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Foraging by Common Redshanks *Tringa totanus* on the polychaete worms *Hediste diversicolor* and *Nephtys hombergii*: a re-analysis of data first published in 1977

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Goss-Custard (1977) constructed an empirical model to test the hypothesis that free-living Common Redshanks *Tringa totanus* selected the size classes of prey that maximised intake rate. Model parameters were estimated during the winters 1969–70, 1970–71 and 1971–72 in Redshanks foraging on 16 mudflats containing two species of polychaete worms, the Ragworm *Hediste diversicolor* and the catworm *Nephtys hombergii*. Model predictions agreed with the predictions of the hypothesis. Subsequent research has found that environmental factors, namely, season, state of the tide and ambient temperature, affect the behaviour of the worms and their availability to shorebirds, including Redshanks. Our initial intention here had been to test by multivariate analysis whether taking the effect of these potentially confounding variables into account would significantly change model parameter values and thus its predictions when testing the rate-maximising hypothesis. The analysis revealed that not only were parameter values substantially changed but that major implicit assumptions in the model had been false. Perhaps most fatal to the model was that the responses of Redshanks to variations in the abundance of the two species of polychaete worms are so different that the two species cannot be considered jointly to comprise the birds' food supply, as had previously been assumed. To our great surprise, intake rate decreased as the numerical density of *Nephtys* increased, exactly opposite to the Type II functional response found in the well-known prey species of Redshanks, *Hediste*. *Nephtys* is now known to be an important predator of *Hediste*. We hypothesise that *Hediste* may avoid *Nephtys* by moving deeper into their burrows below a depth of 5 cm, an anti-predator response that would put them out of reach of the 4 cm long bill of Redshanks. This could reduce the numerical density of accessible *Hediste* when *Nephtys* are present and so the birds' intake rate.

Key words: prey size selection, intake rate-maximising, optimal foraging theory, intake rates, functional response, prey-predator-prey interactions, *Nephtys hombergii*, *Hediste diversicolor*

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Behavioural ecology, the study of behavioural decision-making in animals, was given a powerful boost in the 1960s and early 1970s by the publication of several theoretical papers on what was initially termed 'optimal foraging theory' (OFT; MacArthur & Piana 1966, Schoener 1971, Krebs 1973, Pulliam 1974). The reasoning underlying OFT was that natural selection would be expected to have favoured decisions that enabled animals to obtain their food requirements as quickly as possible so that they could spend as much

time as possible on other behaviours that also contributed to their overall fitness, such as rearing offspring or being alert to predators. The results of early experiments on captive animals by Shimp (1969) and Werner & Hall (1974), for example, were broadly in accordance with the predictions of OFT, a notion that is now more widely known as 'rate-maximising foraging', one aspect of a much broader conceptual framework (Stephens *et al.* 2008). Accordingly, researchers on foraging behaviour in the 1970s began to seek opportunities to test the predictions of OFT in nature.

One such study was that of Goss-Custard (1977) who tested the hypothesis in the field that Redshanks *Tringa totanus* selected the sizes of polychaete worms that maximised intake rate, which, following Zwarts *et al.* (1996), is measured in wading birds (Charadrii) as the ash-free dry mass (mg) consumed per second of active foraging. As only manual statistical analysis was available in 1972, the numerous observational data on each behaviour category investigated were summarised as mean values for each of the 16 study sites. These mean values were used for analysis and proved sufficient to reveal trends from which a model could be constructed to test the rate-maximising hypothesis by simulation experiment. The rate of taking the large and more profitable worms depended mainly on their numerical density in the sediment. The rate of taking the small and less profitable worms, on the other hand, was more influenced by the biomass ingested from the larger worms than by their own density. Small worms were only taken frequently when large ones were scarce, suggesting that small worms were less preferred. Laboratory experiments with captive Redshanks confirmed that the birds varied their response to small prey encountered in linear sequence, as in nature, according to the abundance of large prey (Goss-Custard 1978). The results of simulations with the model of free-living Redshanks foraging on a mixture of small and large worms were consistent with the notion that rejecting small prey when large ones were abundant maximised intake rate (Goss-Custard 1977).

Subsequent research suggests that these conclusions were based on assumptions that should now be challenged. First, the two polychaete species were treated as if they belonged to an equally preferred, single prey type. Although *Hediste* is a well-known and frequent prey species of Redshanks (Goss-Custard & Jones 1976, Goss-Custard *et al.* 1977, Evy Gobbens and Steph Trapp pers. comm.), there is little direct evidence that they regularly eat *Nephtys*, in contrast to a number of other Charadrii species, notably Bar-tailed Godwit *Limosa lapponica*, Dunlin *Calidris alpina* and Eurasian Curlew *Numenius arquata* (Durell & Kelly 1990, Scheiffarth 2001, Bocher *et al.* 2014). In fact, despite much research, there is currently no direct evidence from present-day field observation or eDNA metabarcoding of faeces that Redshanks eat *Nephtys* (Evy Gobbens and Steph Trapp pers. comm.). Second, the behaviour of polychaete worms can change in response to environmental variables, such as the particle composition and wetness of the sediment, the season and ambient temperature and the stage of the tidal cycle, in ways that can affect their detectability and accessibility, i.e. their 'availability', to shorebirds (Smith 1975, Pienkowski 1982, 1983, Esselink & Zwarts 1989a,b, Rosa *et al.* 2007). *Hediste* has been particularly well investigated in this respect, attention focussing on how deeply the worms are buried in the sediment, how frequently they move up to the surface where they are within range of the bills of shorebirds and whether they feed by filter-feeding within their burrows or graze at the surface of the sediment (Esselink & Zwarts 1989a,b, Rosa *et al.* 2007). Accordingly, it was entirely possible that differences between sites in the ambient temperature and the stage of the winter and/or tidal exposure period when foraging observations were being made could have confounded the results of Goss-Custard's (1977) analysis. Another highly relevant finding is that *Nephtys* is a regular predator of *Hediste* of the sizes consumed by Redshanks (Desroy *et al.* 1998). Further, the anti-predator responses of ragworms to the presence of *Nephtys* could change their behaviour in ways likely to affect their availability to Redshanks (Desroy *et al.* 1998). Finally, some Redshanks in Goss-Custard's study foraged singly or in loose flocks while others defended feeding territories. As birds defending a territory may have had different behavioural priorities to non-territorial birds, this difference in social behaviour could also have affected the birds' foraging decisions. Accordingly, research since 1977 has exposed several doubts about the tacit assumptions made by Goss-Custard (1977) and the values of the parameters used in his model.

Here we took advantage of the advent of powerful personal computers and statistical software to use multiple regression to explore whether and how the conclusions of the original paper might have been affected by (1) assuming that the two worm species were treated equally by the Redshank and (2) omitting from the analysis the potentially confounding environmental variables of ambient temperature, season and tidal exposure and the birds' social behaviour. The following hypotheses were tested: (1) If the two worm species did indeed comprise a single prey category, variation in the densities and mean sizes of each of the

worm species would have quantitatively identical effects on the birds' overall intake rate, (2) if the availability of the worms was identical across sites, variation in foraging behaviour would be unaffected by season, stage of the tidal exposure period and the ambient temperature and (3) if a bird's social behaviour did not affect its foraging behaviour, there would be no difference between the intake rates of territorial and non-territorial Redshanks. The main assumptions made in the simulation model were also tested, these being that (1) the number of the large and most profitable worms taken per metre searched would depend solely on their own density in the sediment whereas, in contrast, (2) the number of the less profitable small worms taken per metre would decrease as the bird's consumption of larger worms increased.

METHODS

Study sites, birds and food supply

The 16 study sites, each measuring less than 0.25 ha, were situated on estuaries in southern England and South Wales. They were chosen because of the combined presence of (1) Redshanks feeding primarily on worms that were large enough to be seen as they were being taken by the birds, (2) a muddy sediment that remained wet throughout the tidal exposure period and was free of surface irregularities, such as thick algal matts, and (3) a place nearby from which the birds could be watched from a vehicle using a 30–60 zoom telescope. Observations were made from mid-August to mid-February during the autumns and winters of 1969–70, 1970–71 and 1971–72. Observations in a given site were made at a given time of year and in a given winter over one 'sampling week'. Each sampling week comprised three to five consecutive tidal exposure periods on spring tides when low water occurred around midday – also the time at which the ambient temperature had been recorded. Most foraging data were obtained within 2–3 hours either side of low water which always fell around the middle of the day. The mean value for each behaviour from one site/week provided the 16 data points in Goss-Custard's analysis. As detailed in Goss-Custard (1977), estimates of the numerical densities and sizes (in mg dry weight) of each worm of each species were obtained from core sampling on the last day in each sampling week, i.e. in the several sites where observations were made in two or more winters, the food supply was measured at the end of each sampling week spent in that site and were therefore contemporaneous with the foraging observations. Although some Redshanks defended a foraging territory, non-territorial birds also occurred in most sites, usually foraging in loose flocks or singly. Whether a subject bird was territorial or not had always been recorded.

There were three potentially confounding environmental variables whose possible effect on foraging behaviour could be taken into account: (1) the stage of the winter, represented as the days elapsed since 1 August, (2) the stage of the tidal cycle, represented as the time elapsed since the start of the exposure period and (3) the ambient temperature at midday at approximately the centre of each observation day. The dataset of 16 weekly mean values obtained from the 16 sites that had been used in Goss-Custard's study was clearly inadequate to test by multiple regression the simultaneous effect of each of these variables and that of the food supply on the birds' foraging behaviour. So, to increase sample size, the data for each site/week were sub-setted. Birds had been watched in each site before site boundaries were chosen allowing most sites to be subdivided into two or more 'subsites' in an attempt to achieve uniformity in the polychaete food supply within one food patch. Furthermore, data had been collected from three sites over two or three years between which the polychaete food supply varied. In this way, the data set of 16 weekly mean values could be sub-setted to provide a sample of 107 daily mean values, in which 91 contained a mixture of both species of worms, the remainder only having *Hediste*.

Foraging behaviour

The two sorts of observations used to describe foraging behaviour are detailed in Goss-Custard (1977). To measure the numbers of worms taken per unit time or per metre searched – the 'feeding rate' – an individual was watched for 30 s of active foraging and the numbers of unidentifiable small prey and visible worms swallowed were recorded. The length of visible worms was estimated by comparison with the length of the bill. An adjustment was made by eye when a worm appeared to have contracted or expanded its length as it was being pulled out of the sediment, this being particularly likely to have occurred with the more flexible of the two species, *Hediste*. Intake rate was the product of the feeding rate and the mean weight of the consumed prey. In the 1977 study, prey size (and assumed food value) was established from a length/dry weight relationship obtained from a sample of worms of both species collected from a number of the sites in SW England. As there were small differences between the weight/length ratios of the two species of polychaetes, the average of the two values was used for each

length category on the untested assumption that half the consumed worms were *Hediste* and half *Nephtys*. We use here instead a single function for *Hediste* to convert worm length to ash-free dry mass (AFDM); this is a better measure than dry weight of food value as it excludes indigestible inorganic material such as jaws, chaetae and sediment particles. As the dry weights of *Hediste* and *Nephtys* of the same length were quite similar (Goss-Custard 1977), and most of the large and most profitable worms in the sediment were *Hediste*, this function provided a reasonable standardised estimate of the food value of the consumed worms of both species across all sites and in all seasons and winters. It was obtained from a sample of 151 *Hediste*, of fresh lengths 15 to 150 mm, taken from the Exe estuary in autumn 2001, as described in Durell *et al.* (2005):

$\log_e(\text{AFDM}) =$
$-5.839\ (\pm\ 0.222\ \text{SE}) + 2.190\ (\pm\ 0.055)\ \log_e(\text{length})$,
with AFDM in mg and length in mm ($R^2 = 0.914$).

A second series of observations measured the aspects of foraging behaviour required to convert 'intake rate', the biomass consumed per unit time, to the biomass ingested per linear metre searched. The time taken to make five paces was measured by stop-watch and the numbers of pecks, small and unidentifiable prey and visible worms of measurable length recorded simultaneously to estimate by linear regression the duration – or more precisely, the delay imposed on searching – associated with carrying out each of these components of foraging behaviour (Goss-Custard & Rothery 1976). This allowed the amount of time per 30 s that was spent in pecking at and handling prey to be deducted from the 30 s over which intake rate was measured to estimate the amount of time actively spent searching between prey captures. Dividing this amount by the time taken to make one pace estimated the number of paces made during the 30 s which, when multiplied by the average pace length of 10.3 cm, measured the linear distance searched during 30 s of foraging. Note that, throughout the paper, AFDM (mg) refers to the standardised size of worms ingested by the birds whereas DW (mg) refers to the site-specific size in dry weight of the worms in the sediment.

Probability of small worms being taken

Small worms were defined as worms less or equal half the length of the bill. Although many such prey could clearly be identified as worms as they were being taken, in some sites this was not possible for all small items. It was an assumption in Goss-Custard (1977) that such unidentifiable prey items were in fact very small *Hediste* or *Nephtys*, and this may not always have been the case. Small molluscs, particularly the gastropod *Peringia ulvae*, occurred in many sites along with small bivalve molluscs, such as Baltic Tellin *Limecola balthica*. Unfortunately, it is not possible retrospectively to test the assumption that all unidentifiable prey items were worms and we are therefore forced to make the same assumption as that made in the original study.

Ideally, the probability that a small worm in the sediment is captured and eaten by a Redshank would be measured by dividing the number of worms taken by the Redshank by the number of detectable and accessible small worms in the sediment in the area where it is foraging. This was not possible as neither the width of a Redshank's search path or the proportion of the worms that may have retreated to a depth beyond the reach of an approaching Redshank's bill are known. However, dividing the number of small worms taken per linear metre traversed by the bird by the number of small worms per square metre in the mud provides an index of risk. This measure of risk gave very small values so were multiplied by 1000 to provide more easily comprehended values.

Statistical procedure

Minitab v. 13 (Minitab 1999) was used to perform multiple linear regression analyses, the predominant statistics used in this study. In any one analysis, the approach was to define one of the assumptions made by Goss-Custard (1977) as the hypothesis to be tested (HT) and to explore whether that assumption still held after the simultaneous effects of the ambient temperature, season, tidal exposure and the birds' social behaviour – the potentially confounding variables (PCV) – had been taken into account. That is, the purpose of the analyses was not to derive the statistical model that best described the prey-size selection behaviour of Redshanks. Rather it was to test (1) whether the implicit assumptions made by Goss-Custard would be supported after the effect of potentially confounding variables on the birds' behaviour had been taken into account and (2) whether the parameter values used in his model needed to be changed.

The many (>500) zero scores in the sample of over 4250 30-s estimates of intake rate complicate analysis (Goss-Custard & Durell 1987). This was resolved by using the 'daily mean intake rate' over one low tide period on one day in one subsite as the datum. This greatly reduced the large number of zero scores, yielded a less skewed frequency distribution and greatly reduced the large variation that occurs when

feeding behaviour is recorded over time periods as short as 30 s (Goss-Custard *et al.* 2002). There were 52 estimates of the daily mean intake rates of non-territorial birds and 55 of territorial birds. As sample sizes for estimating daily mean intake rates varied between 2 and 84, all analyses were weighted by sample size.

The size classes used here to describe the food supply of the visible worms large enough to be seen as they were taken were the same fractions of bill length as those used by Goss-Custard (1977): size-class A, the smallest estimated to be visible as they were being taken (Goss-Custard 1977), (0.25 and 0.50 bill length), size class B (0.75 and 1.0), size class C (1.25 and 1.50), size class D (≥1.75). Following Goss-Custard (1977), the category 'large worm' was defined as B+C+D worms and the category 'small worms', termed A* worms here, was defined as A worms combined with small items that were too small to be identified as they were being consumed but assumed to be worms. As in Goss-Custard (1977), the subsite/day values of mean feeding and intake rates and the numerical densities and mean weights of the worms in the sediment were transformed by log10(value)+1. The environmental variables that are known or strongly suspected to affect the worms behaviour and so availability to Redshanks were (1) season, measured as the numbers of days elapsed since 1 August (Day), (2) the ambient temperature measured at midday (Temp) and (3) stage of the exposure period, measured as the hours elapsed after the arbitrary starting time of four hours before low water (Hour). These variables were untransformed but were entered in the quadratic as non-linear effects were anticipated. The interaction between their linear terms was also included. Whether the subject bird foraged in a flock or a territory was represented by a nominal variable with value 0 or 1. When the predictions of a multivariate equation were plotted to reveal the form of the function arising from the final equation, the effect of a given variable was graphed across its observed range in *Hediste* and using in the equation the mean values of each of all the other variables.

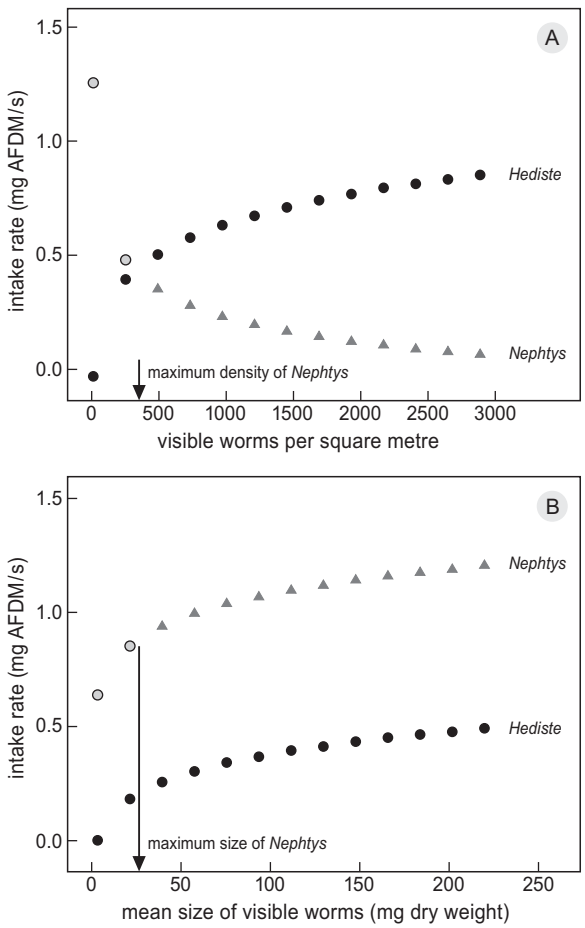

Figure 1. The relationship between the intake rate of Redshanks on visible worms (≥0.25 × bill length) predicted from the equation in Table 1 over the ranges of (A) the numerical densities and (B) mean sizes of *Hediste* of these size classes in the sediment. The maximum density and size of *Nephtys* recorded in the sediment are shown with the predicted intake rates at higher values, and thus beyond the empirical range, indicated by triangles. Values were back-transformed from the equation in Table 1 using the mean values of the other variables.

RESULTS

Intake rate on visible worms ≥0.25 × bill length

Intake rate is measured as the AFDM of visible worms consumed per unit time. Across the 107 values of intake rate obtained from the sample of 107 subsite/days, this size class contributed 97% of the biomass consumed by Redshanks.

The nominal variable representing territoriality was not significant (Table 1). The stage of the season (Day) and tide (Hour) and the ambient temperature (Temp) were significant correlates in at least one of the three terms – as a main effect or within an interaction term – in which each of these variables was represented. With the effect of all the other variables taken into account, the density and size category of each polychaete species were significant correlates in five out of six terms in which each variable was represented. Graphing the prediction of the equation revealed that, as expected, intake rate increased as the numerical density of the large *Hediste* in the sediment increased (Figure 1A). Unexpectedly, however, intake rate decreased very

sharply as the numerical density of *Nephtys* in the sediment increased over the limited range that occurred across the study sites (Figure 1A). Intake rate increased as the size of both the *Hediste* and *Nephtys* in the sediment increased. Nonetheless, the contrasting trends of intake rate against the numerical densities of the two worm species strongly implies that the two worms were not treated by Redshanks as a single prey type.

Feeding rate on large worms

The two expectations tested here were (1) that the feeding rate on large worms (≥ 0.75 × bill length) per metre searched would depend on the densities of these worms in the sediment and (2) that both worm species would have similar coefficients and thus the same quantitative effect on feeding rate.

Territoriality was not a significant factor (Table 2). The stage of the season (Day) and tide (Hour) and the ambient temperature (Temp) were significant, or very nearly significant, correlates in at least one of the three expressions in which each variable was represented. With the effect of other variables taken into account, the numerical density and size of *Nephtys* were significant correlates but neither was significant in *Hediste*. Graphing the predictions of the equation revealed that, accordingly, feeding rate on large worms changed very little as the numerical density of the large *Hediste* in the sediment increased, but decreased very sharply as that

Table 1. Results of a multiple regression analysis of the associations between intake rate and (1) the densities and sizes of the two species of worms, i.e. the hypotheses to be tested (HTs), and (2) three environmental variables and one social variable, i.e. the potentially confounding variables (PCVs). The intake rate (AFDM/s) was from visible worms (≥ 0.25 × bill length) only. The regression was of $\log_{10}$(intake rate + 1), weighted by the number of observations made in each subsite, against (1) $\log_{10}$(numerical Density + 1) and $\log_{10}$(mean Weight + 1) of the visible polychaete worms in the sediment, where Hd = *Hediste diversicolor* and Nh = *Nephtys hombergii*, (2) the birds' social behaviour and (3) the three environmental variables Day, Hour and Temp. Model diagnostics showed acceptable fits with approximately normal residuals and no major heteroskedasticity.

Predictor	**Coefficient**	**SE**	***t***	***P***
Constant	–2.4317	0.7602	–3.20	0.002
HTs:				
$\log_{10}$(vis*Hd*Density + 1)	0.5845	0.1622	3.60	0.001
$\log_{10}$(vis*Hd*Weight + 1)	0.6807	0.1725	3.95	0.000
$\log_{10}$(vis*Nh*Density + 1)	–0.27806	0.07649	–3.64	0.000
$\log_{10}$(vis*Nh*Weight + 1)	0.08604	0.07994	1.08	0.285
$\log_{10}$(*Hd*Den + 1) × $\log_{10}$(*Hd*W + 1)	0.4975	0.2058	2.42	0.018
$\log_{10}$(*Nh*Den + 1) × $\log_{10}$(*Nh*W + 1)	–0.22448	0.09147	–2.45	0.016
PCVs:				
Territorial = 1	0.00683	0.01742	0.39	0.696
Day	0.001025	0.003614	0.28	0.777
Day^2	0.0000311	0.00001189	2.62	0.010
Hour	0.10891	0.06134	1.78	0.079
Hour^2	0.009102	0.005517	1.65	0.102
Temp	0.09498	0.04470	2.13	0.036
Temp^2	–0.001834	0.001136	–1.61	0.110
Day × Hour	–0.0010971	0.0004005	–2.74	0.007
Day × Temp	–0.0002244	0.0001944	–1.15	0.251
Hour × Temp	–0.004673	0.003171	–1.47	0.144
R^2 = 61.3%				

Analysis of Variance

Source	***df***	***SS***	**MS**	***F***	***P***
Regression	16	8.85463	0.55341	8.90	0.000
Residual Error	90	5.59574	0.06217		
Total	106	14.45037			

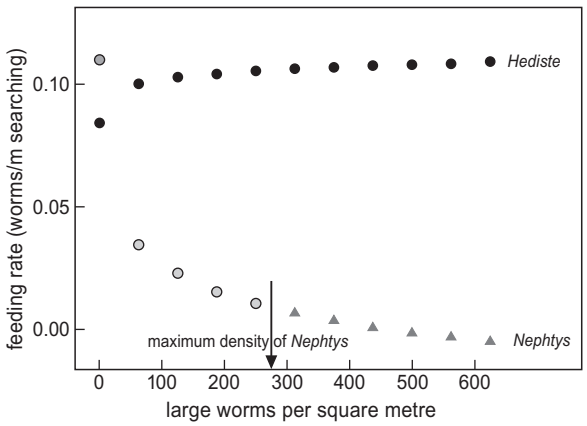

Figure 2. The relationship between the feeding rate of Redshanks on large worms predicted from the equation in Table 2 over the ranges of the numerical density of *Hediste* of these size classes in the sediment. The maximum density of *Nephtys* recorded in the sediment is shown with the predicted intake rates at higher values, and thus beyond the empirical range, indicated by triangles. Values were back-transformed from the equation in Table 2 using the mean values of the other variables.

Table 2. Results of a multiple regression analysis of the associations between the numbers of large worms taken per linear metre searched and (1) the densities and sizes of the two species of worms – the hypotheses to be tested (HTs), and (2) three environmental variables and one social variable – the potentially confounding variables (PCVs). The feeding rate (worms/m searched) was for large worms (≥0.75 × bill length) only. The regression was of $\log_{10}$(feeding rate + 1), weighted by the number of observations made in each subsite, against (1) $\log_{10}$(numerical Density + 1) and $\log_{10}$(mean Weight + 1) of the large polychaete worms in the sediment, where Hd = *Hediste diversicolor* and Nh = *Nephtys hombergii*, (2) the birds' social behaviour and (3) the three environmental variables Day, Hour and Temp. Model diagnostics showed acceptable fits with approximately normal residuals and no major heteroskedasticity.

Predictor	**Coefficient**	**SE**	***t***	***P***
Constant	–0.1349	0.1542	–0.87	0.384
HTs:				
$\log_{10}$(vis*Hd*Density + 1)	–0.01395	0.05377	–0.26	0.796
$\log_{10}$(vis*Hd*Weight + 1)	0.02737	0.04375	0.63	0.533
$\log_{10}$(vis*Nh*Density + 1)	–0.10025	0.0283	–3.54	0.001
$\log_{10}$(vis*Nh*Weight + 1)	–0.10025	0.02835	–3.54	0.001
$\log_{10}$(*Hd*Den + 1) × $\log_{10}$(*Hd*W + 1)	0.00981	0.02922	0.34	0.738
$\log_{10}$(*Nh*Den + 1) × $\log_{10}$(*Nh*W + 1)	0.07305	0.02086	3.50	0.001
PCVs:				
Territorial = 1	0.004348	0.004823	0.90	0.370
Day	0.002509	0.001032	2.43	0.017
Day^2	–0.00000988	0.00000307	–3.22	0.002
Hour	–0.03375	0.01695	–1.99	0.050
Hour^2	0.001996	0.001523	1.31	0.193
Temp	0.02327	0.01199	1.94	0.055
Temp^2	–0.0005363	0.0003148	–1.70	0.092
Day × Hour	0.0000848	0.0001095	0.77	0.441
Day × Temp	–0.00009380	0.00005301	–1.77	0.080
Hour × Temp	0.0009327	0.0008472	1.10	0.274
R^2 = 67.1%				

Analysis of Variance

Source	***df***	***SS***	**MS**	***F***	***P***
Regression	16	0.874333	0.054646	11.49	0.000
Residual Error	90	0.427857	0.004754		
Total	106	1.302190			

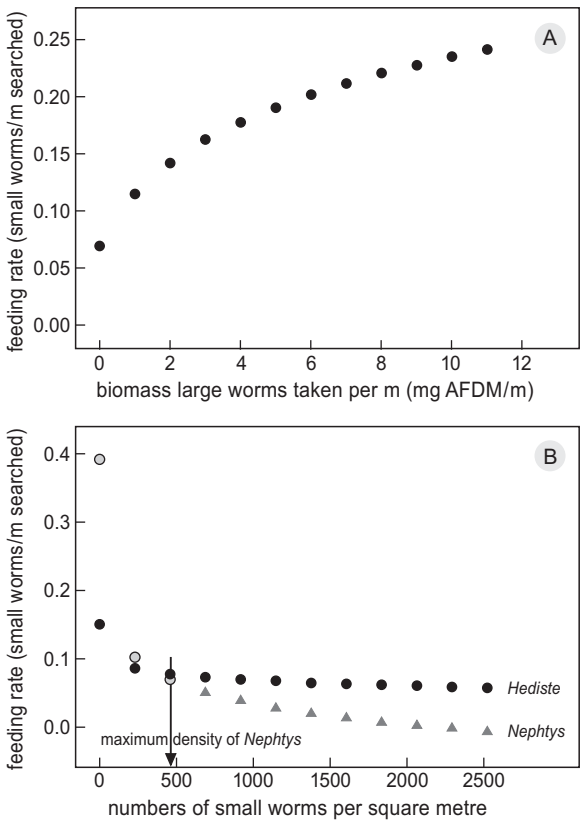

Figure 3. The relationships between the feeding rate of Redshanks on small worms (≤ 0.50 × bill length) and (A) the biomass of large worms (≥ 0.75 × bill length) consumed per metre searched, and (B) the densities of the small worms in the sediment. Values were back-transformed from the equation in Table 4 using the mean values of the other variables. Closed circles, *Hediste*, grey circles, *Nephtys*.

Table 3. The numbers of small worms (≤ 0.50 × bill length) taken per minute and per linear metre searched and the densities (numbers/m^2) of small *Hediste* and *Nephtys* in the sediment in each site. The number of cores taken to sample the worms in each site is also shown.

Site	Subsites	Small worms taken per minute	Small worms taken per metre searched	Small *Hediste*/m^2	Small *Nephtys*/m^2	Cores taken
1	6	3.628	3.213	0.0	177.5	20
2	7	1.720	1.455	305.0	112.5	20
6	8	2.588	2.565	1957.1	0.0	20
7	4	4.277	4.009	1834.3	0.0	20
14	3	1.265	0.247	36.3	0.0	10
15	8	0.328	0.299	0.0	542.5	10
16	7	0.770	0.690	22.5	190.0	10
17	4	0.319	0.264	0.0	61.1	10
18	2	0.264	0.207	0.0	100.0	10
22	9	1.780	1.372	0.0	81.1	20
23	9	1.197	0.928	3.3	95.0	20
24	11	1.084	1.006	5.0	278.1	20
25	14	2.010	1.695	2.5	180.0	20
27	2	1.350	1.244	2583.5	0.0	10
28	1	1.102	0.937	0.0	45.0	10
29	2	0.175	0.138	0.0	45.0	10

of *Nephtys* increased (Figure 2). Although feeding rate on large worms increased as the size of *Nephtys* in the sediment increased, the contrasting trends of feeding rate against the numerical densities of the two worm species again implies that the two worms were not treated by Redshanks as a single prey type.

Number of small worms taken per metre searched

The expectations were (1) that the number of small worms (≤ 0.50 × bill length) taken per metre searched would decrease as the biomass ingested from large worms (≥ 0.75 × bill length) per metre increased, and (2) that the rate of taking small worms would be the same in relation to variations in the density of small *Hediste* and *Nephtys* in the sediment, after the effect of environmental variables had been taken into account. As no small *Hediste* were recorded in the samples taken from 8 of the 16 site/week values, representing a total of 110 sampling cores, yet small worms were consumed in every one (Table 3), it is likely that small worms of both species were taken by Redshanks.

Territoriality had no significant effect (Table 4). The stage of the season (Day), tide (Hour) and ambient temperature (Temp) were significant, or very nearly

Table 4. Results of multiple regression analyses of the associations between feeding on small worms and (1) the biomass of large worms consumed per metre searched, the HT, and (2) three environmental variables and one social variable, the potentially confounding variables (PCVs). The regression was of $\log_{10}$(feeding rate + 1) on worms ≤ 0.50 × bill length taken per metre searched, weighted by the number of observations made in each subsite, and (1) the biomass of worms ≥ 0.75 × bill length consumed per linear metre searched, (2) $\log_{10}$(numerical Density + 1) and $\log_{10}$(mean Weight + 1) of the small polychaete worms in the sediment, where Hd = *Hediste diversicolor* and Nh = *Nephtys hombergii,* (3) the birds' social behaviour and (4) the three environmental variables Day, Hour and Temp. Model diagnostics showed acceptable fits with approximately normal residuals and no major heteroskedasticity.

Predictor	**Coefficient**	**SE**	***t***	***P***
Constant	–0.4310	0.1629	–2.65	0.010
HT:				
Biomass eaten ($\log_{10}$mgAFDM/m)	0.06025	0.01789	3.37	0.001
PCVs:				
Territorial = 1	0.000437	0.007221	0.06	0.952
Day	0.007423	0.001500	4.95	0.000
Day^2	–0.00002615	0.00000454	–5.76	0.000
Hour	–0.06408	0.02479	–2.58	0.011
Hour^2	0.004128	0.002217	1.86	0.066
Temp	0.03239	0.01714	1.89	0.062
Temp^2	–0.0006065	0.0004279	–1.42	0.160
Day × Hour	0.0004138	0.0001581	2.62	0.010
Day × Temp	–0.00018564	0.00007825	–2.37	0.020
Hour × Temp	–0.000160	0.001209	–0.13	0.895
$\log_{10}$(small*Hd*Density + 1)	–0.01597	0.01428	–1.12	0.266
$\log_{10}$(small*Hd*Weight + 1)	–0.01894	0.01551	–1.22	0.225
$\log_{10}$(small*Nh*Density + 1)	0.01455	0.02157	0.67	0.502
$\log_{10}$(small*Nh*Weight + 1)	–0.01164	0.01142	–1.02	0.311
$\log_{10}$(*Hd*Den + 1) × $\log_{10}$(*Hd*W + 1)	0.13077	0.06139	2.13	0.036
$\log_{10}$(*Nh*Den + 1) × $\log_{10}$(*Nh*W + 1)	–0.05272	0.03274	–1.61	0.111
R^2 = 71.5%				

Analysis of Variance

Source	***df***	***SS***	**MS**	***F***	***P***
Regression	17	2.14390	0.12611	13.16	0.000
Residual Error	89	0.85309	0.00959		
Total	106	2.99698			

significant, correlates of the feeding rate on small worms in at least one of the three terms – as a main effect or within an interaction term – in which each of these variables was represented. Of the worm variables, only the interaction between the density and size of *Hediste* was significantly correlated with the feeding rate on small worms. Feeding rate was significantly correlated with the biomass of large worms consumed per metre searched but, contrary to Goss-Custard (1977), positively rather than negatively (Figure 3A). And contrary to Goss-Custard (1977), the correlation between the density of small *Hediste* and feeding rate was negative not positive (Figure 3B).

DISCUSSION

Differences from the 1977 study

Goss-Custard (1977) reported early evidence that a free-living predator, Redshanks, actively selected or rejected small polychaete worms depending on whether doing so would increase its gross intake rate, measured as AFDM consumed per unit time of active foraging. The analysis related a number of foraging behaviours across 16 sites to the numerical densities and sizes of the worms in the sediment. Although a number of environmental measurements were made at the time, the small sample of sites did not allow an in-depth analysis to be carried out. Our initial intention in the present paper had been to re-analyse the data so that any effect of confounding factors on the equations used by Goss-Custard (1977) could be taken into account. That model could then have been re-parameterised and used to re-test the rate-maximising hypothesis in free-living Redshanks. In the event, that aim had to be abandoned because the analysis with the enlarged, sub-setted dataset revealed that unstated assumptions made in the model had been false. Although our results did support the assumption that the birds' social behaviour had no effect on the foraging behaviours investigated here, they were directly contrary to one of the most important assumptions made in Goss-Custard (1977), namely that the birds would respond in quantitatively identical ways to variations in the abundance and sizes of the two worm species in the sediment (Figures 1 and 2).

Our analysis also rejected a second important assumption made in Goss-Custard's (1977) paper that was also fundamental to the test of the predictions of the optimal foraging theory, namely that the rate of taking small worms would be negatively correlated with the rate of biomass consumption of large worms. The findings suggest that environmental variables confounded the site/week mean values in Goss-Custard's (1977) paper in such a way as to generate spurious associations of this critical function in the simulation model (Figure 3). This interpretation is consistent with the results of an analysis of the 107 subsite/day data that was done as a direct comparison with that made by Goss-Custard (1977). A linear regression was carried out using the transformed data of the numbers of small worms taken per metre searched against just two independent variables: (1) the biomass ingested per metre from large worms and (2) the combined numerical density of small (≤ 0.5 bill length) *Hediste* and *Nephtys*. The coefficient for the biomass consumption of large worms was negative and significant and that for the worm density was positive and also significant (Table S1A), as had been found in the original site/week-based analysis in Goss-Custard (1977). But adding the three environmental variables of Day, Hour and Temp to this equation reversed this result: the effect of the biomass of large worms ingested on the feeding rate on small worms now became positive and significant and that for the density of small prey negative, though just failing to reach an accepted level of significance (Table S1B). The percentage of the small worms that comprised *Hediste* was not-significant (Table S1B) which is consistent with the assumption made earlier in this paper that small individuals of both species were probably taken by Redshanks. Our conclusion is that the results in this paper are consistent with the notion that the negative association between feeding rate on small worms and the biomass ingested from large worms obtained by Goss-Custard (1977) arose because of the confounding influence of the environmental effects of seasonal and within-day variation and ambient temperature.

Negative effect of *Nephtys* density and size on intake rate

Intake rate increased as the numerical density of *Hediste* increased, following the type-II functional response curve (Holling 1959). Intake rate also increased as the mean size of *Hediste* in the sediment increased, although the rate of increase slowed down as worm size increased, perhaps reflecting the tendency of large worms to bury themselves deeper in the sediment than small ones and thus to be below the depth at which a Redshank can reach them (Esselink & Zwarts 1989a,b). Redshanks appeared to detect worms when they were at, or very near to, the surface of the sediment. Accordingly, the change in intake rate through the autumn (August to December), with the ambient temperature and the stage of the tidal exposure period

can be understood as a result of worms changing their behaviour in response to these environmental conditions. For example, the increase in intake rate through the exposure period may reflect an increasing tendency as the length of time spent in the burrows increased for *Hediste* to move to the surface to expel accumulating waste products or to forage.

On the assumption that Redshanks took *Nephtys* as readily as they take *Hediste*, we expected that intake rate would increase as the numerical density and mean size of this worm in the sediment increased, as it did with *Hediste*. But to our great surprise, intake rate decreased as *Nephtys* density increased, opposite to the trend in *Hediste*. If Redshanks do indeed consume *Nephtys*, as was indicated by their consumption of small worms in subsites where no small *Hediste* were found in the sediment, the negative effect on intake rate of the increasing abundance of large *Nephtys* was a wholly unexpected result. The finding that intake rate increased as the size of *Nephtys* in the sediment increased may imply that some of these worms are eaten but currently there is no direct evidence of this (Evy Gobbens and Steph Trapp pers. comm.). But whether or not Redshank do ever eat large *Nephtys*, there is still a need to explain why the presence of these worms in the sediment was associated with a decrease in the overall intake rate of Redshanks.

We cannot rule out the possibility that unknown sediment features that made a site suitable for *Nephtys* affected the behaviour of *Hediste* in ways that made it less detectable or accessible to Redshanks: sediment characteristics are of great significance in the natural history of both these species of polychaete worms (Davey & George 1986). However, there are reasons for thinking that *Nephtys* itself may have affected the behaviour of *Hediste* in ways that reduced its availability to Redshanks. *Nephtys* is a predator of *Hediste* and can take worms of a size (c. 100 mg DW) often eaten by Redshanks (Desroy *et al.* 1998). Our observations suggested that Redshanks took *Hediste* from at or near to the surface of the sediment and probably detected them by sight rather than by locating them by touch at depth in the sediment. *Nephtys* search for prey in the upper five centimetres of the sediment (Clavier 1981, Desroy *et al.* 1998) and thus mainly in the range that can be reached by the 4 cm long bill of Redshanks. Where both polychaetes occur together, *Hediste* is known to escape from *Nephtys* by emigrating sideways (Desroy *et al.*1998). If *Hediste* can also avoid *Nephtys* by moving deeper into their burrows below a depth of five centimetres, this anti-predator response would put them out of reach of Redshanks, thereby reducing the numerical density of accessible *Hediste* and thereby the birds' intake rates. The very sharp decrease in intake rate at low densities of *Nephtys* (Figure 1) may reflect a high sensitivity of *Hediste* to the presence of an important predator. And if Redshanks do sometimes eat large *Nephtys*, it would benefit the birds in two ways: (1) by increasing their immediate intake rate, and (2) by reducing the abundance of a predatory worm that not only depletes an important prey species for Redshanks, *Hediste*, but also makes that important food supply less accessible and so available to them. In other words, a combined exploitation and interference competitor.

Our hypothesis yields predictions that can be tested both in the field and laboratory. *Nephtys* have hard parts that can be detected in pellets and faeces (Goss-Custard *et al.* 1977, Durell & Kelly 1990, Scheiffarth 2001). Accordingly, (1) where Dunlins, Bar-tailed Godwits and, if they ever do, Redshanks, take *Nephtys*, they would be expected to be catching prey by tactile means from within the sediment and not from the surface, and (2) Redshanks might be most likely to take *Nephtys* at night when they often use tactile means to detect buried prey (Goss-Custard 1969, Shemmings-Payne 2025). Laboratory and field experiments could test whether (1) *Nephtys* seldom if ever occur at the surface where they could be detected by visually searching birds, and (2) *Hediste* do indeed respond to the presence of *Nephtys* by descending deeper into the sediment and not just by moving sideways, as reported by Desroy *et al.* (1998).

Intake rate maximizing research since 1977

Although Goss-Custard's (1977) particular test of the predictions of optimal foraging theory carried out on prey selection by Redshanks is now known to have been spuriously successful, the notions of 'rate-maximising foraging' and the associated concept of 'prey profitability' have become widely tested and used in a number of areas of shorebird research although as only one aspect of a much broader conceptual framework (Stephens *et al.* 2008). Essentially, the birds are believed to make foraging decisions that maximise their intake rate unless doing so decreases their chances of survival and/or reproduction caused by some other aspect of their natural history. For example, large Common Cockles *Cerastoderma edule* are potentially more profitable to Eurasian Oystercatchers *Haematopus ostralegus* than medium-sized ones but are usually rejected because breaking into them risks damaging the bird's bill and thus its future chances of survival (Rutten *et al.* 2006). Comparable threats to fitness arise from other mortality agents which may deter the most

profitable prey and feeding sites from being selected. Only when a shorebird is seriously threatened by starvation is it thought likely to risk exposing itself to such threats to its fitness. Risk agents involved in these 'trade-off' foraging decisions include parasites (Norris 1999), predators (Whitfield 2003, Cresswell & Quinn 2004, Dekker & Ydenburg 2004, Mindermann *et al.* 2006, Pomeroy 2006, van den Hout *et al.* 2014), digestive constraints (van Gils *et al.* 2005) and even heat stress (Gutierrez 2023). These and other comparable studies have confirmed that the concept of rate maximising in foraging shorebirds has been of great utility in taking forward our understanding of shorebirds as well as many other animals (Stephens *et al.* 2008).

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SAMENVATTING

In de jaren zeventig van de vorige eeuw ontwikkelde Goss-Custard (1977) een empirisch model om de hypothese te toetsen dat in het wild levende Tureluurs *Tringa totanus* die grootteklassen van prooien selecteren die de voedselopname maximaliseren. Modelparameters werden geschat tijdens de winters van 1969/70, 1970/71 en 1971/72 bij Tureluurs die foerageerden op 16 wadplaten met twee soorten borstelwormen, de Zager *Hediste diversicolor* en de Zandzager *Nephtys hombergii*. De voorspellingen van het model kwamen overeen met de voorspellingen van de hypothese. Vervolgonderzoek toonde echter aan dat omgevingsfactoren, met name het seizoen, het getij en de omgevingstemperatuur, het gedrag van de wormen en hun beschikbaarheid voor steltlopers, waaronder Tureluurs, beïnvloeden. Onze oorspronkelijke bedoeling was om door middel van multivariate analyse te toetsen of het meenemen van deze potentieel verstorende variabelen de modelparameterwaarden en daarmee de voorspellingen significant zou veranderen bij het toetsen van de hypothese van een maximale voedselopname. De analyse bracht niet alleen aan het licht dat de parameterwaarden aanzienlijk waren veranderd, maar ook dat belangrijke impliciete aannames in het model onjuist waren. Wellicht het meest fatale effect voor het model was dat de reacties van de Tureluurs op variaties in de talrijkheid van de twee soorten borstelwormen zo verschillend zijn dat de twee soorten niet kunnen worden samengenomen als één voedselbron voor de vogels, zoals eerder werd aangenomen. Tot onze grote verbazing nam de voedselopname af naarmate de numerieke dichtheid van *Nephtys* toenam, precies het tegenovergestelde van de type II functionele respons die werd gevonden bij *Hediste*, de bekende prooisoort van de Tureluurs. *Nephtys* is nu bekend als een belangrijke predator van *Hediste*. We veronderstellen dat *Hediste* mogelijk *Nephtys* vermijdt door zich dieper in hun gangen terug te trekken, tot een diepte van meer dan 5 cm, een anti-predatorreactie die hen buiten het bereik van de 4-cm lange snavel van de Tureluurs zou brengen. Dit zou de numerieke dichtheid van bereikbare *Hediste*, en daarmee ook de voedselopname van de vogels, kunnen verminderen wanneer *Nephtys* aanwezig is.

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SUPPLEMENTARY MATERIAL

Table S1. Correlates of the feeding rate (worms/m searched) on small worms (≤ 0.50 × bill length) in the multiple regression analysis of $\log_{10}$(feeding rate + 1) (worms taken per metre searched), weighted by the number of observations made in each subsite, and (A) the biomass of large worms (≥ 0.75 × bill length) consumed per metre searched ($\log_{10}$AFDM/m) and the $\log_{10}$(numerical Density + 1) of small worms of both species combined, and (B) the biomass of large worms (≥ 0.75 × bill length) consumed per metre searched ($\log_{10}$AFDM/m), the $\log_{10}$(numerical Density + 1) of small worms of both species combined, the percentage of these small worms that were *H. diversicolor* and the three environmental variables Day, Hour and Temp.

(A)

Predictor	**Coefficient**	**SE**	***t***	***P***
Constant	0.058153	0.008435	6.94	0.000
Biomass eaten ($\log_{10}$AFDM/m)	–0.03910	0.01649	–2.37	0.020
$\log_{10}$(smallHd+NhDensity + 1)	0.013624	0.002892	4.71	0.000
R^2 = 0.198				

Analysis of Variance

Source	***df***	**SS**	**MS**	***F***	***P***
Regression	2	0.59326	0.29663	12.83	0.000
Residual Error	104	2.40373	0.02311		
Total	106	2.99698			

(B)

Predictor	**Coefficient**	**SE**	***t***	***P***
Constant	–0.4504	0.1481	–3.04	0.003
Biomass eaten ($\log_{10}$mgAFDM/m)	0.04475	0.01600	2.80	0.006
$\log_{10}$(small*Hd*+*Nh*Density + 1)	–0.015985	0.008716	–1.83	0.070
% small worms *H. diversicolor*	0.0003846	0.0003136	1.23	0.223
Day	0.007306	0.001393	5.25	0.000
Day^2	–0.00002424	0.00000461	–5.26	0.000
Hour	–0.06736	0.02553	–2.64	0.010
Hour^2	0.005700	0.002262	2.52	0.013
Temp	0.04054	0.01473	2.75	0.007
Temp^2	–0.0007634	0.0003793	–2.01	0.047
Day × Hour	0.0003742	0.0001676	2.23	0.028
Day × Temp	–0.00023768	0.00007391	–3.22	0.002
Hour × Temp	–0.000518	0.001268	–0.41	0.684
R^2 = 67.1%				

Analysis of Variance

Source	***df***	**SS**	**MS**	***F***	***P***
Regression	12	1.97124	0.16427	15.05	0.000
Residual Error	94	1.02574	0.01091		
Total	106	2.99698			