THE SEARCHING BEHAVIOUR OF FORAGING REDSHANKS
TRINGA TOTANUS L.

by John Speakman

Introduction

In winter, non-territorial foraging waders usually congregate in areas where their net energy gain rate is greatest (e.g. Bryant 1979). This paper presents some preliminary data concerning the behavioural mechanisms used by waders, in particular Redshanks Tringa totanus L., to remain in favourable areas.

Net rate of energy gain is difficult to measure, and correlating behavioural mechanisms with it, even more so. I attempted, therefore, to establish if a single factor had a major influence on net gain, and hence feeding distribution. Many factors can influence net gain. In many situations a major factor is the density of the prey. In the Knot Calidris canutus, for example, feeding on the mid-estuarine Firth of Forth, Scotland, 98% of the variability in the number of hours spent feeding per tide was explained by variation in the density of the major prey item – a small gastropod mollusc Hydrobia ulvae (Warnes 1981). However, in some situations, other factors are more important and a simple response to density is not found. For example, Sutherland (1982) found size variation in cockles Cerastoderma edule was an important factor influencing the energy gain, and foraging distribution, of Oystercatchers Haematopus ostralegus, on Anglesey, Wales. In this paper I show first that prey density is an important factor influencing the feeding distribution of the Redshank at the study site, and then examine the behavioural mechanisms used by Redshanks to remain in areas of high prey density.

Three potential mechanisms were considered. These were: A) Klinotaxis – walking faster in unfavourable areas. Although this results in birds generally remaining in areas of high density, walking has, like any other behaviour, an energetic cost, and walking faster has a greater cost than walking slower (Fedak et al. 1974). As intake depends on density, a bird performing a klinotaxis encounters its greatest energy demand (i.e. it walks fastest) when it can least afford it. Theoretical models have been developed which suggest that to maximise the net rate of energy gain an animal should only use the high-cost search methods when prey density is high, and use low-cost methods when the density is low (Evans 1976, Norberg 1977, Krebs 1978). B) Klinokinesis – turning more in favourable conditions. C) the Variation response. Both Klinotaxis and Klinokinesis are relatively simple as they involve response only to the absolute level of density at any one time. A bird may, however, integrate information over a longer time-span and respond to changes in density. Such a bird should turn as it encounters a decrease in density but maintain direction at constant or increasing density.

Methods

Diet Choice. Observations were made, from a hide on the edge of the mudflat, of Redshanks foraging in four separate 100m x 100m squares, at Skinflats (NS 924869) on the mid-estuarine Firth of Forth, using a Swift 20 – 60x telescope. The majority of birds were within 50m when observed. At these distances, prey items could be separated into five classes: small and large Macoma balthica a bivalve mollusc; small and large Nereis diversicolor a polycheate worm; and small items, which appeared to be either Hydrobia ulvae or Corophium volutator, an amphipod crustacean. Each observation period lasted for approximately thirty seconds. In each period the total number of each class ingested was recorded.

Pellets ejected by Redshanks at roost at Skinflats were collected. Evidence of all four of the prey species can be found by microscopic analysis of pellets which have been broken up in water. Presence in the diet was identified by whole shells and terminal whorls of Hydrobia, terminal segments of the peripods of Corophium, jaws of Nereis, and shell fragments of Macoma.

Predator responses to prey density. The northern end of Skinflats was divided into 100m x 100m squares and sampling stations were established at the intersections of the squares (n = 22). At each site, four mud samples 5 x 5 x 10cm. deep were collected. Also, at each site between 15 and 50, 50 x 50cm quadrats were thrown at random. In each quadrat the total number of Redshank footprints were counted (total n thrown = 530). In the laboratory, the mud samples were sieved through a 300µ sieve and all the animals retained were identified and counted.

Klinotaxis. Individual Redshanks were observed foraging in 100m x 100m areas at Skinflats from the hide. In each observation period of about 30s, the number of paces, the number of items ingested, and the duration were recorded. Only periods where exclusively small prey items were ingested were included in this analysis. In the same areas, measurements were made of stride length of Redshanks (n = 170) from footprints in the mud.

Klinokinesis/Variation response. Search paths were randomly located on surface of the mudflats at the northern end of Skinflats, within four hours of emersion, on two tides. A metre rule was placed from the apex of a randomly selected print through the apex of the next print made by the same foot (Figure 1), and the distance Xcm was measured. This distance is related to the angularity of the path (A°) by the equation TAN A° = X/100. Over the range considered this is almost linear. The surface density of Hydrobia at the 0, 50 and 100cm marks on the rule was estimated using a 5 x 5 cm quadrat.
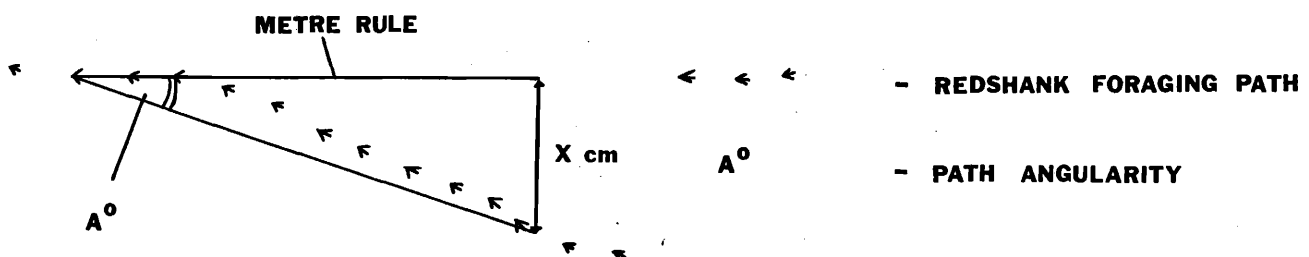

METRE RULE

X cm   A°   – REDSHANK FORAGING PATH

A°   – PATH ANGULARITY

Figure 1. Measurements made on a sample foraging path.

Results

Diet Choice. An example of the direct observation data, for November 1981, is shown in Table 1. At all four sites the major prey were 'small items'. In total, over 90% of the diet was of small items, probably Hydrobia or Corophium. Similar results were found throughout the whole winter period. The analysis of 16 pellets is shown in Table 2. Over 50% of the pellets contained Corophium and over 60% Hydrobia. Only one pellet had no evidence of either. This supports the direct observation that these items constituted numerically the major prey.

Table 1. Diet choice of Redshanks at four 100 x 100m. squares at Skinflats, in November 1981. Figures give the number of each prey type taken.

Site	Small items	Macoma		Nereis	
		Small	Large	Small	Large
1	255	7	12	1	0
2	205	19	11	1	1
3	243	10	24	1	0
4	435	15	1	0	1
Total	1138	51	48	3	2
%	91.6	4.1	3.9	0.2	0.2

Table 2. Microscopic analysis of sixteen pellets collected on the roost site. X indicates some evidence of presence.

Pellet No.	Hydrobia	Corophium	Macoma	Nereis
1	X	X		
2		X		
3	X	X		
4		X		
5		X	X	
6		X		
7	X	X		
8	X	X		
9	X			
10		X		
11	X		X	
12	X			
13	X			
14	X			
15	X			
16				
Total	10	9	2	0
% occurrence	62.5	56.25	12.5	0

Predator responses to prey density. The mean number of footprints per m^2 plotted against the combined density of Hydrobia and Corophium per m^2 at the 22 sites at the northern end of Skinflats is shown in Figure 2. The significant linear regression (F = 6.36, p < .05) shows that the foraging intensity increased with increased prey density.

Klinotaxis. I have assumed that all, or a constant proportion, of Hydrobia and Corophium encountered were ingested. Hence intake per metre walked was a direct measure of prey availability. If the birds did not take a constant proportion, but became more selective as availability increased, the relationship of intake per metre walked to prey availability may be non-linear, but would be expected to remain positive. The distance walked was estimated as the number of paces multiplied by the mean pace length at the site (11.2cm). From studies on captive Redshank (my own unpublished data), it is known pacing rate is directly related to walking speed. Walking speed was therefore calculated from pacing rate using a predictive equation. The walking speed plotted against prey availability is shown in Figure 3. There was a significant non-linear negative relationship (F = 363.4, p < .005) i.e. Redshanks walked more slowly where prey availability was high. Although small items are ingested simultaneously to walking, it is possible that the ingestion retards walking speed (Goss Custard and Rothery 1976). Walking speed was corrected for the time spent in handling behaviour, by subtracting the time spent in handling activity (n items ingested x $\bar{x}$ handling time (0.35s)) from the total time. The corrected walking speed plotted against prey availability is shown in Figure 4. The significant negative relationship (F = 63.78, p < .005) remained.

Klinokinesis. The angularity of the search path (Xcm) plotted against mean prey availability (the mean of the three 5 cm x 5 cm quadrat estimates) is shown in Figure 5. There was a significant linear positive relationship (F = 50.6, p < .01), such that birds turned more when the prey density was high.

Variation response. The difference between the mean of the first two availability estimates and the third estimate was used as a measure of the change in prey availability. The angularity plotted against the change in availability is shown in Figure 6. There was a significant curvilinear response (F = 46.9, p < .01). This means that Redshanks turned most when the increases and decreases in prey density were largest.

Discussion

Predator response to prey density. Redshank did appear to feed more where the preferred prey (Hydrobia ulvae and Corophium volutator) were more dense at the study site. The large variability in the response may be a consequence of the prey density measure not adequately reflecting the prey availability. Availability may differ between sites due to such features as differential drying of the substrate.
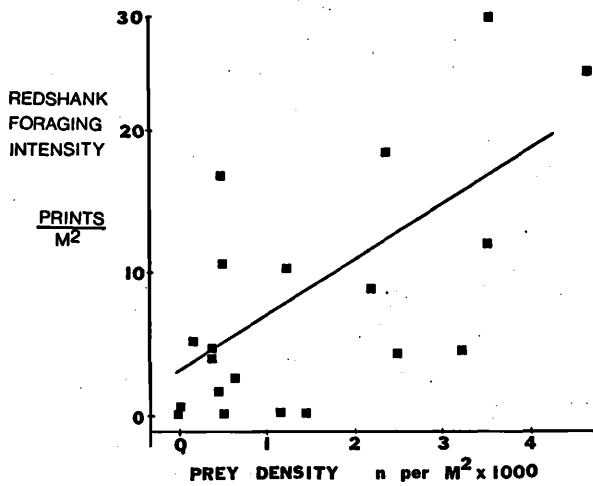
Figure 2. The foraging intensity of Redshanks plotted
against the density of their major prey.
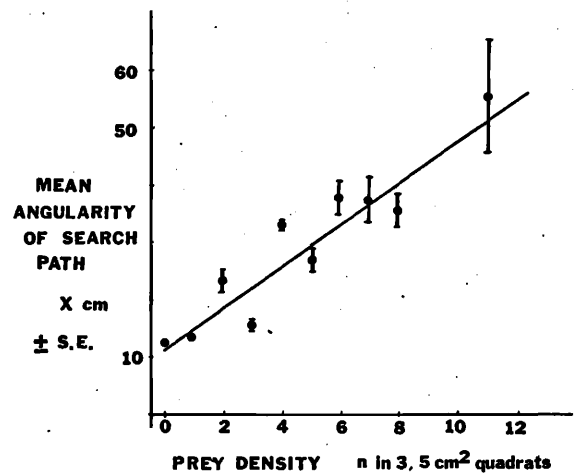$y = 3.77 + 3.17x$, $r = 0.419$, $n = 23$.

Figure 5. The angularity of the search path
plotted against prey availability.
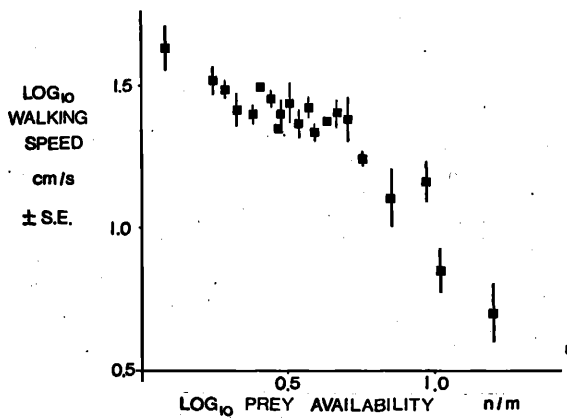$y = 11.6 + 3.62x$, $r = 0.929$, $n = 173$.

Figure 3. The walking speed of Redshanks plotted
against prey availability.
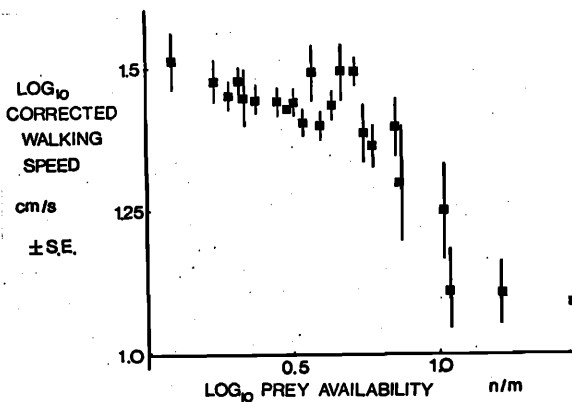$y = 1.58 - 0.55x$, $r = -0.802$, $n = 227$.

Figure 4. The corrected walking speed of Redshanks
plotted against prey availability.
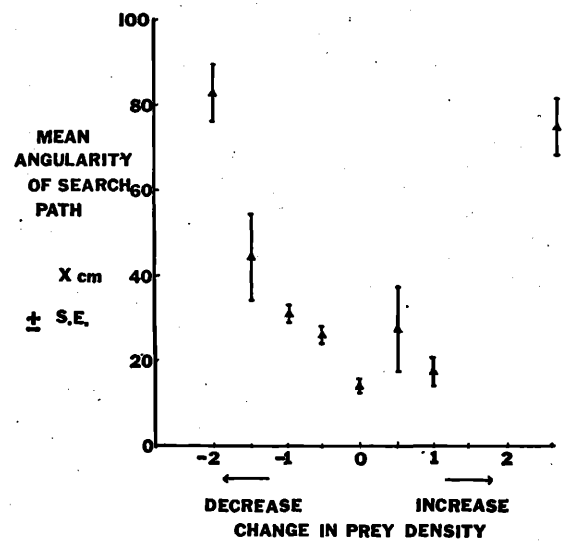$y = 1.59 - 0.31x$, $r = -0.471$, $n = 227$.

Figure 6. Angularity of the search path plotted
against change in prey availability.
$y = 19.1 + 6.64 \ x^2$, $r = 0.465$, $n = 173$.

Klinotaxis. Observed changes in the corrected walking speed (Figure 4) support the hypothesis that the birds perform
a klinotaxis. This refutes the 'optimal foraging' prediction. Redshanks fed sub-optimally in low prey density areas
because this resulted in a faster return to the high prey density areas. Over the short time-scale that the birds
spend in the low prey density areas they may have a lower net gain than they are capable of achieving. However, the
increased time spent in high prey density areas more than offsets this loss, so that in the time-span of a whole
tidal cycle the birds attain an overall greater net gain. It is most probable that the time scale of the whole
tidal cycle is more important than a shorter period, as regards the birds survival. This emphasizes the importance
of time-scales in 'optimal foraging' models.

Klinokinesis/ Variation response. Redshanks appear also to demonstrate a klinokinesis (Figure 5). However I could
not show that the birds exhibit a variation response since they turned more with both decreases (supports prediction)
and increases (contra prediction) in availability. Large changes in availability only occur at overall greater prey
availabilities. The result is therefore a reflection of the klinokinesis. It is possible, however, that the birds
integrate information over a longer or shorter distance than was used in this study. Consequently, a variation
response cannot be rejected until more data are available on the time-scale over which birds integrate information.

Acknowledgements

References

Bryant,D.M. 1979. Effects of prey density and site character on estuarine usage by overwintering waders (Charadrii). Est. Coast. Mar. Sci. 9: 369-384.

Evans,P.R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distribution in the non-breeding season. Ardea 64: 117-139.

Fedak,M.A., Pinshow,B. & Schmidt-Nielson,K. 1974. Energetic cost of bi-pedal running. Am. J. Physiol. 227: 1038-1044.

Goss Custard,J.D. & Rothery,P. 1976. A method for measuring some components of foraging of certain birds in the field. Anim. Behav. 24: 545-550.

Krebs,J.R. 1978. In Behavioural ecology - an evolutionary approach. Krebs,J.R. & Davies,N.B. (Eds.) Oxford, Blackwell Scientific Publications.

Norberg,R.A. 1977. An ecological theory on foraging time and energetics and choice of the optimal food searching method. J. Anim. Ecol. 46: 511-529.

Sutherland,W.J. 1982b. Spatial variation in the predation of cockles by Oystercatchers at Traeth Melynog, Anglesey. II. The pattern of mortality. J. Anim. Ecol. 51: 491-501.

Warnes,J.M. 1981. The impact of overwintering birds on the production ecology of estuarine benthic invertebrates. Ph.D.Thesis, University of Stirling.

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WADER STUDIES IN THE USSR
by Rob Fuller

The choice of Moscow State University as the venue for the XVIII International Ornithological Congress provided a rare chance to learn something about current research on waders in the Soviet Union. The University occupies an imposing position on the Lenin Hills overlooking the city. For six days in August last year, the Congress took over a large part of the ground floor of this massive, spectacular, building.

Surprisingly few papers in the formal sessions focussed on waders. However, vast amounts of free time between these sessions, and an impromptu Round-Table-Discussion on waders gave plenty of opportunities to hear at first hand from Soviet workers. Despite its immensity, the Soviet Union holds very few wintering populations of significance, so breeding studies, with a smattering of work on migrating waders, are prevalent. There is no large-scale programme of co-ordinated research on waders; the most interesting work is being carried out by a handful of predominantly professional wader specialists. Increasing interest in wader studies is reflected in the organization of special symposia in 1973 and 1979. The proceedings of the last meeting were published in 1980 (see Recent Publications on Waders in WSG Bulletin No.30) and the titles give an insight into the range of contemporary work on waders in the Soviet Union.

Regular trapping of migrant waders is carried out at several localities in Kazakhstan under the direction of Dr. E. Gavrilov. The emphasis seems to be on ringing (metal rings) and collection of biometric and moult data. Breeding studies on a variety of species are employing other marking methods, ranging from leg flags to the rather more unconventional use of neck bands and triangular breast plates.

Particularly interesting is the research of P. S. Tomkovich who has worked on several arctic study sites including the extreme north-eastern point of USSR (Chukotski peninsula), and the Taimyr peninsula. He presented a poster paper on "Territoriality of some monogamous species of Calidridinae Sandpipers" based on work carried out at Chukotski between 1978 and 1980. In this region, four monogamous Calidris species are common breeders on the tundra: Rock Sandpiper Calidris ptilocnemis, Dunlin C.alpina, Red-necked Stint C.ruficollis and Western Sandpiper C.mauri. By observing both colour-ringed and unmarked individuals, and by mapping territory boundaries, Tomkovich discerned two distinct types of territorial systems amongst these waders. The main features of the two systems are summarised below, and are taken directly from the paper, with the permission of the author.

Type 1	Type 2
1. Displayed by C.ptilocnemis and C.alpina.	1. Displayed by C.ruficollis and C.mauri.
2. Strong site tenacity with many pairs reuniting.	2. Weak site tenacity; reuniting not recorded.
3. Usually only small changes in territory occurred during the breeding season. But ptilocnemis sometimes established a temporary territory before appearance of snow-free patches at its former territory site.	3. Territories of unmated males were temporary and existed for a few days only. Pairs settled at (or close to) the male's territory and at this time the male defended only some space around the female.
4. In the event of adverse weather before egg-laying, there was a temporary breakdown of the territorial dispersion and a re-appearance of small flocks. When the weather improved, birds re-established their territories.	4. In the event of adverse weather before egg-laying, the unmated males could be forced to leave the unfavourable region. When the weather improved, males (probably new birds) appeared in different places.

For several of us, the Congress was rounded off quite splendidly by an (unofficial) visit to an enormous sewage works in the south of the city. This was an experience long to be cherished. At least 15 species of waders were seen on the endless rows of settling beds. Ruff Philomachus pugnax predominated but Marsh Sandpiper Tringa stagnatilis and Wood Sandpiper Tringa glareola were also amongst the commoner species. It seemed that this place was seldom visited by Russian ornithologists, yet in Britain it would have rated as an inland wetland of very major importance.

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