University of Groningen

Comparative feeding ecology of shorebirds wintering at Banc d'Arguin, Mauritania

Lourenço, Pedro M.; Catry, Teresa; Piersma, Theunis; Granadeiro, José P.

Published in:
Estuaries and coasts

DOI:
[10.1007/s12237-015-0029-1](https://doi.org/10.1007/s12237-015-0029-1)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2016

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Lourenço, P. M., Catry, T., Piersma, T., & Granadeiro, J. P. (2016). Comparative feeding ecology of shorebirds wintering at Banc d'Arguin, Mauritania. *Estuaries and coasts*, 39(3), 855-865.
<https://doi.org/10.1007/s12237-015-0029-1>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Comparative Feeding Ecology of Shorebirds Wintering at Banc d'Arguin, Mauritania

Pedro M. Lourenço¹ · Teresa Catry² · Theunis Piersma^{3,4} · José P. Granadeiro²

Received: 29 April 2015 / Revised: 18 August 2015 / Accepted: 20 August 2015 / Published online: 28 August 2015
© Coastal and Estuarine Research Federation 2015

Abstract Limited knowledge of shorebird feeding ecology in the tropics hinders interpretation of considerable changes in numbers recently observed at the most important shorebird nonbreeding area along the East Atlantic Flyway, the Banc d'Arguin in Mauritania. We used droppings and video recordings to compare the diet and foraging behaviour of six shorebird species at Banc d'Arguin: dunlin, sanderling, red knot, ringed plover, grey plover and bar-tailed godwit. In four of those species, the detail achieved in prey identification allowed us to calculate niche width and foraging niche overlap. Sanderling and ringed plover consumed a wide range of macroinvertebrate taxa, while red knot consumed mainly bivalves with some gastropods, and both grey plover and bar-tailed godwit fed mainly on polychaete worms. A large proportion of dunlin droppings had no recognizable food items, suggesting a soft-bodied prey that we could not identify. Dunlin was the only strictly tactile forager, while sanderling and red knot used both visual and tactile methods. The

remaining species resort to visual cues for catching prey, even though tactile cues may be important for bar-tailed godwits. Dunlin, sanderling, red knot and ringed plover all showed relatively narrow trophic niches and non-significant levels of foraging niche overlap. Overall, the diet of each shorebird was broadly similar to that reported from other parts of their wintering ranges, with more gastropods in the red knot diet than previously described. Our data suggest that the high shorebird densities at Banc d'Arguin despite low benthic food densities (Hydrobiologia 258:211–222, 1993a; Journal of Sea Research 60:235–243, 2008) may result partly from partitioning of available resources via narrow trophic niches with little overlap. Given these distinct trophic niches, the widespread declines in shorebird numbers at Banc d'Arguin may reflect changes in a wide range of prey types and suggest a shift in the overall properties of this unique ecosystem.

Keywords Benthic macroinvertebrates · Diet overlap · Niche width · Tactile forager · Visual forager

Communicated by James Lovvorn

✉ Pedro M. Lourenço
p.m.g.lourenco@gmail.com

¹ Centro de Estudos do Ambiente e do Mar (CESAM)/Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Rua da Escola Politécnica 58, 1250-102 Lisbon, Portugal

² Centro de Estudos do Ambiente e do Mar (CESAM)/Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisbon, Portugal

³ NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands

⁴ Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

Introduction

High Arctic breeding species of shorebirds tend to congregate in large numbers at coastal wetlands during the nonbreeding season, taking advantage of abundant intertidal stocks of macroinvertebrates (van de Kam et al. 2004; Piersma 2012). Shorebirds are recognized as 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). The high densities of shorebirds found at wintering and staging sites often reflect the abundance of their benthic prey (e.g. Piersma 2012), but also their ability to partition trophic

resources by means of morphological and behavioural variation among (Lifjeld 1984; Bocher et al. 2014) and within species (Nebel 2005; Duijns et al. 2014). However, there are few community-wide studies on shorebird trophic ecology (but see Bocher et al. 2014), limiting our understanding of how competition and diet overlap affect resource partitioning among species. Understanding the trophic links between shorebirds and their prey, and among different shorebird species, is also critical to assessing effects of ongoing changes and emerging anthropogenic pressures. Such understanding is particularly relevant from a conservation point of view, as many shorebird populations worldwide are currently facing sharp declines (Stroud et al. 2006). Important examples are key tropical wintering areas such as the Banc d'Arguin in Mauritania, where very little is known about local drivers for ongoing declines in a wide range of species (Zwarts et al. 1998; van Gils et al. 2009; T. Piersma et al. unpublished data).

Located on the tropical Saharan coast, the Banc d'Arguin is the most important wintering area for shorebirds migrating along the East Atlantic Flyway (EAF) and the most important shorebird wintering area in Africa. Here, maximum counts exceed 2 million shorebirds, which represent over one fourth of all shorebirds migrating along the EAF, estimated at ca. 7 million birds (Zwarts et al. 1998; Delany et al. 2009). Such an exceptional site is also a good example 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). On the other hand, this type of information is still very limited for tropical areas of Africa such as Banc d'Arguin. In fact, with the exception of the intensively studied red knot *Calidris canutus* (e.g. Leyrer et al. 2012; Onrust et al. 2013; van Gils et al. 2013), only a few studies looked at the trophic ecology of bar-tailed godwit *Limosa lapponica* (Engelmoer et al. 1984; Zwarts et al. 1990), whimbrel *Numenius phaeopus* (Zwarts 1990; Zwarts and Dirksen 1990) and oystercatcher *Haematopus ostralegus* (Swennen 1990; Zwarts et al. 1990). For other species, and particularly the smaller shorebirds which represent the bulk of the local wintering population (Zwarts et al. 1998), available information on diet and foraging behaviour is very limited or absent (Zwarts et al. 1990).

Measurements of food stocks (Piersma 1982a; Wolff et al. 1993a; Honkoop et al. 2008) suggested that the abundance of harvestable macroinvertebrates was rather low with respect to the exceptionally high numbers of shorebirds using the tidal flats of this wetland during winter (Wolff et al. 1993a; van de Kam et al. 2004; Honkoop et al. 2008). This low food availability may be predicted to lead to increased competition within and among shorebird species.

Here, we take a comparative approach to study the diet and foraging behaviour of six shorebird species within a single time period and over a single study area within the Banc d'Arguin ecosystem. We further estimated the trophic niche width and degree of niche overlap among four of them. If the prediction of food specialization is upheld, the reasons for the decline for the wide range of species would suggest more comprehensive ecosystem problems than if dietary overlap was large.

Methods

Study Area

Field work took place at two intertidal sites at Banc d'Arguin, both located near the village of Iwik: Ebelk Aiznay (19°53'41" N, 16°18'43" W) and Baie d'Aouatif (19°53'48" N, 16°16'58" W), in December 2012, January 2013 and December 2013 (more information on this study area is in Leyrer et al. 2012). Although these study sites represent a very small portion of the whole Banc d'Arguin, they should represent the typical foraging conditions faced by wintering waders over much of this very large intertidal area. Most of the sampling was carried out in muddy intertidal habitats, including both bare and seagrass-covered areas, but we also surveyed sandy intertidal areas which are widely used by foraging sanderlings *Calidris alba*.

Macroinvertebrate Collection and Biomass Content

Randomly taken sediment cores (86.6 cm², approximately 20 cm deep) were sieved through 1 and 0.5 mm meshes to collect the most common macroinvertebrate species in order to build a reference collection and to calculate regression equations relating total structural size and biomass of individuals with the size of 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), individuals of known size were dried to constant mass (60 °C for 48 h) and then incinerated in a muffle furnace (2 h at 500 °C). The samples were weighed after drying and again after incineration, and the AFDM was calculated as the difference between dry mass and ash mass and then used to calculate regression equations (Table 1). Bivalve shells were removed prior to drying. For some prey, it was not possible to estimate sizes based on structures found in droppings, either because these structures

Table 1 Regression equations built to estimate invertebrate size and biomass (AFDM, in mg) based on the remains found in shorebird droppings and on prey structural size (in mm) from invertebrate sampling, respectively

Prey	Equations	N	R ²	Size range
<i>Hydrobia ulvae</i>	TL = 2.094 MW − 0.427 AFDM = 0.248TL ^{0.781}	42	0.98 0.85	0.4–5.0
<i>Bulla adansonii</i>	TL = 2.584 MW + 0.834 AFDM = 0.008TL ^{3.071}	12	0.99 0.99	5.2–17.2
<i>Bittium reticulatum</i>	TL = 3.835 MW − 0.847 AFDM = 0.009TL ^{2.277}	11	0.99 0.78	3.8–10.0
<i>Gibberula miliaria</i>	AFDM = 2.58 ± 0.25	11		1.8–4.1
<i>Dosinia isocardia</i>	APL = 5.998HH + 0.667 AFDM = 0.015APL ^{2.603}	28	0.99 0.98	2.3–15.2
<i>Loripes lucinalis</i>	APL = 9.097HH + 0.165 AFDM = 0.005APL ^{3.241}	25	0.97 0.91	4.2–12.2
<i>Senilia senilis</i>	APL = 3.232HH + 5.476 AFDM = 0.017APL ^{2.706}	12	0.97 0.98	3.8–26.5
<i>Nereis</i> sp.	TL = 40.034ML − 4.227 AFDM = 0.001TL ^{2.259}	18	0.96 0.90	7.5–65.2
<i>Glycera</i> sp.	TL = 59.988ML − 4.365 AFDM = 0.058TL ^{1.295}	15	0.98 0.84	9.6–56.0
Eunicidae	AFDM = 3.80 ± 0.38	8		18.2–36.1
Sedentary polychaetes	AFDM = 1.24 ± 0.21	35		7.6–45.3
<i>Uca tangeri</i>	CW = 2.270CL + 0.494 AFDM = 0.058CW ^{2.782}	25	0.98 0.96	2.4–13.0
<i>Idotea chelipes</i>	TL = 5.697HW + 3.141 AFDM = 0.008TL ^{2.301}	10	0.97 0.84	7.1–14.3
Anthuridae	AFDM = 2.08 ± 0.23	7		8.2–11.4
Amphipoda	TL = 8.042HW + 1.492 AFDM = 0.018TL ^{1.805}	26	0.95 0.84	3.5–9.5
Staphylinidae	AFDM = 0.53 ± 0.22	6		1.3–2.8

Sample size (N), proportion of variance explained (R²) and size range (in mm) are presented for each equation. Sedentary polychaetes include *Scoloplos* sp., *Scolecopsis squamata*, *Capitella capitata* and *Heteromastus filiformis*

APL antero-posterior length, CL claw length, CW carapace width, HH hinge height, HW head width, ML mandible length, MW maximum width, TL total length

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). Ostracods were found in shorebird droppings but were not noticed during invertebrate collection, possibly due to their very small size. In this case, we used a previously published regression equation to estimate their AFDM (Kaeriyama and Ikeda 2002)

Diet Composition and Niche Overlap of Shorebirds

To determine the diet of shorebirds, we collected droppings by following (usually mono-specific) flocks during the outgoing 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 223 droppings from dunlin *Calidris alpina* (n=107), sanderling (n=46), red

knot (n=29) and ringed plover *Charadrius hiaticula* (n=41), which were stored individually in 70 % ethanol until further analysis.

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. All identifiable prey remains were counted and measured to the nearest 0.1 mm. The number of bivalves, large polychaetes and crabs was estimated by pairing shell hinges, mandibles or claws of similar size (Lourenço 2007), respectively, while individual gastropod shells, other crustacean exoskeletons and staphylinid insect thoraxes could be directly counted. Sedentary polychaetes 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). Since we always found few chaetae (<100) in each sample, we assumed that a single individual was present. Still, since we are dealing with different species of sedentary polychaetes, this assumption may cause an underestimation of their real number in some samples. We also recorded the presence of plant fragments in droppings, but we were unable to identify them to species level (see “Discussion”).

Diet composition of shorebirds is expressed both as frequency of occurrence, defined as the proportion of droppings containing a given prey taxon, and numerical frequency, estimated as the number of each prey taxon in one dropping relative to all prey in the same dropping. Furthermore, we estimated the size and biomass content of all prey and used this information to estimate the proportion of consumed biomass represented by each prey type.

Niche width was calculated from dropping data using Levins' measure (B) that calculates the uniformity of distribution of individuals among the resource states using the equation (Levins 1968; Krebs 1999):

$$B = \frac{1}{\sum p_j^2}$$

where p_j is the proportion of food category j in the diet (i.e. based on all samples). For easier comparison with other studies, we standardized B using the method proposed by Hurlbert (1978):

$$B_{st} = \frac{B-1}{n-1}$$

where B_{st} is the standardized Levins' measure and n is the number of possible resource states (number of prey types found in all samples of all four shorebird species). B_{st} varies between 0 and 1. In order to estimate diet similarity among dunlin, sanderling, red knot and ringed plover, we used the Schoener overlap index (D) defined as (Schoener 1968):

$$D_{xy} = 1 - \frac{1}{2} \left(\sum |p_{xi} - p_{yi}| \right)$$

where p_{xi} and p_{yi} are the relative proportions of each prey item i for bird species x and y , respectively. The index value of diet overlap can range from 0, indicating no overlap, to 1, indicating complete overlap between the two species being compared. Index values >0.6 are generally considered to indicate biologically significant dietary overlap (Schoener 1968; Mathur 1977). For the calculation of B_{st} and D_{xy} , we used the average proportion of consumed biomass (i.e. mean percent of all droppings) represented by each prey on the diet of each shorebird species because the numerical frequency of prey would overestimate the importance of small, numerous prey.

In order to calculate mean values and confidence intervals for both B_{st} and D_{xy} , we drew 1000 bootstrap samples, each time randomly selecting (with replacement) the number of samples available for each species. The mean values were the mean of the 1000 bootstrap estimates, and confidence intervals of the mean for each case were estimated as the quantiles 0.025 and 0.975 of the distribution of corresponding bootstrap estimates. We tested differences in mean B_{st} values between each pair of species by estimating the level of significance (P) as the proportion of 1000 bootstrap estimates in which the value for one species was higher than that of the other species (Catry et al. 2014). For each pair of species, we used the proportion of bootstrap estimates of D_{xy} that were lower than 0.6 as the level of significance (P) for rejecting the null hypothesis that diet overlap between two species was lower than 0.6 and, thus, not biologically relevant.

Foraging Behaviour of Shorebirds

In order to study shorebird foraging behaviour, we video recorded a total of 341 focal individuals of all species from which we collected dropping (dunlin: $n=94$, sanderling: $n=99$, red knot: $n=31$ and ringed plover: $n=59$), and also from grey plover *Pluvialis squatarola* ($n=34$) and bar-tailed-godwit *L. lapponica* ($n=24$). Actively foraging individuals were video-taped for periods of 1–2 min, at relatively close range (roughly 5–40 m) using a Canon Hfr56 HD digital camcorder with a $\times 52$ zoom capability. These recordings were subsequently analysed using VLC media player 2.1.5 that allows reducing playing speed to 1/5 of original speed. For each focal bird, we counted the number of steps, turns (sharp direction changes, $>45^\circ$) and feeding attempts (expressed per minute), the latter divided in three categories: pecks, non-random probes and random probes. Pecks were defined as feeding attempts where the bird collects a prey from the surface of the substrate, non-random probes were defined as feeding attempt where the bird inserts its bill in a precise point in the sediment, and random probes were defined as feeding attempts where the bill is kept in the sediment while the bird moves, probing at random. We consider that the first category is a strictly visual strategy, the second is likely to use both visual and tactile cues and the third is a strictly tactile strategy (e.g. Robert and McNeil 1989). In several videos, it was also possible to estimate the success rate of each foraging strategy, by observing either prey being eaten or swallowing movements. Whenever prey taken by birds were visible in the video recording, we tried to quantify the proportion of different prey taxa, although many prey were too small to allow identification, particularly in smaller shorebirds.

The foraging behaviour data obtained from videos were used to compare different species in terms of their foraging strategy. For this purpose, we used four behavioural parameters: the ratio of steps.turn⁻¹, the rates of pecks and non-random probes, and the proportion of time spent random probing. Together, these four parameters characterize the prey search behaviour of each species as more tactile or visual and more linear or sinuous (e.g. Barbosa and Moreno 1999; Dias et al. 2009). The average of each of these parameters for each species was used for an Unweighted Pair Group Method with Arithmetic Mean (UPGMA Algorithm, Gauch 1982) cluster analysis aiming to identify species grouping in terms of foraging behaviour.

Results

Diet Composition of Shorebirds

Sanderling and ringed plover fed on a wide range of macro-invertebrates, including gastropods, bivalves, polychaetes, crustaceans and insects (Table 2). Nonetheless, gastropods, and particularly *Hydrobia ulvae*, represented over 80 % of the individual items eaten by sanderlings and over 50 % of the biomass consumed (Table 2). In the case of ringed plover, large polychaetes (*Nereis* sp., *Glycera* sp. and Eunicidae), the crab *Uca tangeri* and isopods (*Idotea chelipes* and Anthuridae) each represented over 20 % of the biomass

Table 2 Diet composition of sanderling, ringed plover, red knot and dunlin based on the analysis of droppings

Prey	Sanderling <i>N</i> =38			Ringed plover <i>N</i> =36			Red knot <i>N</i> =29			Dunlin <i>N</i> =61		
	FO	NF	PB	FO	NF	PB	FO	NF	PB	FO	NF	PB
Gastropoda												
<i>Hydrobia ulvae</i>	0.42	0.81	0.53	0.31	0.43	0.14	0.41	0.36	0.15	0.11	0.01	0.22
<i>Bulla adansonii</i>							0.24	0.03	0.19			
<i>Bittium reticulatum</i>							0.10	0.03	0.01			
<i>Gibberula miliaria</i>	0.03	0.00	0.01									
Total	0.42	0.81	0.54	0.31	0.43	0.14	0.66	0.42	0.35	0.11	0.01	0.22
Bivalvia												
<i>Dosinia isocardia</i>	0.08	0.01	0.03	0.03	0.02	0.01	0.83	0.36	0.43			
<i>Loripes lucinalis</i>							0.41	0.17	0.16			
<i>Senilia senilis</i>							0.07	0.02	0.06			
Total	0.08	0.01	0.03	0.03	0.02	0.01	0.97	0.55	0.65	0.00	0.00	0.00
Polychaeta												
<i>Nereis</i> sp.	0.16	0.02	0.11	0.19	0.09	0.11						
<i>Glycera</i> sp.	0.03	0.00	0.02	0.06	0.03	0.12						
Eunicidae	0.03	0.00	0.02	0.15	0.03	0.10				0.02	0.00	0.09
Sedent. polychaetes	0.13	0.02	0.03	0.11	0.02	0.02				0.28	0.01	0.47
Total	0.29	0.05	0.18	0.47	0.17	0.35	0.00	0.00	0.00	0.30	0.01	0.56
Crustacea												
<i>Uca tangeri</i>	0.05	0.02	0.09	0.25	0.10	0.24						
<i>Idotea chelipes</i>	0.08	0.01	0.02	0.08	0.03	0.02				0.02	0.00	0.02
Anthuridae	0.11	0.03	0.08	0.36	0.19	0.22				0.03	0.00	0.14
Amphipoda	0.13	0.04	0.03	0.03	0.04	0.02				0.05	0.00	0.02
Ostracoda							0.07	0.03	0.00	0.72	0.99	0.02
Total	0.29	0.09	0.22	0.64	0.36	0.50	0.07	0.03	0.00	0.77	0.99	0.20
Insecta												
Staphylinidae	0.21	0.04	0.03	0.05	0.02	0.01	0.00	0.00	0.00	0.03	0.00	0.02
Other												
Plant fragments	0.12			0.10			0.10			0.10		
Total		352	184.6		244	252.6		172	147.5		5234	44.6

For each shorebird species, we indicate the number of faecal samples used (excluding the ones with no recognizable prey) and the frequency of occurrence (FO), numerical frequency (NF, average proportion of each prey taxon per dropping) and proportion of biomass (PB) for each prey type. Sedentary polychaetes include Orbiniidae, Spionidae, Capitellidae and Cirratulidae. The final line indicates the total number of individual prey items and the sum of their estimated biomass (in mg AFDM) for each shorebird species

consumed (Table 2). The diet of red knot was composed mostly of bivalves, particularly *Dosinia isocardia* which alone represented 43 % of the biomass consumed. Still, three gastropod species (*Hydrobia ulvae*, *Bulla adansonii* and *Bittium reticulatum*) were also found in their droppings, together equating roughly 35 % of the consumed biomass (Table 2). A large proportion (48 %) of dunlin droppings had no recognizable food items, while for the other species, this proportion was much lower (sanderling, 17 %; ringed plover, 17 %; red knot, 3 %). Most of the remaining samples of dunlin (65 %) only had large numbers of very small ostracod crustaceans (total length, 0.44 ± 0.09 mm; range, 0.15–0.90 mm; $n=381$). Overall, sedentary polychaetes and *Hydrobia ulvae* represented most of the biomass consumed by dunlins (Table 2), but only 33 % of droppings with identifiable remains had any of these prey. All four shorebird species had plant fragments in small proportions (<15 % FO) of the analysed droppings (Table 2), a category not included in the analysis of consumed biomass.

The analysis of diets based on video recordings was inevitably biased towards larger and more easily identifiable prey items, particularly worms. Still, if we assume that the small unidentified prey were mainly small gastropods when taken by pecking or small bivalves when taken by probing (e.g. Lourenço et al. 2008; Martins et al. 2013); the observations of foraging sanderlings, dunlins and red knots were consistent with the content of their droppings, with mainly gastropods and worms in the first two cases, and mainly bivalves and gastropods in the latter one (Tables 2 and 3). The observations of foraging ringed plovers and dunlins would suggest a higher proportion of worms in their diet than occurred in droppings (Tables 2 and 3). Bar-tailed godwits appeared to consume almost exclusively worms, while gastropods (small prey) possibly also represent a relevant proportion of the diet of grey plovers in addition to worms (Table 3).

Niche Width and Diet Overlap

Niche width was relatively low in all four studied species. Pair-wise comparisons of niche width between species indicate no significant differences ($P>0.050$), with the exception of ringed plover which had a significantly wider niche than red knot ($P=0.004$; Table 4). Diet overlap was low among the four species, with mean values well below 0.6 in all cases (Table 5). In fact, there were only two pairs of species for which the highest individual bootstrap estimates of D_{xy} reached values above 0.6 (Table 5).

Foraging Behaviour

There was considerable variation in foraging behavioural parameters among shorebird species. Plovers foraged mainly by pecking, while bar-tailed godwits showed high rates of non-random probes and dunlins foraged mostly by random probing (Table 6). Dunlins and ringed plovers showed a more sinuous foraging trajectory, with a low number of steps per turn, while grey plovers and bar-tailed godwits showed a very linear movement with high numbers of steps per turn (Table 6). Despite differences among species, the data suggest that pecks yield very high success rates, while non-random probes and especially random probes have lower success rates (Table 6).

We found significant differences in foraging behaviour between sanderlings foraging in sandy and muddy substrates. In sandy areas, birds showed higher step rates ($t_{97}=8.34$, $P<0.001$) and more steps per turn ($t_{97}=3.62$, $P<0.001$), while also showing a higher pecking rate ($t_{97}=5.62$, $P<0.001$) and a lower rate of random probes ($t_{97}=7.17$, $P<0.001$; Table 6). Red knots also showed two clearly distinct foraging modes, and therefore we present data for this species in two groups on Table 6. Most red knot observations (61 % of videos) show

Table 3 Proportion of different prey types seen being taken by each shorebird species on focal video recordings

Prey	Sanderling			Ringed plover	Red knot		Dunlin			Bar-tailed godwit	Grey plover
	Peck	NRP	RP		Peck	RP	Peck	NRP	RP		
Small prey	0.90		0.21	0.21	0.86		0.77		0.33		0.43
Gastropods					0.14						
Bivalves		0.07	0.17			1.00				0.14	
Worms		0.93	0.62	0.73				1.00	0.67	0.86	0.52
Crabs	0.02			0.05							0.03
Small crustaceans	0.09			0.02			0.23				0.02
<i>N</i>	58	28	24	177	22	33	73	12	9	57	91
<i>N_b</i>	25	15	5	48	7	10	31	5	4	19	25

The types of prey taken are detailed for each feeding categories. *N* is the number of feeding attempts and *N_b* is the number of birds from which the information was obtained. Small prey refers to any prey that was too small to identify. Small crustaceans are most likely isopods and amphipods

NRPs non-random probes, *RPs* random probes (see “Methods”)

Table 4 Estimates of the standardized Levins' measure of niche width for sanderling, ringed plover, red knot and dunlin, based on 1000 bootstrap samples of the proportion of consumed biomass represented by each prey type found in droppings

Species	Mean B_{st}	95 % confidence interval
Sanderling	0.248	0.108–0.476ab
Ringed plover	0.303	0.225–0.367a
Red knot	0.176	0.134–0.218b
Dunlin	0.212	0.082–0.332ab

Different letters indicate significant differences ($P < 0.050$) between species

birds using a tactile foraging behaviour which mostly uses random probing, but the remaining observations (39 % of videos) show birds using a visual foraging behaviour that mainly uses pecking. The first group of observations showed significantly more steps per turn ($t_{28} = 2.92$, $P < 0.01$), a lower pecking rate ($t_{29} = 7.19$, $P < 0.001$) and a higher rate of random probes ($t_{29} = 5.70$, $P < 0.001$; Table 6) than the other group.

In order to quantitatively compare the foraging behaviour of all studied species, we classified them using a UPGMA cluster analysis that delivered three groups (Fig. 1). Group 1 included only dunlin, which spent most of the time random probing, showed a comparatively low number of steps per turn and a high rate of non-random probes. Group 2 was characterized by high pecking rates, low rates of non-random probes and a high proportion of time spent random probing, and included sanderling and red knot. Group 3 included ringed plover, grey plover and bar-tailed godwit and was characterized by lacking random probing behaviour. Moreover, birds in this group forage either with pecks or non-random probes and, in the cases of grey plover and bar-tailed godwit, show a comparatively high number of steps per turn and (Fig. 1 and Table 6).

Discussion

This study presents novel data regarding the diet and foraging behaviour of six shorebird species wintering at the Banc d'Arguin, Mauritania, and was based on a large sample of

droppings (223) and film analysis (8.3 h). Together, these species represent over 80 % of the individual shorebirds wintering at this site (Zwarts et al. 1998). Moreover, with the exceptions of red knot and bar-tailed godwit (e.g. Zwarts et al. 1990; van Gils et al. 2013), there is virtually no published information about the feeding ecology of these species for the Banc d'Arguin. In fact, this type of data is mostly lacking for wetlands located in western Africa, in sharp contrast with the wealth of data originating from European wetlands. Since many species use both European and African wetlands during their annual cycle, this may limit our understanding of their dietary plasticity during the nonbreeding season (e.g. Masero et al. 2007; Martins et al. 2013) and the risks caused by variations in prey abundance in tropical wintering sites.

Our results confirm the importance of bivalves on the diet of red knots. Knots consumed more *D. isocardia* than *Loripes lucinalis* which, although it has a thinner shell, is mildly toxic due to its sulphur-based metabolism (Oudman et al. 2014). Nevertheless, gastropods can contribute substantially to biomass ingested, more than was reported previously (Onrust et al. 2013; van Gils et al. 2013). Red knots apparently consume gastropods by using a visual foraging strategy, which is rather different from the typical tactile foraging strategy widely used by red knots during winter (e.g. Piersma et al. 1998). Still, this behaviour was clearly observed in roughly one third of our focal observations. Since the overall abundance of bivalve species taken by knots tends to be higher than that of the gastropods (Salem et al. 2014), and their average biomass is also generally higher (Salem et al. 2014), this behaviour may reflect a response to small-scale variations in prey abundance. This situation prevails in the upper intertidal near the coast, where *Hydrobia ulvae* can locally achieve very high densities (personal observation) and thus represent an abundant and easily accessible stock of prey compared to buried bivalves.

Ringed plovers and sanderlings hunt a wider range of prey, taking crustaceans, gastropods and polychaetes similarly to their diets in European wintering areas (e.g. Perez-Hurtado et al. 1997; Lourenço et al. 2008). However, the two species differ in terms of foraging behaviour with sanderlings mostly using tactile techniques (probing) when foraging on muddy substrates while ringed plovers specialize in visual foraging (pecking; van de Kam et al. 2004). A previous study

Table 5 Estimates of Schoener diet overlap index for each pair of species based on 1000 bootstrap samples of the proportion of consumed biomass represented by each prey type found in droppings

	Sanderling	Ringed plover	Red knot
Ringed plover	0.439 (0.231–0.636) $P = 0.925$		
Red knot	0.383 (0.236–0.507) $P = 1.000$	0.147 (0.029–0.330) $P = 1.000$	
Dunlin	0.395 (0.236–0.629) $P = 0.964$	0.363 (0.179–0.539) $P = 1.000$	0.203 (0.042–0.396) $P = 1.000$

For each pair of species, we present the mean, the 95 % confidence interval (in parentheses) and the probability (P) that the value is lower than 0.6 (see "Methods")

Table 6 Behavioural parameters of foraging shorebirds, based on the analysis of video recordings. Sanderlings are divided in either sandy (S) or muddy (M) substrates

	Sanderling (S)	Sanderling (M)	Ringed plover	Red knot (T)	Red knot (V)	Dunlin	Bar-tailed godwit	Grey plover
Step rate (min ⁻¹)	262±78 (36)	134±71 (63)	98±29 (59)	82±39 (19)	79±38 (12)	66±38 (94)	84±37 (24)	68±30 (34)
Steps turn ⁻¹	29.3±16.8 (36)	18.8±11.9 (63)	13.1±15.5 (58)	23.5±13.8 (18)	12.2±6.7 (12)	15.1±11.0 (86)	35.7±26.3 (24)	29.4±22.6 (34)
Peck rate (min ⁻¹)	49.0±36.0 (36)	15.9±23.1 (63)	23.4±12.3 (59)	2.7±5.3 (19)	143±77 (12)	9.8±16.8 (94)	2.4±3.1 (24)	6.4±3.5 (34)
Peck success (%)	94±15 % (24)	81±29 % (44)	83±14 % (49)	97±7 % (4)	94±16 % (10)	83±24 % (46)	78±24 % (12)	83±16 % (20)
NRP rate (min ⁻¹)	3.3±6.0 (36)	5.1±7.1 (63)	0.3±0.7 (59)	0.3±0.5 (19)	1.8±2.8 (12)	11.0±26.5 (94)	13.2±4.9 (24)	0.0±0.2 (34)
NRP success (%)	46±26 % (19)	51±22 % (29)	58±39 % (6)	20.3±12.3 (19)	56±44 % (7)	51±33 % (21)	55±14 % (18)	0.0±0.0 (34)
RRP rate (min ⁻¹)	0.0±0.0 (36)	31.9±26.9 (63)	0.0±0.0 (59)	52±19 % (15)	0.0±0.0 (12)	39.9±26.4 (94)	0.0±0.0 (24)	0.0±0.0 (34)
RRP success (%)	0±0 % (36)	37±16 % (30)	0±0 % (59)	86±25 % (19)	0±0 % (12)	46±9 % (26)	0±0 % (24)	0±0 % (34)
% time RP	0±0 % (36)	65±41 % (63)	0±0 % (59)	86±25 % (19)	0±0 % (12)	76±41 % (94)	0±0 % (24)	0±0 % (34)

Red knots are divided in a tactile foraging group (T) and a visual foraging group (V). All values are the mean±SD with sample size in parentheses

NRP non-random probe, RP random probe

Fig. 1 Dendrogram based on Euclidean distances, representing the similarities among shorebird species in foraging behavioural parameters (steps per turn, pecking rate, NRP rate and proportion of time spent random probing). The scale of the horizontal axis represents Euclidean distances as the proportion of the maximum distance (D/D_{max})

suggested that small plovers exploit the abundant *U. tangeri* crabs in the Banc d'Arguin (Zwarts et al. 1990), which our data also shows.

All species had plant remains in a small proportion of faecal samples. Although we were unable to identify these remains, they could reflect the consumption of *Zostera* spp. rhizomes, a food type that is known to be used by red knots in the Banc d'Arguin (J.A. van Gils, personal communication) and by black-tailed godwits *Limosa limosa* in France (Robin et al. 2013). Shorebirds are also known to accidentally consume algae with their animal prey (e.g. Goss-Custard et al. 1977), but plant fragments (including algae) might also have been consumed intentionally as they occurred in all shorebird species studied here. We did not observe birds taking rhizomes in the video recordings, but few of the videos ($n=9$) where made in seagrass-covered areas.

On the video recordings, grey plovers were seen taking both polychaetes and small gastropods by pecking, much like in other parts of their wintering range (e.g. Turpie and Hockey 1993; Lourenço et al. 2008). This species had previously been described as kleptoparasitic in the Banc d'Arguin, obtaining food from robbing larger shorebirds (Zwarts et al. 1990), but we did not observe kleptoparasitism in the present study. Our observation that bar-tailed godwits fed mainly on worms and also take small numbers of bivalves confirm previous studies in the Banc d'Arguin (e.g. Piersma et al. 1982b; Zwarts et al. 1990) and are also in line with what is known for bar-tailed godwits wintering in western Europe (Duijns et al. 2013).

The analysis of dunlin droppings provided somehow unexpected results, with very few recognizable prey items in most samples except for large numbers of very small ostracods. Since ostracods appear to be too small to provide sufficient nourishment for dunlins, even when consumed in very large numbers, the lack of other prey remains would suggest that

this species is eating a food that leaves no trace in droppings, such as the siphons of large bivalves that they take in some other wintering areas (e.g. Santos et al. 2010). The most abundant bivalves in the Banc d'Arguin are relatively small and have short siphons. Moreover, siphon cropping implies a specific feeding behaviour in which the bird keeps its head angled above the surface looking for siphons and then strikes down quickly to capture the siphon (Santos et al. 2010), which was not observed in our focal observations. The presence of plant remains in a small proportion of samples cannot solve this conundrum, as they were also found in similar amounts in the droppings of other shorebirds. Recent studies in coastal wetlands of the northern Pacific have described the consumption of biofilm by small shorebirds including dunlin (Elner et al. 2005; Kuwae et al. 2012), but so far this behaviour has not been described in the Atlantic, and preliminary stable isotope data suggests dunlins do not feed on biofilm in the Banc d'Arguin (unpublished data). At this time, the diet of dunlin, the most abundant wintering shorebird in the Banc d'Arguin, remains unknown.

Foraging behavioural parameters suggest there are three different prey search behaviours used by study shorebirds in the Banc d'Arguin, which do not fit exactly with the traditional classification into visual, tactile and mixed foragers (e.g. Zwarts et al. 1990; Lourenço et al. 2008). The only species that uses only tactile foraging is dunlin, which spent over 75 % of time probing the sediment. Red knots which are usually described as highly specialized tactile foragers (e.g. Piersma et al. 1998) showed a mixed strategy more similar to that used by sanderlings (e.g. Barbosa and Moreno 1999). In fact, on average, red knots show the highest pecking rate of all studied species; although visual foraging was used in only a third of the observations, they then showed remarkably high rates with up to 215 pecks in 1 min and in fact have been observed reaching rates of 10 pecks/second (Piersma et al. 1998). As we would expect, the two plovers which are specialized in visual foraging (Barbosa and Moreno 1999; Lourenço et al. 2008) were included in the same group, together with bar-tailed godwit. Bar-tailed godwits have previously been described as tactile foragers (e.g. Barbosa and Moreno 1999) but, even though they obtain most prey by probing, their prey search behaviour is more similar to that of the two plover species. In fact, they do not probe the sediment randomly, but rather their probes target specific points in the sediment which suggests they use visual cues to some extent. Interestingly, these behavioural groups do not select similar prey, suggesting that availability of different prey types, and possibly differences in how different species perceive their environment (Piersma 2011), allows for resource partitioning even among species using the same feeding areas and strategies.

The narrow niches and the lack of much diet overlap between the four best-studied shorebird species are consistent

with the idea of remarkable inter-specific resource partitioning. Stable isotope data collected in parallel to this study indicated also that the shorebird community at Banc d'Arguin has narrower isotopic niches and lower levels of isotopic niche overlap than communities at other coastal wetlands along the East Atlantic Flyway (Catry et al. 2015). Despite the apparent tight fit between low prey biomass and high predator abundance in tidal flats of the Banc d'Arguin (e.g. Piersma 1982a; Wolff et al. 1993a; Honkoop et al. 2008), our data suggest that shorebirds are able to take advantage of the considerable diversity of benthic macroinvertebrates (e.g. Wolff et al. 1993b; Wijnnsma et al. 1999) to partition available resources among different species. In fact, diet overlap among species may be even smaller than shown here if we take into account that different shorebird species are likely to select different size-classes of the prey taxa they share (Lifjeld 1984). Still, we cannot rule out the occurrence of important levels of competition within species, as has been suggested for red knots (van den Hout et al. 2014).

Previous studies have indicated that there are no systematic differences in the abundance and harvestability of shorebird prey among tropical and temperate intertidal systems (Piersma et al. 1993b; Piersma 2007), even though tropical sites tend to show a higher invertebrate diversity (Piersma et al. 1993b). Therefore, the conclusions reached in the present study should not be applied to other tropical intertidal areas without further investigation. Work in another tropical site which also shows high shorebird densities and low prey abundance, the Bragantian Peninsula in northern Brazil, evidenced that shorebirds had broadly overlapping dietary niches (Kober and Bairlein 2009), while stable isotope data from the Bijagós archipelago, in Guinea-Bissau, indicate relevant resource partitioning among different shorebird species but with wider (isotopic) niches than in the Banc d'Arguin (Catry et al. 2015). Such disparate results suggest considerable variation in the trophic interactions among shorebirds communities in tropical wintering sites.

The low levels of diet overlap among shorebirds suggest that the complexity of the Banc d'Arguin ecosystem offers varied feeding opportunities for wintering shorebirds. However, this may also indicate that the observed widespread declines in shorebird numbers (Zwarts et al. 1998; van Gils et al. 2009; T. Piersma et al. unpublished data) reflect widespread negative changes in the Banc d'Arguin ecosystem since these changes are affecting predators with clearly distinct niches.

Acknowledgments Expeditions to Banc d'Arguin received logistic support from Parc National du Banc d'Arguin (PNBA). We thank the director of PNBA, to Lemhaba Ould Yarba research officer of the Park, and to the PNBA's staff in Iwik. Dr António Araújo (Fondation Internationale du Banc d'Arguin—FIBA) provided crucial support and advice during our expedition preparation, and colleagues from NIOZ Royal Netherlands Institute for Sea Research, particularly Dr Piet van

den Hout and Dr Jan van Gils, are thanked for their help with logistics and sharing their research expertise at PNBA. We would also like to thank José Alves for his help during field work in Mauritania, Camilo Carneiro who collaborated both in field sampling and in the analysis of video recordings, and Mohamed Salem for help identifying benthic macroinvertebrates. Two anonymous reviewers and the associate editor provided constructive comments on an earlier version of this paper. This study was supported by Fundação para a Ciência e Tecnologia (FCT), through Project “Invisible Links” (PTDC/MAR/119920/2010), strategic project UID/AMB/50017/2013 and postdoctoral grants to TC (SFRH/BPD/102255/2014) and PML (SFRH/BPD/84237/2012). The work by TP at BdA has been facilitated by operational grants from Royal NIOZ, by the NWO-ALW TOP grant ‘Shorebirds in space’ (854.11.004) and an NWO WOTRO Integrated Programme grant (W.01.65.221.00).

References

- Barbosa, A., and E. Moreno. 1999. Evolution of foraging strategies in shorebirds: an ecomorphological approach. *Auk* 116: 712–725.
- Bocher, P., F. Robin, J. Kojadinovic, P. Delaporte, P. Rousseau, C. Dupuy, and P. Bustamante. 2014. Trophic resource partitioning within a shorebird community feeding on intertidal mudflat habitats. *Journal of Sea Research* 92: 115–124.
- Catry, T., J.A. Alves, J.A. Gill, T.G. Gunnarsson, and J.P. Granadeiro. 2014. Individual specialization in a shorebird population with narrow foraging niche. *Acta Oecologica* 56: 56–65.
- Catry, T., P.M. Lourenço, R.J. Lopes, C. Carneiro, J.A. Alves, J. Costa, H. Rguibi-Idrissi, S. Bearhop, T. Piersma, and J.P. Granadeiro. 2015. Structure and functioning of intertidal food webs along an avian flyway: a comparative approach using stable isotopes. *Functional Ecology*. doi:10.1111/1365-2435.12506.
- Delany, S., D. Scott, T. Dodman, and D. Stroud. 2009. *An atlas of wader populations in Africa and western Eurasia*. Wageningen: Wetlands International.
- Dias, M.P., J.P. Granadeiro, and J.M. Palmeirim. 2009. Searching behaviour of foraging waders: does feeding success influence their walking? *Animal Behaviour* 77: 1203–1209.
- Duijns, S., N.A. Hidayati, and T. Piersma. 2013. Bar-tailed godwits *Limosa l. lapponica* eat polychaetes worms wherever they winter in Europe. *Bird Study* 60: 509–517.
- Duijns, S., J.A. van Gils, B. Spaans, J. ten Horn, M. Brugge, and T. Piersma. 2014. Sex-specific winter distribution in a sexually dimorphic shorebird is explained by resource partitioning. *Ecology and Evolution* 4: 4009–4018.
- Elner, R.W., P.G. Beninger, D.L. Jackson, and T.M. Potter. 2005. Evidence of a new feeding mode in western sandpiper (*Calidris mauri*) and dunlin (*Calidris alpina*) based on bill and tongue morphology and ultrastructure. *Marine Biology* 146: 1223–1234.
- Engelmoer, M., T. Piersma, W. Altenburg, and R. Mes. 1984. The Banc d'Arguin (Mauritania). In *Coastal waders and wildfowl in winter*, ed. P.R. Evans, J.D. Goss-Custard, and W.G. Hale, 293–310. Cambridge: Cambridge University Press.
- Gauch, H.G. 1982. *Multivariate analysis in community ecology*. Cambridge studies in ecology. Cambridge: Cambridge University Press.
- Goss-Custard, J.D., Jones RE, and P.E. Newbery. 1977. The ecology of the wash. I. Distribution and diet of wading birds (Charadrii). *Journal of Applied Ecology* 14: 681–700.
- Honkoop, P.J.C., E.M. Berghuis, S. Holthuijsen, M.S.S. Lavaleye, and T. Piersma. 2008. Molluscan assemblages of seagrass-covered and bare intertidal flats on the Banc d'Arguin, Mauritania, in relation to characteristics of sediment and organic matter. *Journal of Sea Research* 60: 235–243.
- Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59: 67–77.
- Kaeriyama, H., and T. Ikeda. 2002. Body allometry and developmental characteristics of the three dominant pelagic ostracods (*Discoconchoecia pseudodiscophora*, *Orthoconchoecia haddoni* and *Metaconchoecia skogsbergi*) in the Oyashio region, western North Pacific. *Plankton Biology and Ecology* 49: 97–100.
- Kalejta, B. 1993. Diet of shorebirds at the Berg River estuary, South Africa: spatial and temporal variation. *Ostrich* 64: 123–133.
- Kober, K., and F. Bairlein. 2009. Habitat choice and niche characteristics under poor food conditions. A study on migratory nearctic shorebirds in the intertidal flats of Brazil. *Ardea* 97: 31–42.
- Krebs, C.J. 1999. *Ecological methodology*, 2nd ed. Menlo Park: Addison-Welsey Educational Publishers.
- Kuwae, T., E. Miyoshi, S. Hosokawa, K. Ichimi, J. Hosoya, T. Amano, T. Moriya, M. Kondoh, R.C. Ydenberg, and R.W. Elner. 2012. Variable and complex food web structures revealed by exploring missing trophic links between birds and biofilm. *Ecology Letters* 15: 347–356.
- Levins, R. 1968. *Evolution in changing environments*. Princeton: Princeton University Press.
- Leyrer, J., T. Lok, M. Brugge, A. Dekinga, B. Spaans, J.A. van Gils, B.K. Sandercock, and T. Piersma. 2012. Small-scale demographic structure suggests preemptive behavior in a flocking shorebird. *Behavioral Ecology* 23: 1226–1233.
- Lifjeld, J.T. 1984. Prey selection in relation to body size and bill length of five species of waders feeding in the same habitat. *Ornis Scandinavica* 15: 217–226.
- Lourenço, P.M. 2007. Analysing faecal samples of ragworm predators: not just a matter of counting mandibles. *Ardea* 95: 151–155.
- Lourenço, P.M., A. Silva, C.D. Santos, A.C. Miranda, J.P. Granadeiro, and J.M. Palmeirim. 2008. The energetic importance of night foraging for waders wintering in a temperate estuary. *Acta Oecologica* 34: 122–129.
- Martins, R.J., T. Catry, C.D. Santos, J.M. Palmeirim, and J.P. Granadeiro. 2013. Seasonal variations in the diet and foraging behaviour of dunlins *Calidris alpina* in a south European estuary: improved feeding conditions for northward migrants. *PLoS ONE* 8: e81174. doi:10.1371/journal.pone.0081174.
- Masero, J.A., S.M. Estrella, and J.M. Sánchez-Guzmán. 2007. Behavioural plasticity in foraging mode of typical plovers. *Ardea* 95: 259–265.
- Mathur, D. 1977. Food habits and competitive relationships of the bandfish shiner in Halawakee Creek, Alabama. *American Midland Naturalist* 97: 89–100.
- Nebel, S. 2005. Latitudinal clines in bill length and sex ratio in a migratory shorebird: a case of resource partitioning? *Acta Oecologica* 28: 33–38.
- Onrust, J., J. de Fouw, T. Oudman, M. van der Geest, T. Piersma, and J.A. van Gils. 2013. Red knot diet reconstruction revisited: context dependence revealed by experiments at Banc d'Arguin, Mauritania. *Bird Study* 60: 298–307.
- Oudman, T., J. Onrust, J. de Fouw, B. Spaans, T. Piersma, and J.A. van Gils. 2014. Digestive capacity and toxicity cause mixed diets in red knots that maximize energy intake rate. *American Naturalist* 183: 650–659.
- Perez-Hurtado, A., J.D. Goss-Custard, and F. Garcia. 1997. Diet of wintering waders in Cadiz Bay, southwest Spain. *Bird Study* 44: 45–52.
- Piersma, T. 1982a. Macrobenthic fauna of the intertidal flats. In *Wintering waders on the Banc d'Arguin, Mauritania*, ed. W. Altenburg, M. Engelmoer, R. Mes, and T. Piersma, 49–66. Leiden: Stichting Veth tot steun aan Waddenonderzoek.
- Piersma, T. 1982b. Foraging of bar-tailed godwits. In *Wintering waders on the Banc d'Arguin, Mauritania*, ed. W. Altenburg, M. Engelmoer, R. Mes, and T. Piersma, 49–66. Leiden: Stichting Veth tot steun aan Waddenonderzoek.

- Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology* 148(Suppl. 1): S45–S59.
- Piersma, T. 2011. From spoonbill to spoon-billed sandpiper: the perceptual dimensions to the niche. *Ibis* 153: 659–661.
- Piersma, T. 2012. What is habitat quality? Dissecting a research portfolio on shorebirds. In *Birds and habitat: relationships in changing landscapes*, ed. R.J. Fuller, 383–407. Cambridge: Cambridge University Press.
- Piersma, T., R. Hoekstra, A. Dekinga, A. Koolhaas, P. Wolf, P. Battley, and P. Wiersma. 1993a. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the Western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research* 31: 331–357.
- Piersma, T., P. de Goeij, and I. Tulp. 1993b. An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. *Netherlands Journal of Sea Research* 31: 503–512.
- Piersma, T., R. van Aelst, K. Kurk, H. Berkhoudt, and L.R.M. Maas. 1998. A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proceedings of the Royal Society of London B* 265: 1377–1383.
- Quaintenne, G., P. Bocher, A. Ponsoero, E. Caillot, and E. Feunteun. 2014. Contrasting benthos communities and prey selection by red knot *Calidris canutus* in three nearby bays on the Channel Coast. *Ardea* 101: 87–98.
- Robert, M., and R. McNeil. 1989. Comparative day and night feeding strategies of shorebirds species in a tropical environment. *Ibis* 131: 69–79.
- Robin, F., T. Piersma, F. Meunier, and P. Bocher. 2013. Expansion into an herbivorous niche by a customary carnivore: black-tailed godwits feeding on rhizomes of *Zostera* at a newly established wintering site. *Condor* 115: 340–347.
- Salem, M.V.A., M. van der Geest, T. Piersma, Y. Saoud, and J.A. van Gils. 2014. Seasonal changes in mollusc abundance in a tropical intertidal ecosystem, Banc d'Arguin (Mauritania): testing the 'depletion by shorebirds' hypothesis. *Estuarine, Coastal and Shelf Science* 136: 26–34.
- Santos, C.D., J.M. Palmeirim, and J.P. Granadeiro. 2010. Choosing the best foraging microhabitats: individual skills constrain the choices of dunlins *Calidris alpina*. *Journal of Avian Biology* 41: 18–24.
- Scheiffarth, G. 2001. The diet of bar-tailed godwits *Limosa lapponica* in the Wadden Sea: combining visual observations and faeces analysis. *Ardea* 89: 481–494.
- Schoener, T.W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704–726.
- Stroud, D.A., A. Baker, D.E. Blanco, N. Davidson, S. Delany, B. Ganter, R. Gill, P. González, L. Haanstra, R.I.G. Morrison, T. Piersma, D. Scott, O. Thorup, R. West, J. Wilson, and C. Zöckler. 2006. The conservation and population status of the world's waders at the turn of the millennium. In *Waterbirds around the world*, ed. G.C. Boere, C. Galbraith, and D.A. Stroud, 643–648. Edinburgh: The Stationery Office.
- Swennen, C. 1990. Oystercatchers feeding on giant blood cockles in the Banc d'Arguin, Mauritania. *Ardea* 78: 53–62.
- Turpie, J.K., and P.A.R. Hockey. 1993. Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory grey plovers *Pluvialis squatarola* and whimbrels *Numenius phaeopus* in South Africa. *Ibis* 135: 156–165.
- van de Kam, J., B. Ens, T. Piersma, and L. Zwarts. 2004. *Shorebirds. An illustrated behavioural ecology*. Utrecht: KNNV Publishers.
- van den Hout, P., J.A. van Gils, F. Robin, M. van der Geest, A. Dekinga, and T. Piersma. 2014. Interference from adults forces young knots to forage for longer and in dangerous places. *Animal Behaviour* 88: 137–146.
- van Gils, J.A., M. van der Geest, C. Kraan, E.O. Folmer, E.J. Jansen, and T. Piersma. 2009. How the carrying capacity of the Wadden Sea regulates the number of wintering waders at Banc d'Arguin. *Limosa* 82: 134–140.
- van Gils, J.A., M. van der Geest, J. Leyrer, T. Oudman, T. Lok, J. Onrust, J. de Fouw, T. van der Heide, P.J. van den Hout, B. Spaans, A. Dekinga, M. Bruge, and T. Piersma. 2013. Toxin constraint explains diet choice, survival and population dynamics in a molluscivore shorebird. *Proceedings of the Royal Society of London B* 280: 20130861.
- Wijnsma, G., W. Wolff, A. Meijboom, P. Duiven, and J. de Vlas. 1999. Species richness and distribution of benthic tidal fauna of the Banc d'Arguin, Mauritania. *Oceanologica Acta* 22: 233–243.
- Wolff, W.J., J. van der Land, P.H. Nienhuis, and P.A.W.J. de Wilde. 1993a. The functioning of the ecosystem of the Banc d'Arguin, Mauritania: a review. *Hydrobiologia* 258: 211–222.
- Wolff, W.J., A.G. Duiven, P. Duiven, P. Esselink, A. Gueye, A. Meijboom, G. Moerland, and J. Zegers. 1993b. Biomass of macrobenthic tidal fauna of the Banc d'Arguin, Mauritania. *Hydrobiologia* 258: 151–163.
- Wootton, J.T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. *Ecological Monographs* 67: 45–64.
- Zwarts, L. 1990. Increased prey availability drives premigration hyperphagia in whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in time. *Ardea* 78: 279–300.
- Zwarts, L., and S. Dirksen. 1990. Digestive bottleneck limits the increase in food intake of whimbrels preparing their departure from the Banc d'Arguin, Mauritania, in spring. *Ardea* 78: 257–278.
- Zwarts, L., A.M. Blomert, B.J. Ens, R. Hupkes, and T.M. van Spanje. 1990. Why do waders reach high feeding densities on the intertidal flats of the Banc d'Arguin, Mauritania. *Ardea* 78: 39–52.
- Zwarts, L., J. van der Kamp, O. Overdijk, T.M. van Spanje, R. Veldkamp, R. West, and M. Wright. 1998. Wader count of the Banc d'Arguin, Mauritania, in January/February 1997. *Wader Study Group Bulletin* 86: 55–69.