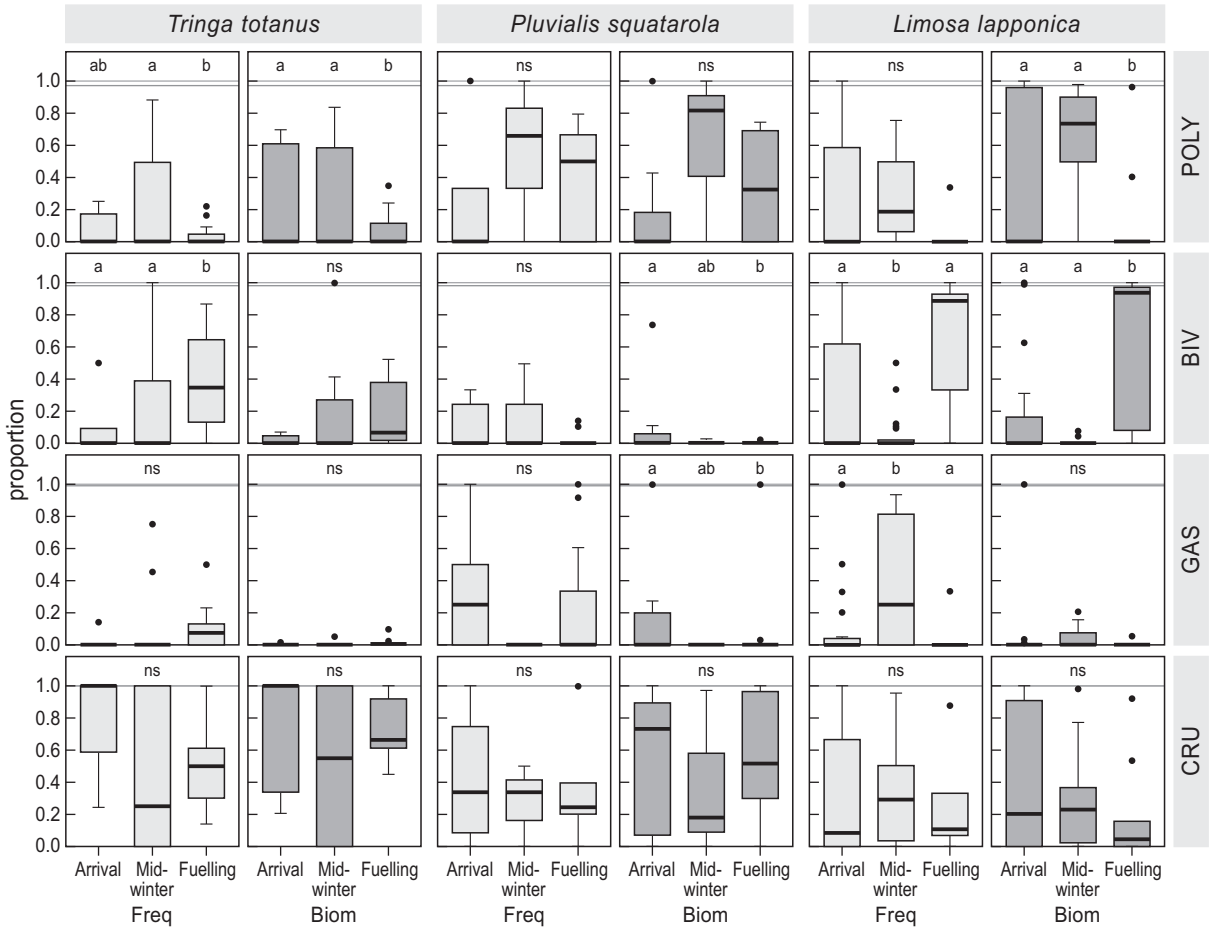


Figure 4. Seasonal variation in diet composition across three periods of the non-breeding season, for the smaller shorebirds (Ringed Plover, Curlew Sandpiper and Sanderling, indicated in the top row), expressed as the proportion of individuals ('Freq', light grey boxplots) and proportion of biomass ('Biom', estimated as mg AFDM, dark grey boxplots) of each given prey group (one per row), as indicated to the left of the plots ('POLY' = polychaetes, 'BIV' = bivalves, 'GAS' = gastropods, 'CRU' = crustaceans). Each species therefore has two columns of plots: 'Freq' and 'Biom'. Letters above each plot indicate significant differences between periods. See Table S2 and S3 for model and pairwise test results and associated *P*-values.

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group is smaller than that of errant polychaetes (Coelho *et al.* 2022). Bivalve syphons also have low levels of digestible biomass. In fact, recent DNA metabarcoding confirmed a low occurrence of sedentary polychaetes in faeces of shorebird wintering in the Bijagós (Correia *et al.* 2023), but further comparisons are not warranted due to different sampling effort and methods used between studies.

Shorebird diet reconstruction in the Bijagós

The diet of most species was in line with the few previous descriptions for the Bijagós and also with the much wider contributions from other wintering sites (Pienkowski 1982, Moreira 1996, Lourenço *et al.* 2016b, 2017). For example, Ringed Plovers and Curlew Sandpipers were found to consume a high proportion of polychaetes (Puttick 1978, Pienkowski 1982, Perez-Hurtado *et al.* 1997, Lourenço *et al.* 2017), while Red Knots almost exclusively consumed bivalves, just as they do in most parts of the world (Piersma 1991, Moreira 1994, van Gils *et al.* 2013, Yang *et al.* 2013, Sturbois *et al.* 2015, Lourenço *et al.* 2017). Redshanks, on the other hand, are more generalist predators, targeting different prey groups according to local availability at different sites throughout the flyway (Goss-Custard 1977, Moreira 1996, Sánchez *et al.* 2005). This is in line with the present findings, as Redshank diet consisted of wide range of prey of the most abundant groups, from polychaetes to crustaceans and bivalves. The diet of the crab specialist Whimbrel was also similar to what had previously been reported for this area, feeding almost exclusively on West African Fiddler Crabs *Afruca tangeri* (Zwarts 1985, 1988, Lourenço *et al.* 2017).

However, likely due to the larger spatio-temporal sampling achieved in this study, with seven mudflats sampled throughout the non-breeding season, some results deviated considerably from what was expected from literature. Bar-tailed Godwits mostly target polychaetes in wintering areas in Europe (Scheiffarth 2001, Duijns *et al.* 2013), however, in the Bijagós they consumed as many polychaetes as Ghost Shrimps *Balsscallichirus balssi* (23% of total consumed individuals for each prey). In terms of biomass, this translated to about 50% polychaetes but only about 30% crustaceans, including other species besides the low energy but easy digestible ghost shrimps, such as the more energetic but harder to digest crabs. Another high-Arctic breeding species, the Grey Plover is known to feed mostly on polychaetes in European estuaries (Kersten & Piersma 1984, Pienkowski 1982, Moreira 1996), whilst in the Bijagós it consumed almost as many crustaceans as polychaetes (33% and 44%, respectively).

Some authors have demonstrated the importance of Fiddler Crabs, a widely available species in the Bijagós (Paulino *et al.* 2021), as a key prey in the diet of the most of shorebirds in the archipelago (Zwarts 1985, Lourenço *et al.* 2017, Carneiro *et al.* 2021). Our findings corroborate this, but their relative importance appears to be much lower than previously suggested. In particular, Curlew Sandpiper and Sanderling diets contained a proportion of crustacean biomass estimated to be less than half of what was previously reported (only 8% and 17%, respectively). For Redshank and Grey Plover, crustaceans consistently represented about 60% of consumed biomass, including not only Fiddler Crabs but also other crustaceans such as Ghost Shrimp and Anthuridae, revealing a much lower proportion of this prey group than the c. 85% previously reported by Lourenço *et al.* (2017). These differences in diet composition are likely due to the much wider sampling effort of the present study, which encompasses seven different sites on different islands, with distinct macrozoobenthic community compositions (Coelho *et al.* 2022), and consequently different prey availability and abundance, thus likely representing more completely shorebird diet in the Bijagós Archipelago. Our results also indicate that the Ringed Plover's main prey are polychaetes, as recently reported (Lourenço *et al.* 2017) and not (or no longer) the Fiddler Crab as reported several decades ago (Zwarts 1985). Interestingly, Whimbrel, Redshank and Bar-tailed Godwit also occasionally include fish in their diet, which suggests that despite the difficulty in catching and handling such prey, these shorebirds are able to take advantage of its very high quality when conditions allow, for example when fish get trapped in small pools after the receding tide.

This was a surprising finding particularly for Whimbrel, which have previously been reported to feed exclusively on crabs in the Bijagós (Lourenço *et al.* 2017), although a more recent study indicates that Ghost Shrimp is also consumed (Carneiro *et al.* 2021). Our results show that despite crabs being indeed the main source of biomass (90%), Whimbrel also occasionally included a much more varied prey set in their diet, specifically mud snails (Hydrobiidae), Ghost Shrimps and fish (Table2).

Seasonal variation of shorebird diet

Shorebird diet changed seasonally with some species showing opposite patterns of change. Two of the smaller sized species, the Ringed Plover and Curlew Sandpiper, included more polychaetes in their diet towards the end of the season, while simultaneously

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decreasing the amount of gastropods and crustaceans. Soft-bodied polychaetes are theoretically very profitable and are in fact preferred by many shorebirds even when other prey with a high shell:flesh ratio are available in higher densities (Kalejta 1993). While both these shorebird species consume mostly polychaetes, this result appears to be intuitive if seen as an increase of the most preferred and profitable prey for these species, the polychaetes. Interestingly, the opposite pattern was found for larger bodied species, in particular for Redshank and Bar-tailed Godwit that displayed a change in diet from polychaetes to bivalves by the end of the season. This is an interesting result, as it was expected that polychaetes would also be the most profitable prey item for these two larger species, specifically for the polychaete specialist Bar-tailed Godwit (Scheiffarth 2001, Duijns *et al.* 2013). Even though polychaete abundance does not decrease in the Bijagós towards the end of winter, the average size of polychaetes found in the archipelago is very small (mean size of 5 mm; Coelho *et al.* 2022). Given such small size, in relation to polychaetes found in other sites, this prey may still be relatively profitable for smaller sized shorebirds, but less so for larger ones. Instead, the increase in the proportion of bivalves in the diet of these larger shorebirds may be due to the increasing abundance of these prey in the Bijagós towards the end of the season, possibly due to recruitment during this period (Coelho *et al.* 2022).

The macrozoobenthic community in the Bijagós is diverse and spatially variable, with different sites having distinct macrozoobenthic compositions (Lourenço *et al.* 2018, Coelho *et al.* 2022). Bivalves represent the majority of the biomass available and increase in density during the shorebirds' presence in the archipelago, but other prey groups show spatial differences (Coelho *et al.* 2022). Polychaetes, the most abundant group, as well as gastropods and crustaceans, increase in density in only a few sites, while remaining constant in others (Coelho *et al.* 2022). The observed changes in shorebird diet could be influenced by this spatial variation in prey availability, and future studies should take this into consideration. While this study was not designed to address spatial variation in shorebird diet (Table S1), the fact that several species showed opposite patterns in diet variation (e.g. some increasing consumption of bivalves and other decreasing), and that prey density does not decrease (Coelho *et al.* 2022), suggests that diet variation is caused by the responses of shorebirds to increased energetic requirements.

Some species however showed much smaller dietary variation. For example, Grey Plover maintained the proportion of its two main prey groups constant throughout the season (polychaetes and crustaceans), but there was a significant reduction of the other two less important prey groups (bivalves and gastropods) in the fuelling period compared to the arrival period, despite both increasing in abundance in the archipelago (Coelho *et al.* 2022). These results suggest that despite having the capacity to change their diet in accordance with the available prey species in a certain site (Pienkowski 1982), Grey Plover wintering in the Bijagós actively select their preferred prey groups during the fuelling period. However, as the proportion of those least preferred prey was so small to begin with, these results should be interpreted with caution. Similarly, Sanderling diet varied only in the proportion of polychaetes, that was lower during fuelling compared to mid-winter, although it is unclear which prey group replaced polychaetes in the fuelling period, possibly due to the consumption of soft-bodied prey that was therefore missed.

The shorebird species that demonstrated least dietary variation throughout the season was the Whimbrel, which may be explained by the extremely high local availability of its most consumed prey, the Fiddler Crab (Paulino *et al.* 2021). This may also be an important factor contributing to the Whimbrel's increasing population in the Bijagós, whereas on the rest of the flyway the species remains stable (Henriques *et al.* 2022a).

Dietary overlap between the three periods

Intraspecific seasonal overlap between periods was often high, corroborating the previous results and indicating the existence of only small adjustments in the proportion of consumed prey groups. Given that shorebirds tend to display high levels of site-fidelity (Alves *et al.* 2013, Lourenço *et al.* 2016a), dietary changes within the same season are expected to be minimal. However, the reported temporal change in the macrozoobenthic community in the Bijagós towards the end of the shorebird season (Coelho *et al.* 2022), contemporaneous with the fuelling phase of these species, could lead to dietary changes. In fact, the most pronounced seasonal changes in diet were indeed recorded between fuelling and another period for all shorebird species (except Grey Plovers), indicating that almost all species adjusted their diet closer to their departure, thus likely responding to the higher energetic requirements of this period. While some species made this dietary adjustment gradually over the season, with the largest differences found between the arrival and fuelling periods, others changed more rapidly, between mid-winter and

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fuelling. The lowest overlap, between Grey Plovers' diet in arrival and mid-winter, suggests that it may have been less selective upon arrival, consuming some of its least preferred prey (gastropods and bivalves), but changing shortly after, to the preferred polychaetes and crustaceans, which it kept consuming in similar proportions during mid-winter and fuelling.

Understanding dietary flexibility in shorebirds may be important to better assess their resilience to environmental change. However, despite their general ability to change their diet in the Bijagós, particularly during fuelling, it remains unknown if such a dietary shift provides the required energetic input. The fact that the biomass densities of the most consumed prey groups do not decrease in the course of the season in the Bijagós (Coelho *et al.* 2022) may point towards a frequent renewal of resources, but this merits further investigation. Daily energy budget estimates are necessary in order to understand how the shorebirds make ends meet.

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SAMENVATTING

Net als elders op de wereld voeden wadvogels die de (noordelijke) winter op de tropische wadplaten van de Bijagós Archipel in Guinee-Bissau in West-Afrika doorbrengen, zich met ingegraven schelp- en schaaldieren en borstelwormen. In deze studie beschrijven we voor het eerst het menu (de samenstelling op basis van gereconstrueerde biomassawaarden) van acht wadvogelsoorten (Bontbekplevier *Charadrius hiaticula*, Zilverplevier *Pluvialis squatarola*, Drieteenstrandloper *Calidris alba*, Krombekstrandloper *C. ferruginea*, Kanoet *C. canutus*, Tureluur *Tringa totanus*, Rosse Grutto *Limosa lapponica* en Regenwulp *Numenius phaeopus*) in de Bijagós Archipel. We beschrijven ook hoe hun menu gedurende de drie hoofdperioden van het winterseizoen (aankomstperiode, midwinterperiode, opvetperiode) veranderde, en beschrijven hoe groot, binnen elk van de soorten, de overlap in het menu tussen de drie perioden is. Het voedsel van de kleinere wadvogels bestond voornamelijk uit borstelwormen, met een aandeel van 83% in het menu van de Krombekstrandloper en bijna 70% in dat van de Drieteenstrandloper en Bontbekplevier. De laatste twee soorten aten ook kleine schaaldieren (respectievelijk 9% en 16%). Tureluurs en Rosse Grutto's hadden het meest diverse menu, met een groter aandeel schaaldieren (rond 40%), maar ook aanzienlijke percentages tweekleppigen en borstelwormen (beide tussen 20% en 30%). Zilverplevieren aten ook veel schaaldieren (33%), maar de meest voorkomende prooidieren waren borstelwormen (44%). Bij de overige twee soorten bestond het menu voornamelijk uit één prooigroep: 78% tweekleppigen bij Kanoeten en 76% schaaldieren (de wenkkrab *Afruca tangeri*) bij Regenwulpen. In de loop van de winter, tijdens de opeenvolgende perioden, vonden we bij de meeste soorten significante veranderingen in het menu, maar niet bij Regenwulpen, die vrijwel altijd wenkkrabben aten. Bij enkele kleine wadvogels (Bontbekplevier, Krombekstrandloper) werd het aandeel aan wormen groter tijdens de opvetperiode, terwijl bij Tureluurs en Rosse Grutto's het aandeel tweekleppige schelpdieren dan groter werd. Dat tijdens het opvetten het menu zozeer veranderde ten opzichte van de rest van overwinteringsperiode in de Bijagós Archipel kan het gevolg zijn van veranderingen in de beschikbaarheid van de benthische prooidieren, maar ook van de criteria voor prooiselectie van de wadvogels, of van een combinatie van de twee factoren.

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SUPPLEMENTARY MATERIAL

Table S1. Total number of analysed droppings containing prey remains, collected in each site, by period, for each shorebird species.

		ANRUMEI	ABU	BIJANTE	BRUCE	ESCADINHAS	IMBONE	RATUM
Charadrius hiaticula	Arrival	–	4	6	4	–	–	–
	Mid-winter	–	–	5	27	–	–	–
	Fuelling	–	–	–	16	–	–	–
Calidris ferruginea	Arrival	–	8	5	–	–	–	–
	Mid-winter	–	13	–	5	12	–	–
	Fuelling	–	3	–	8	–	–	–
Calidris alba	Mid-winter	–	2	4	12	–	–	–
	Fuelling	–	4	4	6	–	–	–
Tringa totanus	Arrival	–	1	3	–	1	–	–
	Mid-winter	–	8	1	–	8	–	–
	Fuelling	–	–	12	–	–	–	–
Pluvialis squatarola	Arrival	2	–	1	7	–	–	–
	Mid-winter	1	–	–	–	2	–	–
	Fuelling	–	–	3	–	15	–	–
Limosa lapponica	Arrival	1	18	–	1	–	–	–
	Mid-winter	–	13	2	6	–	–	1
	Fuelling	–	6	2	1	–	–	–
Numenius phaeopus	Arrival	–	1	6	1	11	–	1
	Mid-winter	1	1	–	4	15	1	–
	Fuelling	3	3	–	–	1	–	–

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Table S2. Results of Generalized linear models (GLM) exploring the variation on proportion of individuals (frequency) and biomass of the most common prey groups ('POLY' = polychaetes, 'BIV' = bivalves, 'GAS' = gastropods, 'CRU' = crustaceans) between periods. Arrival was used as the reference period for all shorebird species, except for *Calidris alba*, where Mid-winter was used as reference (as no samples were attained for arrival). *T*-values refer to the models with binomial family, whereas *Z*-values refer to the models with quasibinomial error distribution. Significant results are highlighted in bold.

			FREQUENCY						**BIOMASS**					
			Estimate	Std. Error	*t*-value	*Pr*(>|*t*|)	*z*-value	*Pr*(>|*z*|)	Estimate	Std. Error	*t*-value	*Pr*(>|*t*|)	*z*-value	*Pr*(>|*z*|)
Charadrius hiaticula	POLY	Intercept	–1.540	0.670	–2.298	**0.025**	NA	NA	–0.330	0.642	–0.514	0.609	NA	NA
		Mid-winter	1.655	0.731	2.264	**0.027**	NA	NA	1.147	0.744	1.542	0.129	NA	NA
		Fuelling	3.620	0.783	4.626	**0.000**	NA	NA	1.390	0.720	1.931	0.058	NA	NA
	BIV	Intercept	–3.199	0.721	NA	NA	–4.434	**0.000**	–1.956	0.879	–2.226	**0.030**	NA	NA
		Mid-winter	–0.740	0.927	NA	NA	–0.797	0.425	–4.674	4.457	–1.049	0.299	NA	NA
		Fuelling	–0.313	0.832	NA	NA	–0.376	0.707	0.630	0.935	0.674	0.503	NA	NA
	GAS	Intercept	–0.039	0.527	–0.074	0.941	NA	NA	–2.237	0.812	–2.754	**0.008**	NA	NA
		Mid-winter	–0.635	0.615	–1.032	0.306	NA	NA	–0.328	0.959	–0.342	0.733	NA	NA
		Fuelling	–2.941	0.806	–3.648	**0.001**	NA	NA	–2.378	1.363	–1.745	0.086	NA	NA
	CRU	Intercept	–0.875	0.433	–2.022	**0.048**	NA	NA	–0.569	0.496	–1.148	0.256	NA	NA
		Mid-winter	–1.169	0.559	–2.092	**0.041**	NA	NA	–0.618	0.584	–1.059	0.294	NA	NA
		Fuelling	–2.477	0.693	–3.572	**0.001**	NA	NA	–2.670	0.750	–3.562	0.001	NA	NA
Calidris ferruginea	POLY	Intercept	0.525	0.475	1.104	0.275	NA	NA	0.246	0.365	0.675	0.503	NA	NA
		Mid-winter	1.588	0.615	2.583	**0.013**	NA	NA	1.945	0.517	3.759	**0.000**	NA	NA
		Fuelling	1.920	0.779	2.464	**0.017**	NA	NA	3.078	0.954	3.228	**0.002**	NA	NA
	BIV	Intercept	–2.040	0.572	–3.569	**0.001**	NA	NA	–1.433	0.481	–2.979	**0.004**	NA	NA
		Mid-winter	–1.546	0.823	–1.877	0.066	NA	NA	–1.308	0.683	–1.915	0.061	NA	NA
		Fuelling	–2.618	1.491	–1.756	0.085	NA	NA	–2.291	1.215	–1.887	0.065	NA	NA
	GAS	Intercept	–1.802	0.535	–3.371	**0.001**	NA	NA	–4.018	0.749	NA	NA	–5.363	**0.000**
		Mid-winter	–0.885	0.669	–1.324	0.191	NA	NA	–0.148	0.896	NA	NA	–0.165	0.869
		Fuelling	–2.446	1.270	–1.926	0.060	NA	NA	–2.124	2.044	NA	NA	–1.039	0.299
	CRU	Intercept	–2.040	0.597	–3.415	**0.001**	NA	NA	–1.217	0.316	–3.856	**0.000**	NA	NA
		Mid-winter	–2.008	0.977	–2.056	**0.045**	NA	NA	–2.459	0.609	–4.039	**0.000**	NA	NA
		Fuelling	–0.778	0.848	–0.917	0.363	NA	NA	–3.481	1.288	–2.703	**0.009**	NA	NA
Calidris alba	POLY	Intercept	0.379	0.255	NA	NA	1.491	0.136	1.334	0.339	3.936	**0.000**	NA	NA
		Fuelling	0.813	0.336	NA	NA	2.419	**0.016**	0.017	0.458	0.038	0.970	NA	NA
	BIV	Intercept	–2.708	0.925	–2.928	**0.006**	NA	NA	–4.221	1.651	–2.557	0.016	NA	NA
		Fuelling	0.232	1.114	0.209	0.836	NA	NA	1.033	1.887	0.548	0.588	NA	NA
	GAS	Intercept	–1.946	0.378	NA	NA	–5.148	**0.000**	–4.257	0.873	NA	NA	–4.878	**0.000**
		Fuelling	–1.154	0.593	NA	NA	–1.946	0.052	–0.571	1.361	NA	NA	–0.420	0.675
	CRU	Intercept	–1.273	0.421	–3.027	**0.005**	NA	NA	–1.516	0.340	–4.460	**0.000**	NA	NA
		Fuelling	–0.797	0.587	–1.358	0.185	NA	NA	–0.157	0.469	–0.334	0.741	NA	NA
Tringa totanus	POLY	Intercept	–1.642	0.637	–2.578	**0.015**	NA	NA	0.159	0.727	0.218	0.828	NA	NA
		Mid-winter	1.387	0.723	1.919	**0.064**	NA	NA	–0.532	0.917	–0.580	0.566	NA	NA
		Fuelling	–2.107	0.963	–2.188	**0.036**	NA	NA	–2.961	0.845	–3.503	**0.001**	NA	NA
	BIV	Intercept	–1.856	0.776	–2.391	**0.023**	NA	NA	–2.844	1.258	–2.262	**0.031**	NA	NA
		Mid-winter	–0.207	0.985	–0.211	0.835	NA	NA	1.047	1.404	0.746	0.461	NA	NA
		Fuelling	2.134	0.815	2.619	**0.014**	NA	NA	1.761	1.271	1.386	0.176	NA	NA
	GAS	Intercept	–2.110	0.529	NA	NA	–3.986	**0.000**	–4.571	1.158	NA	NA	–3.947	**0.000**
		Mid-winter	0.047	0.649	NA	NA	0.072	0.943	–0.309	1.546	NA	NA	–0.200	0.842
		Fuelling	–0.799	0.630	NA	NA	–1.267	0.205	–2.218	1.506	NA	NA	–1.473	0.141
	CRU	Intercept	0.383	0.539	0.711	0.483	NA	NA	–0.426	0.595	–0.715	0.480	NA	NA
		Mid-winter	–1.055	0.673	–1.567	0.127	NA	NA	0.194	0.743	0.262	0.795	NA	NA
		Fuelling	–0.974	0.596	–1.635	0.112	NA	NA	1.220	0.620	1.967	0.058	NA	NA

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Table S2. Continued.

			FREQUENCY						BIOMASS					
			Estimate	Std. Error	*t*-value	*Pr*(>|*t*|)	*z*-value	*Pr*(>|*z*|)	Estimate	Std. Error	*t*-value	*Pr*(>|*t*|)	*z*-value	*Pr*(>|*z*|)
Pluvialis squatarola	POLY	Intercept	–1.642	0.580	–2.832	**0.008**	NA	NA	–0.976	0.734	–1.329	0.195	NA	NA
		Mid-winter	1.930	1.150	1.678	0.104	NA	NA	1.211	1.010	1.199	0.241	NA	NA
		Fuelling	1.382	0.646	2.140	**0.041**	NA	NA	0.640	0.788	0.812	0.424	NA	NA
	BIV	Intercept	–2.428	0.602	NA	NA	–4.031	0.000	–3.442	0.459	NA	NA	–7.491	**0.000**
		Mid-winter	0.636	1.237	NA	NA	0.514	0.607	–1.018	0.912	NA	NA	–1.116	0.264
		Fuelling	–1.298	0.935	NA	NA	–1.388	0.165	–2.126	0.721	NA	NA	–2.951	**0.003**
	GAS	Intercept	–0.272	0.524	–0.519	0.608	NA	NA	–3.242	0.419	NA	NA	–7.745	**0.000**
		Mid-winter	–17.725	2931.045	–0.006	0.995	NA	NA	–18.333	2460.155	NA	NA	–0.007	0.994
		Fuelling	–0.661	0.648	–1.020	0.317	NA	NA	–2.450	0.724	NA	NA	–3.386	0.001
	CRU	Intercept	–0.734	0.351	NA	NA	–2.090	**0.037**	0.653	0.671	0.972	0.339	NA	NA
		Mid-winter	–0.182	0.907	NA	NA	–0.201	0.841	–0.934	0.953	–0.980	0.335	NA	NA
		Fuelling	–0.318	0.430	NA	NA	–0.740	0.459	–0.346	0.726	–0.477	0.637	NA	NA
Limosa lapponica	POLY	Intercept	–1.935	0.541	–3.580	**0.001**	NA	NA	0.107	0.428	0.249	0.804	NA	NA
		Mid-winter	0.122	0.646	0.189	0.851	NA	NA	0.645	0.557	1.157	0.253	NA	NA
		Fuelling	–2.151	1.407	–1.529	0.133	NA	NA	–3.539	1.126	–3.142	**0.003**	NA	NA
	BIV	Intercept	0.579	0.386	1.501	0.140	NA	NA	–1.794	0.514	–3.493	**0.001**	NA	NA
		Mid-winter	–3.999	0.818	–4.890	**0.000**	NA	NA	–3.962	2.547	–1.555	0.126	NA	NA
		Fuelling	0.669	0.563	1.188	0.241	NA	NA	3.352	0.652	5.140	0.000	NA	NA
	GAS	Intercept	–2.783	0.878	–3.168	**0.003**	NA	NA	–5.543	1.181	NA	NA	–4.694	**0.000**
		Mid-winter	3.029	0.923	3.282	**0.002**	NA	NA	2.631	1.209	NA	NA	2.176	**0.030**
		Fuelling	–2.005	2.273	–0.882	0.382	NA	NA	–2.124	3.120	NA	NA	–0.681	0.496
	CRU	Intercept	–1.552	0.613	–2.532	**0.015**	NA	NA	–0.722	0.410	–1.760	0.085	NA	NA
		Mid-winter	0.542	0.711	0.763	0.449	NA	NA	–0.294	0.533	–0.552	0.583	NA	NA
		Fuelling	0.156	0.816	0.191	0.850	NA	NA	–1.075	0.622	–1.728	0.091	NA	NA
Numenius phaeopus	POLY	Intercept	–20.909	3369.370	NA	NA	–0.006	0.995	–21.507	4571.314	–0.005	0.996	NA	NA
		Mid-winter	18.157	3369.370	NA	NA	0.005	0.996	17.559	4571.314	0.004	0.997	NA	NA
		Fuelling	–0.183	6394.533	NA	NA	0.000	1.000	–1.090	8736.459	0.000	1.000	NA	NA
	BIV	Intercept	–2.918	0.726	NA	NA	–4.019	**0.000**	–4.710	1.529	–3.080	**0.003**	NA	NA
		Mid-winter	–0.260	1.024	NA	NA	–0.254	0.799	–0.263	2.162	–0.121	0.904	NA	NA
		Fuelling	1.308	0.963	NA	NA	1.359	0.174	0.294	1.975	0.149	0.883	NA	NA
	GAS	Intercept	–2.485	0.739	–3.360	**0.002**	NA	NA	–6.665	4.641	–1.436	0.158	NA	NA
		Mid-winter	1.540	0.835	1.845	0.071	NA	NA	1.667	4.971	0.335	0.739	NA	NA
		Fuelling	–0.348	1.466	–0.238	0.813	NA	NA	–1.899	12.231	–0.155	0.877	NA	NA
	CRU	Intercept	1.917	0.582	3.292	**0.002**	NA	NA	4.575	1.749	2.616	**0.012**	NA	NA
		Mid-winter	–1.427	0.682	–2.094	**0.042**	NA	NA	–1.182	1.954	–0.605	0.548	NA	NA
		Fuelling	–0.664	0.902	–0.736	0.465	NA	NA	–0.175	2.315	–0.076	0.940	NA	NA

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Table S3. Results of Pairwise Post-hoc Tukey tests, following the GLMs (see Table S2) exploring the variation on proportion of individuals (frequency) and biomass of the most common prey groups ('POLY' = polychaetes, 'BIV' = bivalves, 'GAS' = gastropods, 'CRU' = crustaceans) between periods. Significant results are highlighted in bold.

			FREQUENCY				BIOMASS			
			Estimate	Std. Error	*Z*	*P*	Estimate	Std. Error	*Z*	*P*
Charadrius hiaticula	POLY	Mid-winter: Arrival	1.65	0.73	2.26	0.060	1.15	0.74	1.54	0.266
		Fuelling: Arrival	3.62	0.78	4.63	**<0.001**	1.39	0.72	1.93	0.126
		Fuelling: Mid-winter	1.96	0.50	3.95	**<0.001**	0.24	0.50	0.49	0.875
	BIV	Mid-winter: Arrival	–0.74	0.93	–0.80	0.700	–4.67	4.46	–1.05	0.516
		Fuelling: Arrival	–0.31	0.83	–0.38	0.924	0.63	0.93	0.67	0.760
		Fuelling: Mid-winter	0.43	0.71	0.60	0.820	5.30	4.38	1.21	0.160
	GAS	Mid-winter: Arrival	–0.63	0.61	–1.03	0.552	–0.33	0.96	–0.34	0.936
		Fuelling: Arrival	–2.94	0.81	–3.65	**<0.001**	–2.38	1.36	–1.75	0.184
		Fuelling: Mid-winter	–2.61	0.69	–3.35	**0.002**	–2.05	1.21	–1.70	0.202
	CRU	Mid-winter: Arrival	–1.17	0.56	–2.09	0.090	–0.62	0.58	–1.06	0.536
		Fuelling: Arrival	–2.48	0.69	–3.57	**0.001**	–2.67	0.75	–3.56	**0.001**
		Fuelling: Mid-winter	–0.31	0.65	–2.02	0.105	–2.05	0.64	–3.20	**0.004**
Calidris ferruginea	POLY	Mid-winter: Arrival	1.59	0.61	2.58	**0.026**	1.94	0.52	3.76	**<0.001**
		Fuelling: Arrival	1.92	0.78	2.46	**0.036**	3.08	0.95	3.23	**0.003**
		Fuelling: Mid-winter	0.33	0.73	0.45	0.891	0.13	0.95	1.19	0.449
	BIV	Mid-winter: Arrival	–1.55	0.82	–1.88	0.138	–1.31	0.68	–1.91	0.128
		Fuelling: Arrival	–0.62	1.49	–1.76	0.176	–2.29	1.21	–1.89	0.136
		Fuelling: Mid-winter	–1.07	0.49	–0.72	0.747	–0.98	1.22	–0.81	0.690
	GAS	Mid-winter: Arrival	–0.88	0.67	–1.32	0.370	–0.15	0.90	–0.16	0.984
		Fuelling: Arrival	–2.45	1.27	–1.93	0.124	–2.12	2.04	–1.04	0.536
		Fuelling: Mid-winter	–1.56	1.22	–1.28	0.394	–1.98	1.96	–1.01	0.557
	CRU	Mid-winter: Arrival	–2.01	0.98	–2.06	0.099	–2.46	0.61	–4.04	**<0.001**
		Fuelling: Arrival	–0.78	0.85	–0.92	0.658	–3.48	1.29	–2.70	**0.017**
		Fuelling: Mid-winter	1.23	0.98	1.25	0.419	–1.02	1.35	–2.75	0.719
Calidris alba	POLY	Fuelling: Mid-winter	0.81	0.34	2.42	**0.016**	0.02	0.46	0.38	0.970
	BIV	Fuelling: Mid-winter	0.23	1.11	0.21	0.835	1.03	1.89	0.55	0.584
	GAS	Fuelling: Mid-winter	–1.15	0.59	–1.95	0.052	–0.57	1.36	–0.42	0.675
	CRU	Fuelling: Mid-winter	–0.80	0.59	–1.36	0.175	–0.16	1.47	–0.33	0.739
Tringa totanus	POLY	Mid-winter: Arrival	1.39	0.72	1.92	0.130	–0.53	0.92	–0.58	0.829
		Fuelling: Arrival	–2.11	0.96	–2.19	0.071	–2.96	0.84	–3.50	**0.001**
		Fuelling: Mid-winter	–3.49	0.80	–4.37	**<0.001**	–2.43	0.71	–3.43	**0.002**
	BIV	Mid-winter: Arrival	–0.21	0.98	–0.21	0.975	1.04	1.40	0.75	0.723
		Fuelling: Arrival	2.13	0.81	2.62	**0.023**	1.76	1.27	1.39	0.331
		Fuelling: Mid-winter	2.34	0.65	3.58	**<0.001**	0.71	0.65	1.10	0.497
	GAS	Mid-winter: Arrival	0.05	0.65	0.07	0.997	–0.31	1.55	–2.20	0.978
		Fuelling: Arrival	–0.80	0.63	–1.27	0.411	–2.22	1.51	–1.47	0.304
		Fuelling: Mid-winter	–0.84	0.51	–1.66	0.217	–1.91	1.41	–1.36	0.363
	CRU	Mid-winter: Arrival	–1.05	0.67	–1.57	0.255	0.19	0.74	0.26	0.962
		Fuelling: Arrival	–0.97	0.59	–1.63	0.226	0.22	0.62	1.97	0.115
		Fuelling: Mid-winter	0.02	0.48	0.17	0.984	1.02	0.48	2.14	0.077

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Table S3. Continued.

			FREQUENCY				BIOMASS			
			Estimate	Std. Error	*Z*	*P*	Estimate	Std. Error	*Z*	*P*
Pluvialis squatarola	POLY	Mid-winter: Arrival	1.93	1.15	1.68	0.204	1.21	1.01	1.20	0.446
		Fuelling: Arrival	1.38	0.65	2.14	0.077	0.64	0.79	0.81	0.689
		Fuelling: Mid-winter	–0.55	1.03	–0.53	0.851	–0.57	0.75	–0.76	0.720
	BIV	Mid-winter: Arrival	0.64	1.24	0.51	0.863	–1.02	0.91	–1.12	0.501
		Fuelling: Arrival	–1.30	0.93	–1.39	0.343	–2.13	0.72	–2.95	**0.009**
		Fuelling: Mid-winter	–1.93	1.30	–1.50	0.290	–1.11	0.96	–1.15	0.480
	GAS	Mid-winter: Arrival	–17.72	2931.04	–0.01	1.000	–18.33	2460.15	–0.01	0.999
		Fuelling: Arrival	–0.66	0.64	–1.02	0.521	–2.45	0.72	–3.39	**0.001**
		Fuelling: Mid-winter	17.06	2931.04	0.01	1.000	15.88	2460.15	0.01	0.999
	CRU	Mid-winter: Arrival	–0.18	0.91	–0.20	0.977	–0.93	0.95	–0.98	0.582
		Fuelling: Arrival	–0.32	0.43	–0.74	0.729	–0.35	0.73	–0.48	0.879
		Fuelling: Mid-winter	–0.14	0.87	–0.16	0.986	0.59	0.73	0.80	0.694
Limosa lapponica	POLY	Mid-winter: Arrival	0.12	0.64	0.19	0.980	0.64	0.56	1.16	0.465
		Fuelling: Arrival	–2.15	1.41	–1.53	0.263	–3.54	1.13	–3.14	**0.004**
		Fuelling: Mid-winter	–2.27	1.35	–1.68	1.197	–4.18	1.10	–3.80	**<0.001**
	BIV	Mid-winter: Arrival	–4.00	0.82	–4.89	**<0.001**	–3.96	2.55	–1.55	0.241
		Fuelling: Arrival	0.67	0.56	1.19	0.454	3.35	0.65	5.14	**<0.001**
		Fuelling: Mid-winter	4.67	0.83	5.63	**<0.001**	7.31	2.23	2.89	**0.009**
	GAS	Mid-winter: Arrival	3.03	0.92	3.28	**0.002**	2.63	1.21	2.18	0.067
		Fuelling: Arrival	–2.00	2.27	–0.88	0.634	–2.12	3.12	–0.68	0.761
		Fuelling: Mid-winter	–5.03	2.12	–2.38	**0.041**	–4.76	2.90	–1.64	0.211
	CRU	Mid-winter: Arrival	0.54	0.71	0.76	0.723	–0.29	0.53	–0.55	0.845
		Fuelling: Arrival	0.16	0.82	0.19	0.980	–1.07	0.62	–1.73	0.194
Numenius phaeopus	POLY	Mid-winter: Arrival	18.16	3369.37	0.01	1	17.56	4571.31	0.01	1
		Fuelling: Arrival	–0.18	6394.53	0.00	1	–1.09	8736.46	0.00	1
		Fuelling: Mid-winter	–18.34	5435.83	–0.01	1	–18.65	7445.05	–0.01	1
	BIV	Mid-winter: Arrival	–0.26	1.02	–0.25	0.965	–0.26	2.16	–0.12	0.992
		Fuelling: Arrival	1.31	0.96	1.36	0.362	0.29	1.97	0.15	0.988
		Fuelling: Mid-winter	1.57	0.96	1.63	0.231	0.56	1.97	0.28	0.957
	GAS	Mid-winter: Arrival	1.54	0.83	1.84	0.148	1.67	4.97	0.33	0.94
		Fuelling: Arrival	–0.35	1.47	–0.24	0.968	–1.90	12.23	–0.15	0.97
		Fuelling: Mid-winter	–0.89	1.32	–1.43	0.316	–3.57	11.45	–0.31	0.94
	CRU	Mid-winter: Arrival	–1.43	0.68	–2.09	0.089	–1.18	1.95	–0.60	0.815
		Fuelling: Arrival	–0.66	0.90	–0.74	0.739	–0.17	2.31	–0.07	0.997
		Fuelling: Mid-winter	0.76	0.77	0.98	0.582	1.01	1.75	0.58	0.830

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