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Seasonal variation in the diet of Redshank *Tringa totanus* in the Odiel Marshes, southwest Spain: a comparison of faecal and pellet analysis

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Capsule Redshank diet from southern Europe during migration shows spatial and seasonal variations.

Aims To assess seasonal variation in Redshank diet at a major passage site, and to compare data derived from analysing pellets or faeces.

Methods At the Odiel Marshes in 2001, pellets from spring migration (39), autumn migration (121) and midwinter (15) were analysed, together with faecal samples from autumn (84).

Results The abundance of different invertebrate groups in pellets varied between seasons. In spring, *Chironomus salinarius* pupae and larvae dominated by volume, followed by Ephydridae larvae and the beetle *Paracymus aenus*. Polychaetes and molluscs dominated in autumn, and isopods in midwinter. In autumn, chironomid larvae, *Mesembryanthemum nodiflorum* seeds and *Artemia* cysts were relatively more abundant in faeces, whereas polychaetes, isopods, molluscs and cestode cysticercoids were more abundant in pellets. Harder and/or larger items were thus relatively more abundant in pellets than faeces. Pellet analysis gave more emphasis to mudflat prey, and faeces to saltpan prey.

Conclusion Pellet and faecal analysis give different results for wader diet, and it is useful to combine the two methods. However, they show significant correlations both in diet range and rank abundance of prey items. Redshank diet shows much seasonal and spatial variation in southern Europe.

The Odiel Marshes in southwest Spain are protected as a Biosphere Reserve, Ramsar site, EU-SPA and Natural Park owing to their importance for migratory waterbirds. They are internationally important for six species of waders including the nominal subspecies of the Redshank *Tringa totanus totanus*. Here we present a detailed study of the diet of Redshank using the saltpan complex within the Odiel Marshes. This subspecies is under decline at a flyway scale (Wetlands International 2002). Loss of habitat on passage sites may be one cause of decline since energetic requirements are particularly high during migration (Recher 1966, Davis & Smith 1998, Pfister *et al.* 1998).

We compare Redshank diet during spring migration, autumn migration and winter and assess the relative importance of prey items from salt pans and from surrounding tidal mudflats in each period. Salt pans are known as important foraging habitat for waders on the

Atlantic coast (Velasquez *et al.* 1991, Masero 2003) although their relative importance at different times of the annual cycle has not previously been assessed. This is the first study of Redshank diet in southern Europe during migration. Previous studies during migration were carried out in northern Europe where different prey are available (Goss-Custard & Jones 1976, Goss-Custard *et al.* 1977).

Many species of shorebirds produce pellets containing the indigestible hard parts of their prey. Shorebirds known to produce pellets include Turnstone *Arenaria interpres* (Jones 1975), Grey Plover *Pluvialis squatarola* (Goss-Custard & Jones 1976), Curlew *Numenius arquata* (Pérez-Hurtado *et al.* 1997) and Common Sandpiper *Actitis hypoleucos* (Arcas 2001).

Comparisons of diet between wader species, seasons or sites (e.g. Pérez-Hurtado *et al.* 1997, Kalejta 1993) are complicated by the use of various methods with distinct biases (analyses of stomach contents, faeces, pellets or direct observations). We compare the data on

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Redshank diet provided by analyses of faeces and pellets. Although several authors have pointed out the need to combine the results of different methods (Duffy & Jackson 1986, Jenni *et al.* 1989, Arcas 1999, Harris & Wanless 1993, Scheiffarth 2001), to our knowledge this is the first study to make a detailed comparison of methods used at the same time and place. Previous comparisons of analyses of faeces and pellets have focused only on the size of prey items of a given type (Goss-Custard *et al.* 1977, Dekinga & Piersma 1993), whereas we focus on the whole range of prey items including their relative abundance and overall diversity.

STUDY AREA

The Odiel Marshes (37°17′N 06°55′W) is an estuarine complex formed at the mouths of the rivers Odiel and Tinto, southwest Spain. They contain 6000 ha of intertidal mudflats and 1185 ha of salt pans. Our study area occupied 27% of the total area of salt pans. During weekly counts throughout 2001 we counted up to 20 775 waders including up to 2170 Redshank. Numbers of Redshank peak during spring and autumn migration.

METHODS

Samples were collected at different times of the year in 2001 from Redshank at a high-tide roost. We collected 15 pellets from midwinter on 13 January. We then collected a total of 39 pellets during spring migration from late February to late April. Likewise, 121 pellets were collected during autumn migration. In autumn, we collected 84 faecal samples. To avoid repeated sampling from the same individuals, we collected only fresh samples and did not collect more than one sample where several were found within 20 cm of each other. We took samples only when a monospecific group of Redshank was observed with a telescope at the sampling spot for at least 30 minutes.

Samples were stored at 5°C. Prior to analysis, they were rehydrated and separated in water, then observed with a binocular microscope in a Petri dish. Prey items were identified using suitable keys (see Sánchez *et al.* 2000). The volume of each diet component was estimated as a proportion of the total sample volume, using the following seven categories of relative abundance: absent (assigned the rank of 1 for non-parametric analysis), <10% (rank of 2), 10–25% (3), 26–50% (4), 51–75% (5), 76–90% (6) and >90% (7). The percentage of individual samples in which each food item was recorded (i.e. the percentage occurrence,

PO) was calculated for faecal and pellet samples for each season. Differences in PO of different diet components in pellets between the three seasons (spring, autumn and winter) were analysed using Kruskal–Wallis tests employing Statistica 5.5 (StatSoft 1999). Only food items with a PO > 10% in at least one season were analysed, and *P* values were Bonferroni corrected to avoid type I errors. Mann–Whitney *U*-tests were used as post hoc tests to determine significant differences between each season. The numbers of readily countable items (*Artemia* cysts (eggs), seeds and cestode cysticercoids) in pellets were compared between seasons in the same way. All these items were counted, including those that were partially digested.

The relative abundance of prey items and number of countable items were compared for faecal samples and pellets collected in autumn in a similar way, using Bonferroni-corrected Mann–Whitney *U*-tests and analysing those items with PO > 10% in at least one type of sample. In order to compare the diversity of faecal and pellet contents, we compared the number of prey items recorded in each with Mann–Whitney *U*-tests. To assess the similarity and repeatability of pellet and faecal contents, we calculated the average abundance for each prey item (i.e. the average of the seven ranks defined above), and compared these average ranks with a Spearman's rank correlation. We excluded green plant material (mainly Chenopodiaceae) from our comparison of pellets and faeces because, in the case of faeces (but not pellets), we were unable to distinguish reliably between material excreted and material that had become stuck to the faeces after excretion.

In order to compare the relative abundance of chironomid larvae and pupae in pellets for a given season, we used a sign test for each season.

RESULTS

Seasonal differences in pellet contents

The prey item recorded most often in spring pellets was chironomid *C. salinarius* pupae (74% of pellets). The other prey items occurring in more than 50% of pellets were (in order of decreasing frequency) the beetle *Ochthebius corrugatus*, *Artemia* cysts, *C. salinarius* larvae, unidentified Coleoptera and green plant material (Table 1). In winter pellets, Isopoda were the most frequently recorded prey (67% of pellets), followed by unidentified Coleoptera, polychaetes and green plant material (Table 1). In autumn pellets, polychaetes

Table 1. Contents of Redshank pellets and faeces, showing the percentage occurrence (PO) of each food item and the percentage of samples in which each item represented more than 10% of the sample volume (V > 10%).

Prey	Habitat	Autumn faeces (n = 84)		Autumn pellet (n = 121)		Spring pellet (n = 39)		Winter pellet (n = 15)		U	H	PCS
		PO	V > 10%	PO	V > 10%	PO	V > 10%	PO	V > 10%			
Green plant material		26	7	36	1	51	3	53	–			
Angiospermae	S	24	7	33	1	51	3	53	–			
Algae		5	–	4	–	–	–	–	–			
Seeds		32	19	12	–	46	3	17	–			
Arthrocnemum macrostachyum	M/S	4	1	3	–	13	–	13	–		5.8	
Salicornia		–	–	2	–	–	–	–	–			
Suaeda		1	–	–	–	–	–	–	–			
Sonchus oleraceus	S	1	–	–	–	31	3	–	–		44.6****	S > Au
Mesembryanthemum nodiflorum	S	26	18	2	–	8	–	–	–	3820**		
Unidentified seeds		4	1	6	–	–	–	13	–		4.2	
Invertebrates		100	90	100	100	100	100	100	100			
Bryozoan statoblast		–	–	1	–	–	–	–	–			
Chironomus salinarius (L)	S	35	18	7	1	59	10	–	–	3615.5****	58.6****	S > Au,W
Chironomus salinarius (P)	S	33	15	10	5	74	62	7	–	3889**	77.6****	S > Au,W
Chironomus salinarius (A)		–	–	1	–	–	–	–	–			
Dolychopodidae (L)		–	–	2	–	–	–	–	–			
Stratiomyidae (L)	S	–	–	4	–	26	–	7	–		16.4****	S > Au
Ephydridae (L)		–	–	1	–	8	5	7	7			
Ephydridae (P)	S	1	1	11	2	28	18	27	20	4766.5	13.8***	S > Au
Unidentified Diptera (L)		4	1	6	–	3	–	–	–			
Unidentified Diptera (P)		10	1	1	–	–	–	–	–			
Ochthebius notabilis (A)	S	54	10	26	11	23	–	33	7	3848.5**	0.70	
Ochthebius corrugatus (A)	S	12	1	16	–	67	–	40	–	4898.5	37.8****	S > Au
Ochthebius (L)	S	6	–	1	–	–	–	–	–			
Paracymus aenus (A)	S	–	–	1	–	41	21	20	13		48.1****	S > Au
Unidentified Coleoptera (A)		42	12	33	2	54	3	60	20	4511.5	8.9*	
Formicidae (A)		6	2	17	3	26	–	33	7	4553.5	3.10	
Unidentified Hymenoptera (A)		1	–	1	–	–	–	13	–		13.1***	
Corixidae (A)		4	–	1	–	–	–	13	–		13.1***	
Unidentified Insecta (A)		14	1	14	–	18	3	13	–	5061.5	0.40	
Artemia parthenogenetica		17	12	2	1	–	–	–	–	4348.5		
A. parthenogenetica cyst	S	61	8	38	4	64	–	–	–	3900**	17.6****	S,Au > W
Flamingolepis liguloides cysticercoids		23	1	27	2	28	3	–	–	4844	5.4	
Isopoda	M	4	–	45	6	3	3	67	60	2985****	33.2****	W,Au > S
Anphipoda		1	–	12	3	–	–	–	–	4510.5	7.2*	
Decapoda		–	–	7	–	3	–	27	7		9.7**	
Cirripedia		–	–	1	–	–	–	–	–			
Ostracoda	M	1	–	20	–	–	–	–	–	4134.5*	12.3**	
Unidentified Crustacea		1	–	3	–	10	–	–	–		4.02	
Araneida		7	–	10	–	21	–	7	–		3.5	
Acarina		2	–	1	–	–	–	–	–			
Polychaeta	M	77	39	84	72	8	3	60	20	3466.5****	71.1****	Au,W > S
Foraminifera	M	1	–	18	–	–	–	–	–	4218.5*	11.1**	
Gastropoda		–	–	7	2	8	–	13	7		0.50	
Unidentified Mollusca (shells)	M	18	4	74	37	15	3	20	–	1999.5****	48.9****	Au > W,S
Cestoda		4	1	2	–	–	–	–	–			
Nematoda		1	–	–	–	–	–	–	–			
Unidentified invertebrate		8	2	7	–	–	–	–	–	5027.5		
Invertebrate eggs		11	1	10	–	13	–	–	–		5.7	
Fish		12	4	22	2	3	3	7	–	4584	9*	
Grit	M/S	1	–	56	18	23	18	47	–	2275.5****	9.1*	
Others		–	–	7	–	3	–	7	7			

Prey: A = adults, L = larvae, P = pupae; others = nylon line and other artificial objects. Habitat: S = salt pan; M = tidal mudflats. *U* = Mann–Whitney *U* post hoc tests for differences between faeces and pellets in autumn; *H* = Kruskal–Wallis tests for seasonal differences for pellets: *P < 0.05, **P < 0.01 without Bonferroni correction, ***P < 0.05 after Bonferroni correction, ****P < 0.01 after Bonferroni correction. PCS = summary of significant pairwise seasonal comparisons for pellet composition with Mann–Whitney *U* post hoc tests: Au = autumn, S = spring, W = winter. Dashes indicate 'not present'.

occurred most frequently (84%) followed by molluscs (Table 1).

Chironomid pupae also dominated in spring pellets by volume (Table 1), representing >90% of the volume in 13 (33%) of the samples (*n* = 39). The next most important prey by volume were Ephydridae larvae and the beetle *Paracymus aenus*, representing >50% of volume in six (15%) and five (13%) samples respectively. In winter pellets, isopods were dominant, representing >90% of the volume in six (40%) of the samples (*n* = 15). In autumn pellets, polychaetes were dominant, representing >90% of the volume in 29 (24%) of the samples (*n* = 121), followed by molluscs which made up >50% of the volume in 18 (15%) samples. Grit was unusually abundant in autumn pellets, constituting >50% of the volume in 11 (9%) samples.

There were significant differences between seasons in the abundance of different food items in pellets (Table 1). *Sonchus oleraceus* seeds, chironomid larvae and pupae, Stratiomyidae larvae, Ephydridae pupae, *O. corrugatus*, *P. aenus* and *Artemia* cysts were more abundant in spring than in autumn. Chironomid larvae and pupae and *Artemia* cysts were more abundant in spring than in winter. Isopods, polychaetes and molluscs were more abundant in autumn than in spring. *Artemia* cysts, polychaetes and molluscs were more abundant in autumn than in winter. Isopods were more abundant in winter than in the other two seasons, and polychaetes were more abundant in winter than in spring (Table 1).

We also found significant differences between seasons in the numbers of countable items recorded in pellets: *S. oleraceus* seeds were more abundant in spring than in autumn (*U* = 1633.5, *P* < 0.05). *Artemia* cysts were more numerous in spring than the other two seasons (autumn: *U* = 1670, *P* < 0.05; winter: *U* = 562.5, *P* < 0.05), and more numerous in autumn than in winter (*U* = 105, *P* < 0.01). There were no significant differences between seasons in numbers of *Arthrocnemum macrostachyum* seeds, *Mesembryanthemum nodiflorum* seeds or cestode cysticercoids (*Flamingolepis liguloides*).

As measured by categories of volumetric abundance, chironomid pupae were relatively more abundant in spring pellets than chironomid larvae (sign test, *z* = 2.04, *P* < 0.05), whereas differences in their relative abundance for other seasons (Table 1) were not significant.

Differences between pellets and faeces in autumn

The diversity of items varied, with more classes of food items being recorded in pellets (46) than in faeces (38).

Suaeda seeds, *S. oleraceus* seeds and nematodes were found only in faeces, while *Salicornia* seeds, bryozoan statoblasts, adult chironomids, Dolichopodidae, Stratiomyidae, Ephydridae larvae, *P. aenus*, decapods, cirripeds and gastropods were found only in pellets.

Polychaetes were the most frequently recorded prey items in both pellets and faecal samples (Table 1). However, whereas molluscs were the next most important items for pellets, *Artemia* cysts and *O. notabilis* beetles were the next most important for faeces (Table 1).

Polychaetes were dominant in volumetric terms in both pellets (see above) and faeces, representing >90% of the volume in 13 (15%) faecal samples (*n* = 84). Unlike pellets, in which molluscs and grit were abundant (see above), the next most important items in faeces were chironomid larvae, *M. nodiflorum* seeds and *Artemia* cysts (Table 1) which made up >50% of the volume in eight (10%), nine (11%) and two (2%) samples respectively.

There were significant differences in the relative abundance of different components between pellets and faeces. Chironomid larvae were more abundant in faeces, whereas isopods, polychaetes, molluscs and grit were more abundant in pellets (Table 1). Amongst countable items, *M. nodiflorum* seeds and *Artemia* cysts were more abundant in faeces (*U* = 3828, *P* < 0.01; *U* = 3824.5, *P* < 0.01), whereas the number of cestode cysticercoids was higher in pellets (*U* = 2714, *P* < 0.01).

The relative abundance of different components in pellets and faeces showed a highly significant correlation (r_s = 0.56, *P* < 0.01, *n* = 48) when comparing mean values of volumetric ranks (see Methods). The correlation for percentage occurrence of each item was equally significant (r_s = 0.51, *P* < 0.01). However, each method gave a different ranking to the abundance of different items (Table 2).

DISCUSSION

The diet of waders can be very variable at different times of the tidal cycle, and waders can excrete various pellets differing in composition during the course of one cycle (Goss-Custard & Jones 1976, Worral 1984). In our study area, it was not possible to collect samples throughout the tidal cycle, as only roost sites used at high tide were accessible for sample collection. However, we collected all samples from the same place and at the same point of the tidal cycle, so that samples were comparable.

Table 2. Order of importance (by ranks) of different prey items found in autumn faeces and pellets, and by both methods combined. The ranks were based on the mean values of seven volumetric categories (see Methods). Combined ranks were based on the means of the two means for pellets and faeces.

Prey	Pellet	Faeces	Pellet + faeces
Polychaeta	1	1	1
A. parthenogenetica cyst	5	3	2
Ochthebius notabilis (A)	4	5	3
Unidentified Mollusca (shells)	2	9.5	4
Mesembryanthemum nodiflorum	8	4	5
Unidentified Coleoptera (A)	7	7	6
Flamingolepis liguloides cysticercoids	9	9.5	7
Chironomus salinarius (P)	13.5	6	8
Fish	10	11	9
Chironomus salinarius (L)	21	2	10
Isopoda	6	21	11.5
Formicidae (A)	11	16	11.5
Ochthebius corrugatus (A)	16.5	13	12
Grit	3	27	13
Invertebrate eggs	19.5	12	14
Artemia parthenogenetica	26	8	15
Ephydridae (P)	13.5	21	16
Araneida	19.5	17	17
Arthrocnemum macrostachyum	23	14	18
Ostracoda	12	27	19
Foraminifera	15	27	20
Cestoda	28	15	21
Anphipoda	16.5	27	22.5
Algae	24.5	19	22.5
Ochthebius (L)	33.5	18	24
Gastropoda	18	35.5	25
Corixidae (A)	33.5	21	26
Acarina	33.5	23	27
Decapoda	22	35.5	28
Stratiomyidae (L)	24.5	35.5	29
Salicornia	28	35.5	30.5
Dolychopodidae (L)	28	35.5	30.5
Suaeda	39	27	35.5
Sonchus oleraceus	39	27	35.5
Nematoda	39	27	35.5
Bryozoan statoblast	33.5	35.5	35.5
Chironomus salinarius (A)	33.5	35.5	35.5
Ephydridae (L)	33.5	35.5	35.5
Paracymus aenus (A)	33.5	35.5	35.5
Cirripedia	33.5	35.5	35.5

A = adults, L = larvae, P = pupae.

Many studies of Redshank diet have been carried out in northern Europe, where different prey items are available (e.g. Goss-Custard 1970, Goss-Custard & Jones 1976). In southern Europe, the few previous studies have been made in winter. In faeces from the Tagus Estuary in Portugal, the gastropod *Hydrobia ulvae* was dominant (Moreira 1996). In pellets collected from salt pans in Cádiz Bay, the dominant prey were Diptera, Coleoptera and *H. ulvae* (Perez-Hurtado *et al.* 1997). In our winter pellet samples, isopods, Coleoptera and polychaetes were dominant.

The contrast between our study and that in the Tagus may be explained by the different composition of faeces and pellets (see below). The difference with the Cádiz Bay study is probably explained by different management of salt pans. In Cádiz, the depth of many evaporation ponds is reduced in autumn and winter (Masero & Pérez-Hurtado 2001), allowing waders to feed efficiently on chironomids and other prey in the ponds. In Odiel, 90 km to the northwest, there are no drawdowns in this period, and almost all the ponds remain too deep in winter for Redshank, forcing them to feed in the mudflats on isopods and polychaetes.

Based on pellet composition, insect prey from salt pans were most important in the diet in spring, whereas prey from mudflats (polychaetes, molluscs, isopods) were most important in autumn and winter, suggesting a switch in habitat use (Table 1). The relative value of the salt pans and mudflats as foraging habitat changes between seasons, since fluctuations in available biomass in these two habitats are asynchronous (Masero *et al.* 1999, Masero & Pérez-Hurtado 2001). Thus, in mudflats in Cádiz the biomass of available prey dropped by a third from February to March (Masero *et al.* 1999), when the biomass of chironomid prey in the Odiel salt pans increased. Furthermore, in Odiel the depth in salt pans is reduced in spring, favouring their use by waders (Sánchez *et al.* unpubl. data). Hence it is not surprising that the relative importance of mudflat and salt pan species in Redshank diet changed between seasons. Our data confirm the complementary importance of both habitat types for Redshank in the Iberian peninsula at different times of the year (see Masero *et al.* 1999).

In benthic samples from the salt pans, we have found the density of chironomid pupae to be low compared with that of larvae (one pupa per 125–162 larvae in January, March and September 2001). Thus, the greater relative abundance of *C. salinarius* pupae in Redshank pellets suggests the pupae are taken from the surface during emergence events (Armitage *et al.* 1995), as supported by observations of feeding behaviour. Pupae were most abundant in pellets in spring, when we recorded the highest density of pupae in the sediments (64/m^2; Sánchez *et al.* unpubl. data).

The consumption of seeds by waders is common, but the reasons for this are poorly understood (Green *et al.* 2002). In our study, *S. oleraceus* seeds were consumed mainly in spring, coinciding with the time of seed production (Valdés *et al.* 1987). *Artemia* cysts were

most abundant in autumn and spring, the peak in cyst production being in summer (Martínez 1989).

As we have shown, the use of different methods to study wader diet can produce important differences in results and their associated biases. We found pellets to contain a greater diversity of prey items than faeces, but all items recorded in more than 7.5% of general samples were also recorded in pellets and vice versa. Thus, both kinds of samples include all major prey items, contrary to previous suggestions (Goss-Custard *et al.* 1977, Worral 1984). Although most items are present, those found in faeces are often more fragmented and harder to identify. Moreby (1988) suggested that the value of faecal analysis is limited by poor detectability following digestion. In our study, almost all arthropod groups left detectable hard parts in faeces, although their identification is time-consuming.

These two methods give different, but correlated, indices of the relative importance of prey, with polychaetes, isopods and molluscs being particularly abundant in pellets, and chironomids in faeces. These differences appear to be related to differences in digestibility, with harder items being more frequent in pellets. They also appear related to size, with smaller items being excreted as faeces. Thus, M. *nodiflorum* seeds (<1 mm diameter) and *Artemia* cysts (<0.3 mm) were more frequent in faeces, despite their hardness. For a given mollusc species, individuals in pellets are larger than those in faeces (Goss-Custard *et al.* 1977, Dekinga & Piersma 1993). At Cádiz Bay, the selection of prey size by Redshank was studied by comparing the size of prey in faeces with those available (Masero & Pérez-Hurtado 2001). Our results suggest it is important to compare both faecal and pellet contents in such studies, since they represent different fractions of the prey sizes consumed. They also suggest that studies comparing the diet of wader species that use faecal analysis for some species and pellet analysis for others (e.g. Pérez-Hurtado *et al.* 1997) may produce misleading results.

In general, larger, harder prey items consumed on mudflats are represented more in pellets, and softer, smaller items consumed in the salt pans more in faeces. We used the average volumetric category for each prey item to rank them in importance for faeces and pellets (Table 2). The sum of these rankings gives a more reliable indication of the diet composition (Duffy & Jackson 1986). This suggests that polychaetes were most important in autumn diet, followed by *Artemia* cysts and *O. notabilis* (Table 2). Nevertheless, even this combined method is biased owing to different digestibilities and detectabilities between prey items. Indeed, to confirm that a combined method is more representative than either pellets or faeces alone, it would be necessary to undertake controlled experiments with known ingesta composition. Polychaetes were ranked first in both sample types because they contained both hard, indigestible mandibles (recorded mainly in pellets) and fine chaetae (detectable in faeces).

Although pellet and faecal analyses produce different results and a combination of both methods is the best option, the abundances and frequencies of prey items recorded by the two methods are highly correlated. Thus, either method provides a useful and related assessment of Redshank diet.

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