

THE DIET OF BAR-TAILED GODWITS *LIMOSA LAPPONICA* IN THE WADDEN SEA: COMBINING VISUAL OBSERVATIONS AND FAECES ANALYSES

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Estimating diet composition of Bar-tailed Godwits *Limosa lapponica* by visual observations was hampered by large amounts of unidentified prey items. Therefore, additional analyses of faeces were conducted. Overall, 17 prey species were found in the droppings, but only four polychaetes, the Lugworm *Arenicola marina*, the Estuary Ragworm *Nereis diversicolor*, the Catworm *Nephtys hombergii*, *Scoloplos armiger* and one crustacean, the Shore Crab *Carcinus maenas* were taken regularly by the birds. In faecal samples the number of polychaete chaetae, hooks, jaws and bivalve umbos were estimated, which allowed in the case of *Nereis diversicolor*, *Nephtys hombergii*, *Scoloplos armiger* and the Baltic Tellin *Macoma balthica* an estimation of the minimum number of prey individuals per dropping. The ratios of these prey species to each other in the faeces were used to correct for the unidentified prey taken during observations. The diet of Bar-tailed Godwits showed a seasonal pattern, as well as differences between males and females. Diet was similar between the sexes in winter with *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger* comprising 99% of the prey items taken. In spring 20% of the prey items of males were *Macoma balthica*, whereas females took the Sand Mason *Janice conchilega* instead. In late summer *Arenicola marina* was an important prey for females but its importance decreased with decreasing prey availability in autumn. Towards winter the proportion of small polychaete species like *Scoloplos armiger* and *Nereis diversicolor* increased in the diet.

Key-words: *Limosa lapponica* - diet composition - polychaetes - reconstruction of prey size - sex differences - Wadden Sea

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INTRODUCTION

The knowledge of diet composition of predators is fundamental for the understanding of their foraging ecology. For birds, several methods have been proposed to quantify diet composition (Hartley 1948; Pienkowski *et al.* 1984; Duffy & Jackson 1986; Rosenberg & Cooper 1990). However, each method has its drawbacks, so that relying on one method alone may lead to biased results. Indirect

methods such as analyses of stomach contents, regurgitates, pellets, or droppings have in common that prey organisms have already entered the digestive tract before analysis. Thus, problems with differential digestibility or detectability in the samples have to be taken into account when estimating the composition of the consumed diet (Greenwood & Goss-Custard 1970; Jenni *et al.* 1990; Rosenberg & Cooper 1990). On the other hand, direct visual observations of foraging birds

often yield large amounts of unidentified prey, even for waders which forage in open, accessible habitats and are relatively easy to observe (Goss-Custard *et al.* 1977; Evans *et al.* 1979; Altenburg *et al.* 1982; Kalejta 1993; Pérez-Hurtado *et al.* 1997). For a quantification of the diet two possibilities are feasible. Firstly, a recalculation of the diet from indirect methods on the basis of feeding experiments (Green 1978, 1984; Galbraith 1989; Jenni *et al.* 1990). This can go as far as the calculation of intake rates on the basis of faecal analysis (Dekinga & Piersma 1993). Analyses of pellets, droppings, or stomach contents often have the advantage that prey size can be calculated, if any indigestible parts of the prey species exist which relate to the size of the individual prey eaten. Secondly, the correction of visual observations by means of the indirect methods. Until now this has not been carried out and results of both methods have been presented separately.

In this paper seasonal and sexual differences in diet composition of Bar-tailed Godwits *Limosa lapponica* are presented on the basis of the combination of visual observations and dropping analysis, as visual observations alone resulted in 64% unidentified prey items. Bar-tailed Godwits breed in northern Scandinavia and western Siberia and winter mainly in the western Wadden Sea, Britain, and West Africa (Cramp & Simmons 1983; Drent & Piersma 1990). During their stop-over in the Wadden Sea in spring birds increase their body mass, fuelling up for their up to 4000 km long-distance flights (Prokosch 1988; Drent & Piersma 1990). Individuals that winter in the Wadden Sea must cope with highly seasonal fluctuations of prey availability (Zwarts & Wanink 1993). Furthermore, Bar-tailed Godwits are highly sexually dimorphic (Prokosch 1988), so that differences in prey choice between the sexes are expected.

METHODS

Collection of droppings and observations were carried out at tidal flats near List, Sylt in the northern European Wadden Sea (55°01'N,

8°26'E). Sediments consist mainly of coarse sand (Austen 1994; see Reise 1985 for a further description of the study area). On an annual average, Bar-tailed Godwits make up 17% of the bird community of this area (Scheiffarth & Nehls 1997). The phenology of Bar-tailed Godwits shows the typical pattern of a stopover and wintering site for arctic breeding waders with high numbers from March to May, a low in June/July during the breeding season with almost no Bar-tailed Godwits present in the study area, and again higher numbers from August onwards to mid January (Scheiffarth *in press*).

Analysis of droppings

Droppings were collected during low tide at least once per month from August 1991 to April 1992. Radio tracking data confirmed that the median time Bar-tailed Godwits foraged on the same patch is one hour (Scheiffarth unpubl. data). Observations of captive Bar-tailed Godwits showed that the mean time between the start of feeding and the production of the first dropping took 28 min (Scheiffarth unpubl. data), which makes it likely, that at least part of the droppings collected on the mudflats represent local prey. Droppings were found and identified by following the tracks of Bar-tailed Godwits on the mudflats (*cf.* Durell & Kelly 1990). Entire droppings were scraped off the surface and preserved in 70% ethanol. For analysis the samples were treated with ultrasound for at least for 10 min, resulting in a separation of sand and soft parts. After sedimentation for 1-2 min the supernatant was put over a 64 µm sieve and the parts retained were analysed in a 25 cm³ cylindrical chamber with a diameter of 25 mm. All chaetae and aciculae of polychaetes were identified to species level (Friedrich 1938; Hartmann-Schröder 1971) by means of an inverted microscope (x 25 - 400). All parts were counted on three transects which allowed a calculation of the number of chaetae per species in the entire sample (see Table 1 for species and parts counted). Specific identification of the chaetae was facilitated by a reference collection of specimens from the study area (see also Dernerde 1993).

Table 1. Parts of species counted in droppings.

Species	parts counted
<i>Nereis diversicolor</i>	jaws, aciculae, chaetae
<i>Nephtys hombergii</i>	jaws, aciculae, chaetae
<i>Arenicola marina</i>	chaetae, thoracic hooks
<i>Lanice conchilega</i>	chaetae, thoracic hooks
<i>Scoloplos armiger</i>	chaetae, thoracic hooks
other polychaetes	chaetae
<i>Macoma balthica</i>	umbos

Chaetae for the reference collection were obtained by digesting the worms in a bath of pepsin (from porcine gastric mucosa, 700 FIP-U g⁻¹, 0.7 Ph Eur-E mg⁻¹, Merck, Darmstadt) and HCl (10% pepsin concentration in fresh water, pH 1.6). The sand fractions were searched for hard parts of crustaceans and molluscs, and polychaete jaws with a stereo-microscope (8x - 64x). For the umbos of the Baltic Tellin *Macoma balthica*, the jaws of the Estuary Ragworm *Nereis diversicolor* and the Catworm *Nephtys hombergii* calibration curves were constructed from locally collected specimens (Fig. 1) which allowed the estimations of body lengths (shell length or worm length) from these parts. For the calculation of calibration lines the function giving the best fit for the available data were used. Worm lengths were taken, after anaesthetising the worms with MgCl₂ (80 g l⁻¹, Hulings & Gray 1971), from relaxed individuals without stretching them to maximum length. The umbos of *Macoma balthica* were measured according to Zwarts & Blomert (1992). The jaws of *Nereis diversicolor* were measured from the base of the proximal 'tooth' to the distal end of the jaw, which differs from the method applied by Zwarts & Esselink (1989). They measured from the tip of the proximal 'tooth' to the distal end of the jaw, resulting in slightly shorter jaw lengths. From *Nephtys hombergii* maximum jaw length was measured from the base to the distal end. As this method was developed in parallel to the analysis of the droppings, length estimates for this species are only available for spring samples. As a control, on each sampling date and place a 0-sam-

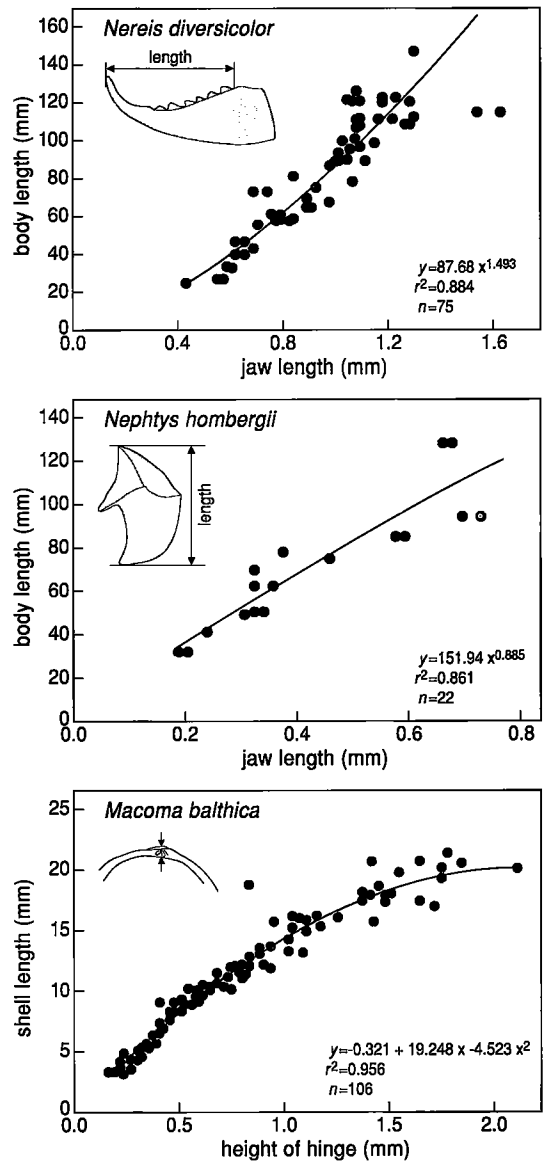


Fig. 1. Regressions for estimating worm lengths of *Nereis diversicolor* and *Nephtys hombergii* on the basis of jaw length, and the shell length of *Macoma balthica* on the basis of umbo width. Regression statistics for *Nereis diversicolor* and *Nephtys hombergii* were calculated with ln-transformed data.

ple was taken, which consisted only of surface sediment and was treated in the same way as the droppings. Usually no prey remains were found in the 0-sample, otherwise a species was only counted in a sample, when the number of chaetae or other parts was larger than in the corresponding 0-sample.

Although usually more than one type of fragment per species was counted in one sample, the most obvious part which was easiest to count was chosen to be representative in all samples. If instead only other parts were counted in a sample, for comparability the numbers of the 'representative' part was calculated on the basis of the regressions from Table 2. For all calculations, only droppings with at least one identifiable part were considered. Empty droppings were discarded. After some practise with the identification of chaetae, the entire procedure for analysing one sample took 2-3 h.

Counting all different parts in a sample, especially small ones like hooks, aciculae, and chaetae was not always possible, therefore the contents of all samples could not be quantified. Depending on the difficulty of the identification of various parts, the proportion of quantified parts differs between species. Counting chaetae and hooks of *Scoloplos armiger* proved to be particularly difficult, since these parts require a high microscopic magnification to identify. If large amounts of undigested flesh, pieces of carapaces or other undigested remainings of food made visibility poor, it was impossible to count these small parts. However, for most prey species in 85 - 95% of all samples

collected at least one body part could be quantified.

Calculation of the number of individuals in a sample

The number of individuals per sample could be determined for *Nereis diversicolor*, *Nephtys hombergii*, *Macoma balthica*, and *Scoloplos armiger*. In all other species either no unique body part was found in the droppings (e.g. Shore Crab *Carcinus maenas*) or these species have no parts which allow the calculation of the number of individuals represented in the droppings. For *Nephtys hombergii* and *Nereis diversicolor* the number of jaws in a sample divided by two was taken as the minimum number of individuals. If no jaws were found, regressions between the number of jaws and the number of chaetae or aciculae (Table 2) were used to estimate the number of jaws. Similarly, the minimum number of *Macoma balthica* was calculated by dividing the number of umbos by two.

Since *Scoloplos armiger* has no jaws or other indigestible structures which allow a direct conclusion on the number of individuals, a different approach was used. *Scoloplos armiger* has 12 - 22 thoracic segments (Hartmann-Schröder 1971). Each segment has 40 thoracic hooks, hence each individual should have 480 - 880 thoracic hooks. Usually, in faecal analysis not all chaetae or other soft parts are retained for analysis, so that a correction has to be made (e. g. Jenni *et al.* 1990). Since no feeding experiments with *Scoloplos armiger* were carried out, the probability that a

Table 2. Relation between different countable parts in droppings within species.

Species	Regression	r ²	P	n
<i>Nereis diversicolor</i>	# aciculae = 0.0517 * # chaetae + 35.08	0.395	0.001	28
	# jaws = 0.0265 * # aciculae + 0.11	0.742	< 0.001	56
	# jaws/# chaetae		n.s.	
<i>Nephtys hombergii</i>	# aciculae = 0.159 * # chaetae - 11.5	0.659	< 0.001	30
	# jaws = 0.0171 * # aciculae - 0.294	0.605	< 0.001	54
<i>Arenicola marina</i>	# chaetae/# thoracic hooks		n.s.	
<i>Scoloplos armiger</i>	# thoracic hooks = 0.348 * # chaetae + 89.1	0.658	< 0.001	34

thoracic hook was found in the faeces was based on a calculation with the chaetae of *Nereis diversicolor*. Moreira (1995) gives a regression between the length of *Nereis diversicolor* and the number of setigers. Furthermore, he estimated the mean number of chaetae per setiger as 28.2. Alternatively, the calculation can be carried out with the number of aciculae per setiger (4; Hartmann-Schröder 1971), which provides the same final result. Since the length of the *Nereis diversicolor* in the faeces was known from the relationship between jaw-length and worm-length and furthermore the minimum number of *Nereis diversicolor* in the droppings was known, the number of chaetae or aciculae which should be present in a dropping could be calculated. According to these calculations, 17.5% of *Nereis diversicolor* chaetae were retained in the sample. Assuming the same proportion for the thoracic hooks of *Scoloplos armiger*, 84 - 154 hooks per individual should be in a sample. In order to calculate the number of *Scoloplos armiger*, an intermediate number of 119 thoracic hooks per individual was used. If visibility for *Scoloplos armiger* thoracic hooks as a result of their smaller size is poorer than for *Nereis diversicolor* chaetae, this calculation would lead to an underestimate of *Scoloplos armiger* in the diet of Bar-tailed Godwits.

Visual observations

From August 1991 to October 1993 individual birds foraging on tidal flats were observed for as long as possible and behaviour was recorded on a continuously running tape recorder (focal animal sampling, continuous recording; Martin & Bateson 1986). Observations were conducted from observation towers, dikes, and by following flocks of foraging Bar-tailed Godwits on foot. All ingested species and their estimated sizes were recorded. Ingested prey were converted into biomass according to Scheiffarth (1995). Only birds observed longer than 270 s were included in the analysis. Sex of the birds was determined through a telescope by the relationship between bill length and body size which is different for males and females (Scheiffarth *in press*; Zwarts *et al.* 1990).

For statistical analysis of diet composition, the proportion of the different prey organisms in the diet was calculated for each bird. Thereafter the mean proportion per sex and month for each prey organism was calculated. Before testing for differences in diet composition, all proportions were arcsine transformed (Sachs 1984). With these data a two-factorial MANOVA was performed. As test criterion Pillai's Trace statistic, transformed to approximate the F distribution was taken (Norusis 1986).

RESULTS

Overall, 17 prey species were found in droppings of which 10 were polychaetes (Table 3). Only the polychaetes Lugworm *Arenicola marina*, *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger*, as well as the crustacean Shore Crab

Table 3. Species found in droppings and mean percentage (\bar{x}) of droppings with occurrence per sampling date. CV = Coefficient of variation; *n* date is number of sampling dates with occurrence of species; total number of droppings: 131; total number of sampling dates: 10.

Species	\bar{x}	CV	<i>n</i> date
<i>Arenicola marina</i>	38.0	83.0	8
<i>Nereis diversicolor</i>	48.1	40.8	9
<i>Nephtys hombergii</i>	60.6	54.1	9
<i>Scoloplos armiger</i>	78.1	31.1	10
<i>Lanice conchilega</i>	9.0	122.2	6
<i>Anaitides</i> sp.	3.0	234.9	2
<i>Pygospio</i> sp.	2.3	173.9	3
<i>Eteone longa</i>	2.4	216.0	2
<i>Lumbricus</i> sp.	2.1	316.2	1
<i>Harmothoë impar</i>	2.8	223.3	2
<i>Carcinus maenas</i>	14.3	84.8	9
<i>Crangon crangon</i>	6.9	117.6	5
<i>Gammarus</i> sp.	0.8	316.2	1
Crustacea sp.	5.5	152.0	4
<i>Cerastoderma edule</i>	1.7	235.8	2
<i>Macoma balthica</i>	17.5	155.0	6
<i>Ensis</i> sp.	2.1	216.0	2
<i>Pisces</i> sp.	1.9	213.5	2

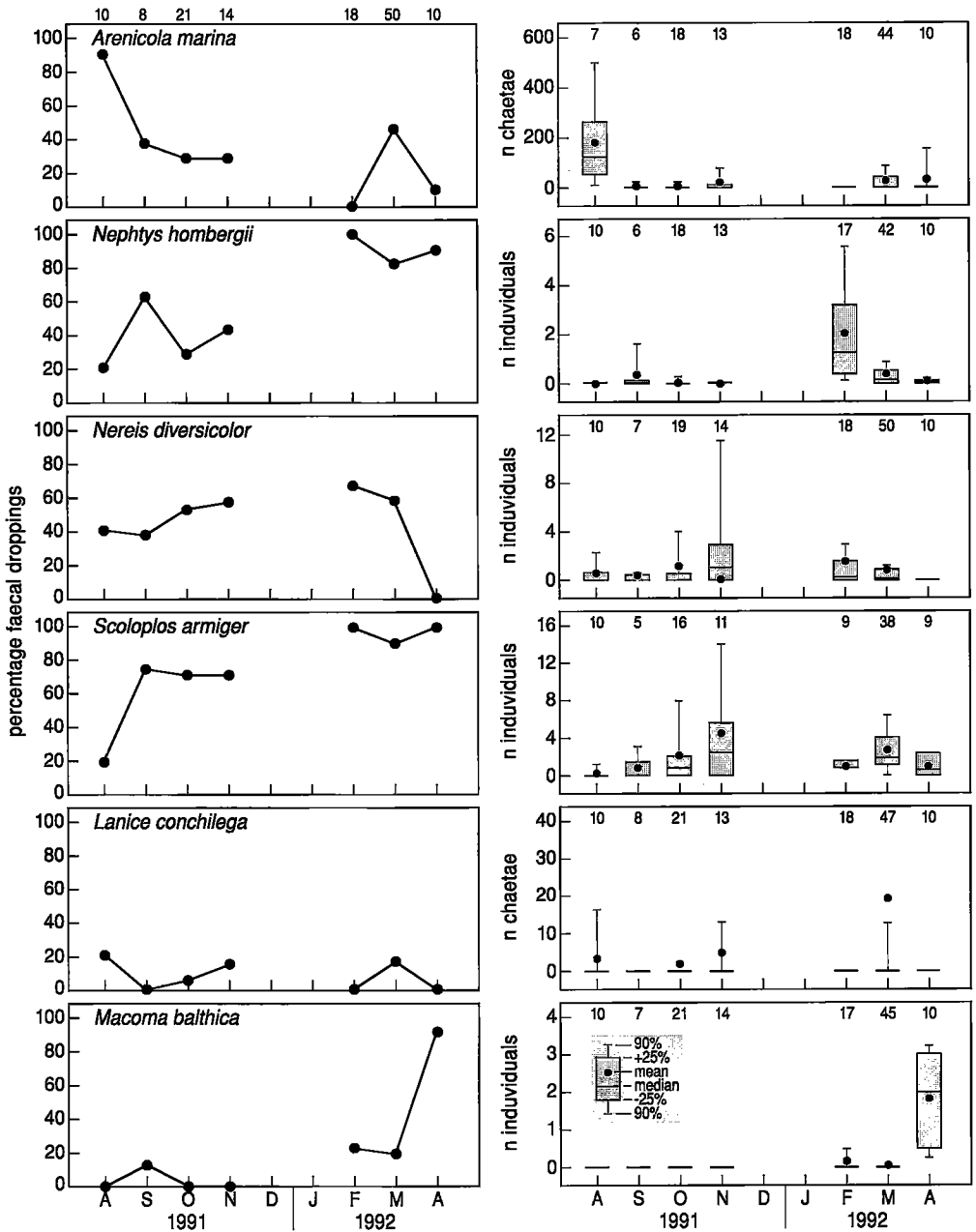


Fig. 2. Left: monthly variation of occurrence of main prey species in droppings, 100% = all droppings collected each month with at least one identifiable part. Right: box plots of seasonal variation of number of chaetae or minimum number of individuals per dropping. Numbers represent the number of samples analysed.

Carcinus maenas were regularly taken by Bar-tailed Godwits. The other species showed low frequencies of occurrence in the droppings and/or a high coefficient of variation. The occurrence of most of these species was restricted to autumn.

The occurrence of major prey species in droppings likewise showed a distinct monthly variation within the study year (Fig. 2, left). In August Bar-tailed Godwits took relatively many *Arenicola marina*. Towards winter, the proportion of droppings with small polychaete species, namely *Nephtys hombergii*, *Nereis diversicolor*, and *Scoloplos armiger*, increased in concurrence with a decrease of the proportion of *Arenicola marina*. In February these small polychaetes dominated the diet. In spring *Scoloplos armiger* and *Nephtys hombergii* were taken regularly and the importance of *Macoma balthica* rose sharply, whereas *Nereis diversicolor* disappeared.

For most prey species a similar monthly pattern in the study year emerged if the mean numbers of individuals or chaetae per dropping are considered (Fig. 2, right). However, there are also marked differences between the two patterns. Although the proportion of droppings containing *Nephtys hombergii* remained high during spring, the number of individuals decreased from 2.05 to 0.08 dropping⁻¹. The number of *Scoloplos armiger* per dropping remained low throughout winter and spring despite the fact, that this species was present in almost every dropping.

Besides the seasonal pattern in prey choice also the sizes of prey taken by the birds varied between the months studied (Fig. 3). In *Nereis diversicolor* the mean worm length increased from 51.7 mm in September/October to 85.6 mm in February (Kruskal-Wallis, $\chi^2 = 21.12$, $df = 4$, $P < 0.01$). In February the same mean worm size as in *Nereis diversicolor* was taken in *Nephtys hombergii* (Mann-Witney *U*-test, $U = 561$, $P > 0.05$). In both species no change in prey size between February and March could be detected (*Nereis diversicolor*: $U = 704$, $P > 0.05$, *Nephtys hombergii*: $U = 286$, $P > 0.05$). *Macoma balthica* taken by Bar-tailed Godwits increased in average shell length from 9.2 mm in February to 13.6 mm in April (Kruskal-

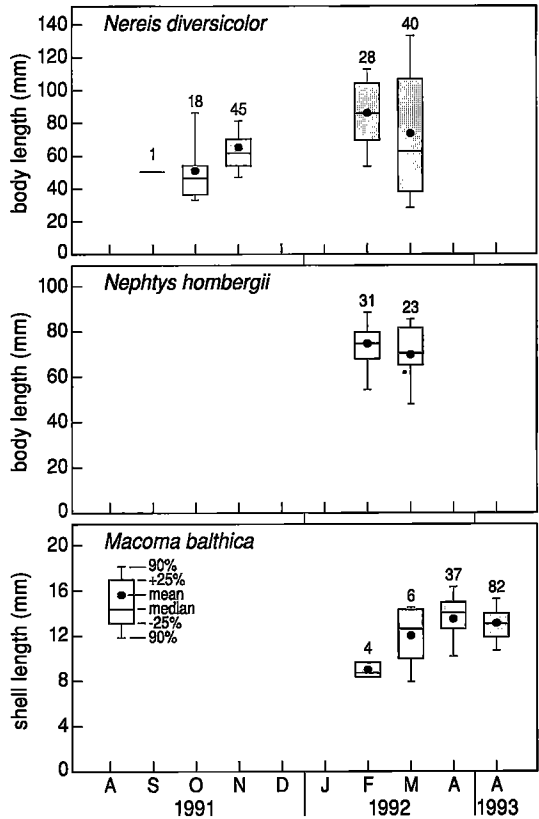


Fig. 3. Variation of prey size for *Nereis diversicolor*, *Nephtys hombergii*, and *Macoma balthica*. Prey-size was calculated from contents of droppings using the regressions from Fig. 1. Numbers represent the number of parts measured. Note that *Macoma balthica* was found both in April 1992 and April 1993.

Wallis, $\chi^2 = 7.9$, $df = 2$, $P < 0.05$). The same *Macoma* sizes were taken as prey one year later, in April 1993, the only month when samples containing *Macoma balthica* were collected in that year (Mann-Witney *U*-test, $U = 1851$, $P > 0.05$).

The results from faecal analyses were used to correct the visual observations. For a correction of the prey category 'Nereis/Nephtys' for each month the relative proportions of the two species in the droppings were used. Likewise, for the prey category 'unidentified' it was assumed that it consisted of *Nereis diversicolor*, *Nephtys hombergii*,

and *Scoloplos armiger*. All other prey species detected in the faeces were either considered to be insignificant (Scaleworm *Harmothoe impar*, *Eteone longa*, Paddleworm *Anaitides sp.*, *Pygospio sp.*, Earthworm *Lumbricus sp.*, gammarids *Gammarus sp.*, American Jackknife Clam *Ensis directus*, fish *Pisces sp.*) or showed a similar pattern between observations and droppings, so that a correction was not considered to be necessary. Thus, the relative proportions of *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger* were calculated for each month. For each individual bird observed, the categories 'Nereis/Nephtys' and 'unidentified' were multiplied with the corresponding proportions.

Prey composition based on the corrected number of individuals taken during observations (Fig. 4) showed a clear difference between months (MANOVA, $F_{56,1449} = 11.14$, $P < 0.001$), as well as, a marked difference between males and females (MANOVA, $F_{8,201} = 4$, $P < 0.001$). Furthermore, the monthly patterns differed between the two sexes (two-way interactions, MANOVA, $F_{56,1449} = 1.7$, $P < 0.01$). Overall, 94% of all prey items taken by Bar-tailed Godwits were polychaetes (males 91%, females 96%), of which the largest proportion comprised *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger*. The importance of these polychaetes was most pronounced in winter, with an increasing importance of *Scoloplos armiger* in autumn and a large proportion of *Nephtys hombergii* in February. Crustaceans played a minor role, and only so in autumn which is related to the availability of these species on intertidal flats (Boddeke 1976; Beukema 1991 & 1992; Herrmann *et al.* 1998). Sex differences in diet composition were due to *Arenicola marina* and Sand Mason *Lanice conchilega*, which were more often taken by females than by males (ANOVA, *Arenicola marina*: $F_{1,208} = 14.33$, $P < 0.001$, *Lanice conchilega*: $F_{1,208} = 13.02$, $P < 0.001$). For females *Arenicola marina* was an important prey species in August, but towards winter it nearly disappeared from the diet (ANOVA, $F_{7,97} = 4.68$, $P < 0.001$), whereas *Lanice conchilega* was most often taken in spring

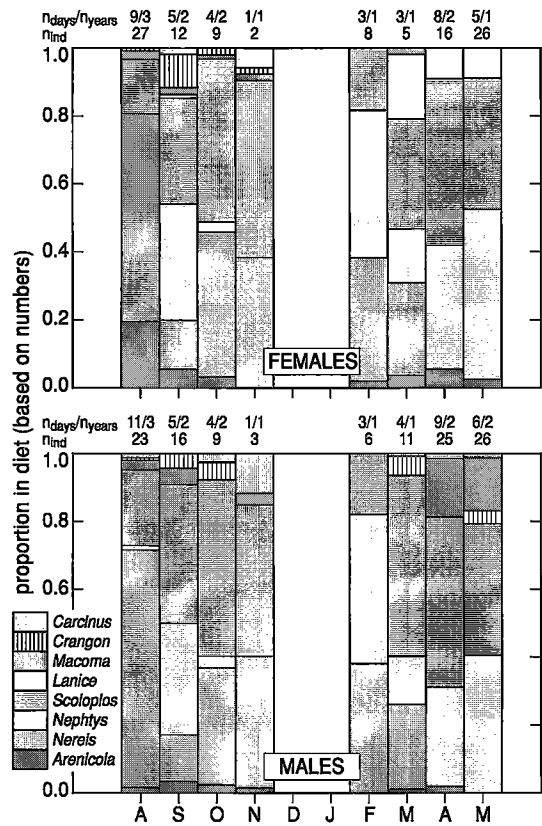


Fig. 4. Seasonal variation of diet composition (by numbers) for female and male Bar-tailed Godwits as determined by corrected visual observations on the basis of faeces analyses. Numbers above bars represent number of birds observed (n_{ind}), number of years with observations (n_{years}) and number of days with observations (n_{days}).

(ANOVA, $F_{7,97} = 2.66$, $P < 0.02$). On the contrary, *Macoma balthica* was an important prey for males in spring (ANOVA, $F_{7,111} = 2.88$, $P < 0.01$). Diet composition differed most strongly between sexes in August and became more similar towards winter. In February the diet of males and females was almost identical, *Nereis diversicolor*, *Nephtys hombergii*, and *Scoloplos armiger* together comprising 99% of all prey by numbers. From March onwards, diet composition differed again between

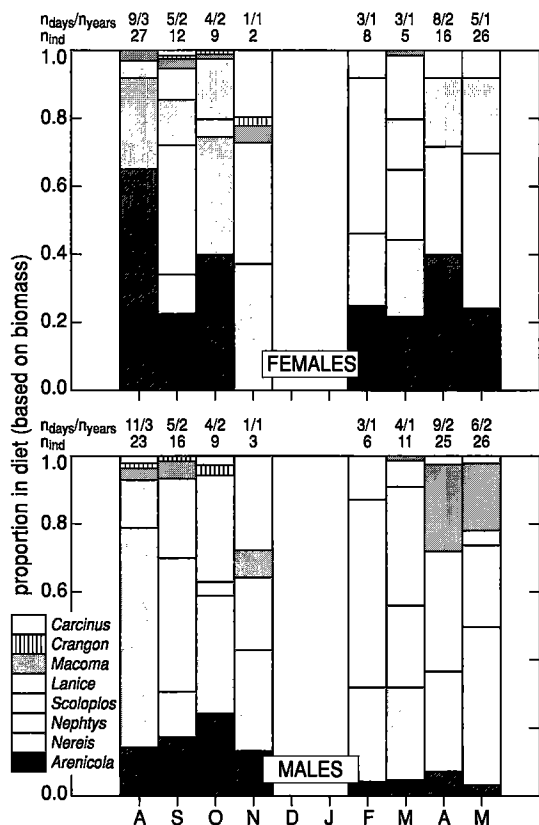


Fig. 5. Seasonal variation of diet composition (by biomass) for female and male Bar-tailed Godwits as determined by corrected visual observations on the basis of faeces analyses. Numbers above bars as in Fig. 4.

the sexes with the largest differences within the annual cycle in April and May.

When considering prey biomass composition, the importance of *Arenicola marina* in the diet of females becomes even more pronounced, particularly in August (65%, Fig. 5). Even for males the proportion of *Arenicola marina* comprised up to 24% of the diet. Although overall prey composition based on biomass differs between the two sexes (MANOVA, $F_{8,201} = 3.94$, $P < 0.001$), *Arenicola marina* is the only species where a significant difference can be found (ANOVA, $F_{1,208} = 10.9$, $P < 0.01$). In contrast to *Arenicola marina*, the importance of *Scoloplos armiger* is much low-

er as compared to the proportions based on numbers (see Fig. 4). Nevertheless, this species still makes up 25% of the diet of males and 17% of the diet of females, by mass.

DISCUSSION

Like in many other wader studies (Goss-Custard *et al.* 1977; Altenburg *et al.* 1982; Kalejta 1993; Pérez-Hurtado *et al.* 1997), a high proportion of the prey remained unidentified during the observations. However, for the construction of energy budgets (Scheiffarth 1995; Scheiffarth & Bairlein 1998), prey intake has to be estimated with the highest possible precision and diet composition must be known quantitatively. Goss-Custard (1973) recommended, that 'as much as possible should be described by the observations and any gaps should be filled by the analysis of pellets and droppings'. Many alternatives for determining diets, based on the examination of contents or remainings from the digestive tract, exist (Pienkowski *et al.* 1984; Duffy & Jackson 1986; Rosenberg & Cooper 1990). In the case of Bar-tailed Godwits the analysis of faeces has several advantages over other methods (see Verkuil 1996). Bar-tailed Godwits are difficult to catch on the feeding grounds, so that stomach flushing is no serious alternative. Since Bar-tailed Godwits seldom produce pellets and have never been observed doing so during this study, the vast majority of the indigestible remainings of prey organisms must pass the gut and leave the birds within the faeces. Furthermore, analysing droppings is a non-invasive method and samples are easy to collect (Durell & Kelly 1990; Verkuil 1996).

The analysis of faeces only by means of a binocular microscope is insufficient for detecting the remains of all prey species. Many small parts may be missed in this way and a compound microscope with a x 250 magnification or a phase contrast microscope must be used (Moreira 1995). At least all polychaetes have some indigestible parts (chaetae, hooks) which are detectable in this way. The method used in this study, using an

Table 4. Diet composition of Bar-tailed Godwits in different stop-over and wintering sites: Banc d'Arguin (Mauritania), Cádiz Bay (Spain), The Wash, Tees and Lindisfarne (Britain) and Königshafen (Germany). Figures are percentages of occurrence of prey species in gizzards or proventriculus, pellets, and faeces or the percentage of the total number of prey ingested, as determined by visual observations. If more than one area or period was available, the mean percentage was calculated.

Species	Banc d'Arg. observ. ^a	Cádiz Bay faeces ^b	Cádiz Bay observ. ^b	The Wash faeces, pellet, gizzard ^c	The Wash observ. ^c	Tees observ. ^d	Lindisfarne oesoph., proventr. ^e	Lindisfarne observ. ^e	Königs- hafen corr. observ. ^f
<i>Coleoptera spec.</i>		5.5							
<i>Mollusca spec.</i>	9.5	16.6			13.8				
<i>Macoma balthica</i>				95.7		2	52.4	2.6	3.3
<i>Cerastoderma edule</i>				16.3			9.5		
<i>Scrobicularia plana</i>							4.8		
<i>Tellina tenuis</i>							4.8		
<i>Hydrobia ulvae</i>			9.3	9.8					
<i>Nereis diversicolor</i>		83.3	61.7	13.0		80	9.5	1.4	27.6
<i>Nephtys hombergii</i>				1.1					21.6
<i>Lanice conchilega</i>					15.2			0.9	2.9
<i>Arenicola marina</i>					1.2		66.7	37.7	3.3
<i>Scoloplos armiger</i>							14.3	57.4	38.2
<i>Diopatra spec.</i>		11.1							
<i>Polychaeta spec.</i>	13.5				21.0				
<i>Crangon crangon</i>									1.6
<i>Carcinus maenas</i>				12.0	0.1	2			1.5
Seeds		38							
unidentified	77		29	9.8	48.8	16			

^aPiersma 1982; ^bPeréz-Hurtado *et al.* 1997; ^cGoss-Custard *et al.* 1977; ^dEvans *et al.* 1979; ^eSmith 1975; ^fthis study

inverted microscope, has the advantage that the entire sample can be surveyed and no extra preparations have to be made nor do subsamples have to be taken.

Assessing the numbers of different parts in a dropping goes one step further than determining the percentage of samples with the occurrence of a prey species. Counting parts offers the opportunity to estimate the minimum number of individuals per prey species and dropping, and seasonal changes in the relative importance of prey species can be determined (Mouritsen 1994). When presenting both the frequency of occurrence and the mean number of parts per dropping, as recommended by Duffy & Jackson (1986) and Rosenberg & Cooper (1990), it becomes obvious that these are not always correlated (contrary to Goss-

Custard & Jones 1976). As shown by the example of *Scoloplos armiger*, some prey species are taken regularly by most of the birds (a high proportion of droppings contain this species) but the importance in the diet varies seasonally (the mean number of individuals per dropping fluctuates). Although *Scoloplos armiger* is also the prey of *Nephtys hombergii* (Schubert & Reise 1986; Beukema 1987) and therefore parts of *Scoloplos armiger* may have entered the birds via *Nephtys hombergii*, observations have shown that *Scoloplos armiger* was regularly taken by Bar-tailed Godwits as prey in all months of observation.

Nevertheless, the method of analysing the droppings as presented here still has some shortcomings. The number of jaws, chaetae, or hooks counted must be in some way related to the num-

ber of prey organisms actually ingested, but this relationship is yet unknown. The processes which act on these parts during digestion have not been studied in detail, so that feeding experiments are needed for the interpretation of the number of parts found in the faeces (Green 1978, 1984; Galbraith 1989; Jenni *et al.* 1990; Robinson & Stebbings 1993). Furthermore, different prey species are digested at various rates or have different detection rates. This might result in a different relation of the indigestible parts to each other in the faeces as compared to the ingested prey (Greenwood & Goss-Custard 1970; Jenni *et al.* 1990).

As Carss & Parkinson (1996) concluded from feeding trials, analysing faeces gives a good estimate of the ranks of different prey species in the diet but offers a poor indicator for the true proportions consumed. This problem was circumvented in the present study. By combining observations and faeces analyses the true proportions of the staple food species could be estimated. Only prey of minor importance were missed by the observations, so that the entire spectrum of prey organisms was not covered by this method, resulting in only 8 prey species as opposed to 17 by faecal analysis. However, the missing nine prey species in the observations were taken so rarely, that they can be considered insignificant in the diet of Bar-tailed Godwits. For further progress it would be desirable to distinguish between the faeces from males and females. In this study a distinction between droppings of both sexes was impossible, so that a single correction factor for the observations had to be used. A solution to this problem could be the measurement of steroid hormones in the faeces (Totzke *pers. comm.*) or the distinction of the size of footprints between males and females on the mudflat.

In this study several prey species have been described for the first time in the diet of Bar-tailed Godwits, but most of these were of minor importance. Like in most other studies, polychaetes form the main prey (Table 4, see Piersma 1982). In Europe *Nereis diversicolor*, *Lanice conchilega*, *Arenicola marina*, and *Scoloplos armiger* are the

most important ones. Additionally, some molluscs are taken, in Europe mainly *Macoma balthica*. Compared to other waders, the prey choice of Bar-tailed Godwits appears relatively constant between areas and between seasons. Although some 94% of the diet of Bar-tailed Godwits around List consisted of polychaetes, some seasonal variation was apparent, but the total proportion of polychaetes in the diet never dropped below 85%. Furthermore, an apparent difference existed between males and females which was based mainly on the choice of large polychaete species like *Arenicola marina* and *Lanice conchilega* by females and the bivalve *Macoma balthica* by males in spring.

Males and females were not equally separated in prey choice throughout the year. Prey choice differed most in late spring and summer but became similar towards winter. The differentiation in diet composition coincided with a separation in habitat choice. In late spring and summer males utilised exposed mudflats, while females tended to feed at the waterline instead, as all Bar-tailed Godwits do in winter (*pers. obs.*; C. Both *pers. comm.*). This partitioning of the sexes in spring may be density related. As densities of Bar-tailed Godwits increase in spring, the smaller males may avoid competition with females (C. Both *pers. comm.*). Alternatively, it may also be that when temperatures rise in spring, *Macoma balthica* and small polychaetes become available on the exposed mudflats, which for some reason can be exploited in a profitable way by the males.

In all, the results show that quantitative dropping analyses offer the opportunity for the reproducible correction of observations and therefore result in a more complete picture of diet composition of birds. Especially, when the major interest lies in the calculation of energy intake or male-female differences, the combination of both approaches should be favoured to a separate presentation of droppings and observations.

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SAMENVATTING

Om de problemen die Rosse Grutto's *Limosa lapponica* ervaren, die in de Waddenzee doortrekken en overwinteren beter te leren begrijpen, zijn gedetailleerde voedselstudies gedaan. In de winter hebben de vogels te maken met een wisselend voedselaanbod en lage temperaturen; tijdens de korte opvetpieken tijdens de doortrek met een enorme voedselbehoefte. Mannen en vrouwen hebben een groot verschil in snavellengte, wat wijst op een verschillende aanpak van de voedsel-ecologische problemen. Pogingen om het menu in detail te beschrijven middels directe waarnemingen aan foeragerende vogels, strandden op het feit dat veel van de ogenschijnlijk bemachtigde en ingeslikte prooien zo klein waren, of zo sterk op elkaar leken, dat specifieke herkenning vaak niet mogelijk was. De auteur heeft daarom gezocht naar aanvullende methoden om de gegeten prooien tot op soortsniveau te kunnen determineren. Hiertoe werd microscopisch onderzoek gedaan aan feces van de vogels. Feces werden op het wad verzameld bij Sylt, in de Duitse Waddenzee. Onder een omkeermicroscop werden harde delen van wormen (chitineuze haren, haken en kaken) en slotjes van schelpdieren verzameld. Door een vergelijking met referentiemateriaal van wormen en schelpdieren uit het studiegebied konden op deze wijze 17 soorten prooidieren worden geïdentificeerd, waarvan het merendeel kleine wormen betrof. Slechts enkele soorten waren echt belangrijke prooidieren, de rest werd slechts af en toe gevonden. In de winter bestond het voedsel van zowel mannen als vrouwen voor het overgrote deel uit slechts drie soorten wormen: de Zeeduizendpoot *Nereis*

diversicolor, de Zandzager *Nephtys hombergii* en de Wapenworm *Scoloplos armiger*. In het voorjaar aten mannen en vrouwen deels verschillende prooien. De mannen namen veel (20% van alle prooien) Nonnetjes *Macoma balthica*, de vrouwen namen in plaats daarvan een vergelijkbaar aandeel Schelpkokerwormen *Lanice conchilega*. Wadpieren *Arenicola marina* waren in de nazomer een belangrijke prooi voor vrouwen (65% van de prooimassa) en in mindere mate voor mannen (24%). Voor een aantal prooi-soorten (Zeeduizendpoot, Zandzager, Wapenworm en Nonnetje) was het mogelijk om op grond van de gevonden kaken, respectievelijk slotjes, een schatting te geven van de minimaal gegeten aantallen prooien. Voor soorten die dergelijke relatief grote structuren missen, moest op grond van de aantallen gevonden haren, gecorrigeerd voor een aangenomen verlies van haren in de monsters, het aantal prooien worden geschat. Daarnaast was het mogelijk, door metingen aan kaken en slotjes, de groottes te reconstrueren van de gegeten Zeeduizendpoten, Zandzagers en Nonnetjes, zodat ook verschillen in prooigroottes door het jaar heen konden worden beschreven. Een opvallende conclusie van de studie is, dat voedselverschillen tussen mannen en vrouwen veel kleiner zijn dan op grond van het grote verschil in snavellengte mocht worden verwacht. Deze conclusie behoeft echter nog enige nadere onderbouwing, omdat de feces van mannen en vrouwen niet van elkaar konden worden onderscheiden. Terugkoppeling met de zichtwaarnemingen was hiervoor nog noodzakelijk. (MFL)

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