SHOREBIRD FOOD HABITS IN THE EASTERN CANADIAN ARCTIC

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This report compares food habits among shorebirds of ten species breeding near Fort Churchill, Manitoba, Canada. Nutrition may be the most critical niche dimension for birds (see Hespenheide 1973), yet dietary studies on a community-wide basis are rarely encountered. The reports of Ashmole and Ashmole (1967) and of Holmes and Pitelka (1968) are important exceptions.

Ecological segregation along behavioral and structural niche dimensions has been documented for six species of this shorebird community (Baker and Baker 1973). Here, I examine the community from the point of view of the relationships between shorebird body size and food size. I also consider the degree of species distinctness along the food size parameter of the niche in relation to the theory of species packing. Data on food size and body size are examined in view of the hypothesis that larger species of shorebirds consume larger average prey and are more selective foragers than small species (Baker and Baker 1973). The hypothesis resulted from the discovery that within a community of six species, the heavier species foraged more slowly (number of prey capture attempts per unit time). To maintain a caloric intake higher than that required by a smaller species (Nice 1938), larger shorebirds may select larger food items and thus may require more time to find each item in the array of food items of different size.

METHODS

Shorebirds and their prey populations were studied in breeding habitats near Fort Churchill, Manitoba, Canada (58°45′N, 94°00′W). Stomachs of individuals of 10 of the 12 most common species breeding were collected by R. L. Zusi in 1967 and by me in 1968–69 (table 1). Species included are: Lesser Yellowlegs (*Tringa flavipes*), Northern Phalarope (*Lobipes lobatus*), Short-billed Dowitcher (*Limnodromus griseus*), Stilt Sandpiper (*Micropalama himantopus*), Least Sandpiper (*Calidris minutilla*), Dunlin (*Calidris alpina*), Semipalmated Sandpiper (*Calidris pusilla*), Hudsonian Godwit (*Limosa haemastica*), Golden Plover (*Pluvialis dominica*), and Semipalmated Plover (*Charadrius semipalmatus*). Approximately equal numbers of males and females made up the sample for each species. Sixty-five percent of the specimens were collected in June, 25% in July, and 5% each in May and August. The content of each stomach was examined with a binocular dissecting microscope fitted with an ocular measuring scale. Food types were divided into 20 categories on the basis of taxonomic affiliations (table 2). In all, 7,253 items were identified and their lengths measured. I found little digestion of stomach contents. One reason for this is that I collected individuals that I watched foraging for a period of time, and so each bird had a freshly-caught complement of food. Secondly, viscera of birds I collected were injected immediately with formalin and the stomachs removed and preserved within an hour. I found no differences between the contents of stomachs I collected and those collected by Zusi, although he did not preserve them as soon as I did.

In 1968–69, I sampled the prey in foraging habitats using three techniques. An insect net 30 cm in diameter with a 1 mm mesh was swept 50 times through emergent vegetation and standing water along edges of meltwater ponds and channels or through dry vegetation. Forty-six 50-sweep samples were collected. Twenty-three mud samples, 25 × 25 × 3 cm deep were collected from marl flats (muskeg, pond porridge). Ten sod samples, 25 × 25 × 5 cm deep, were cut out of dry tundra surface. All samples were from microhabitats used by foraging shorebirds. In all but a few instances, they were taken from the habitat where the birds were foraging after the bird was collected for stomach analysis. Mud and sod samples were sieved with a screen of 1 mm mesh, then samples were hand sorted under the dissecting microscope. Food items were so abundant that I doubt that the foraging bird significantly altered availability, but I have no controls for this.

The 79 habitat samples yielded 15,546 items of the categories and sizes found in the stomachs. Items outside the size range or food categories were not considered. Excluded were 30 small fish, 18 tadpoles, and 1 leech, none of which were represented in any stomach. Large snails accounted for most of the exclusions made because of size.

RESULTS

TAXONOMIC CATEGORIES OF FOOD EATEN

Each species uses about 10 food categories (fig. 1, table 2). Short-billed Dowitchers and Golden Plovers eat substantial numbers of seeds, but obtain them differently. Dowitchers usually probe deep into the ground whereas plovers typically peck from the surface. Morphologically the seeds used by the two species were the same. I believe that two somewhat distinct resources are created from the seeds of the same plant depending on whether they fall on a hard dry surface or into wet mud and sedge microenvironments.

Larval chironomids, tipulids, and dolichopodids are common in the diets of Stilt Sandpiper, Dunlin, Semipalmated Plover, Lesser Yellowlegs, Least Sandpiper, and Semipalmated Sandpiper, but seldom does any one of

TABLE 1. Numbers of food items found in stomachs of shorebirds.

Species	Number stomachs collected Zusi (1967)	 Baker (1968–69)	No. food items
Dunlin	13	16	387
Least Sandpiper	15	18	967
Semipalmated Plover	12	21	1,098
Golden Plover	6	7	1,100
Northern Phalarope	14	10	996
Lesser Yellowlegs	15	17	260
Short-billed Dowitcher	13	11	740
Semipalmated Sandpiper	10	23	748
Stilt Sandpiper	12	10	259
Hudsonian Godwit	6	6	698
Total	116	139	7,253

these birds eat all three larval forms with great frequency. Diptera larvae of the Cyclorrapha group predominate in Hudsonian Godwit stomachs. Northern Phalarope eat heavily on adult chironomids. In summary, the prey taken by the shorebird species overlap substantially, but some notable foci of specialization exist in diets when each species is examined individually.

BODY SIZE AND FOOD SIZE

Data presented elsewhere (Baker and Baker 1973) suggested that larger shorebirds take fewer items per unit time than smaller ones. This led to the prediction that larger species may select larger food, because they require more food. A large bird could simply spend more time foraging and harvest all its energy from small items, but in my experience the time budgets for all the species appear roughly similar.

TABLE 2. Prey identified from the stomachs of ten species of shorebirds.

Identification	Category no.
Dipteran eggs	1
Plant seeds	2
Chironomidae, larvae (Diptera)	3
Tipulidae, larvae (Diptera)	4
Dolichopodidae, larvae (Diptera)	5
Cyclorrapha, larvae (Diptera)	6
Chironomidae, adult (Diptera)	7
Unidentified snails	8
Chrysomelidae, *Donacia* adult (Coleoptera)	9
Unidentified spiders	10
Muscidae, *Lispe* larvae (Diptera)	11
Ceratopogonidae, larvae (Diptera)	12
Dytiscidae, *Agabus* larvae (Coleoptera)	13
Tipulidae, adult (Diptera)	14
Psychodidae, *Pericoma* larvae (Diptera)	15
Unidentified adult Coleoptera	16
Dytiscidae, Hyrgotus adult (Coleoptera)	17
Unidentified larval Diptera	18
Chrysomelidae, *Donacia* larvae (Coleoptera)	19
Misc. Tipulidae, Ephydridae, Gyrinidae, Syrphidae, Trichoptera, and Homoptera	20

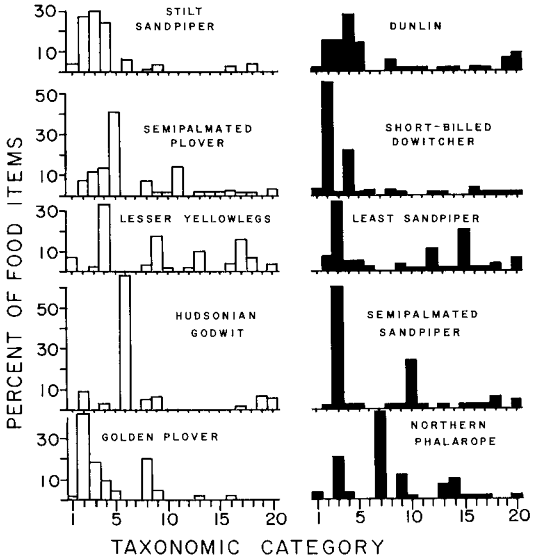

FIGURE 1. Frequency histograms of food categories utilized by ten species of shorebirds. Category numbers correspond to those in table 2.

Size frequency distributions of the foods eaten by shorebirds of the ten species are given in figure 2. Distributions for several of the species, such as Lesser Yellowlegs, tend to be bimodal, independent of the sex of the bird. Bimodality may reflect some relationship between size and taxonomic identity of food items as pointed out by Hespenheide (1973). For example, in the Golden Plover, the smaller food items are seeds and the larger ones are mostly snails. Diets of the remaining species did not follow such a simple pattern. In most instances, modal food size comprised a diverse array of taxa.

I calculated correlation coefficients between

TABLE 3. Spearman rank correlation data for size of shorebirds and prey.

Species	Rank body[a] weight	Rank prey length Mean	 Median	 Mode
Hudsonian Godwit	1	6	3	4
Golden Plover	2	3	6	6
Short-billed Dowitcher	3	1	1	1.5
Lesser Yellowlegs	4	2	2	1.5
Stilt Sandpiper	5	5	7	8
Dunlin	6	4	4	4
Semipalmated Plover	7	7	5	4
Northern Phalarope	8	8	9	10
Semipalmated Sandpiper	9	9	8	8
Least Sandpiper	10	10	10	8

[a] Body weight vs. median, Spearman $r_s = 0.75$, $P < 0.01$. Body weight vs. mean, Spearman $r_s = 0.77$, $P < 0.01$. Body weight vs. mode, Spearman $r_s = 0.60$, $P < 0.05$.

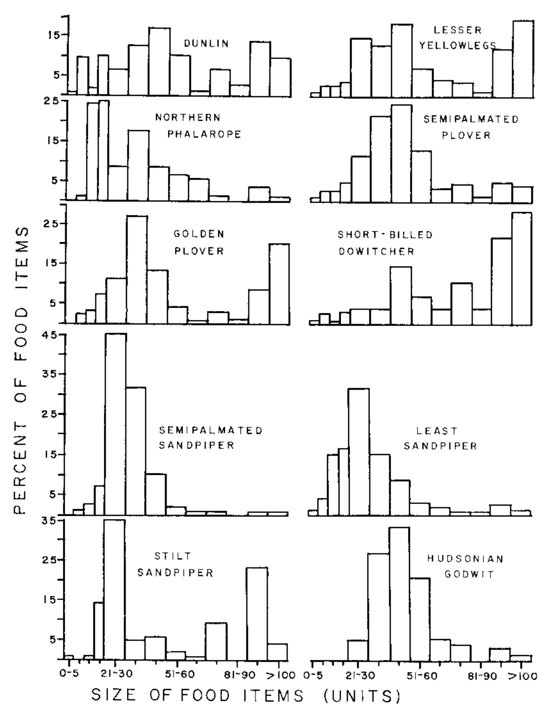

FIGURE 2. Size-frequency histograms of foods utilized by ten species of shorebirds. The widths of the histogram bars correspond to the size range of prey. This scaling was done to provide more detail on the small food sizes. Each unit on the abscissa equals 0.105 mm in body length.

TABLE 4. Body weight, coefficient of variation (CV) of food size, diversity of food size (H)[a], and indices of selectivity (IS)[b] for 10 species of shorebirds.

Species	x̄ Body[c] wt. (g)	CV	H	IS (%)
Least Sandpiper	24.3	68.9	0.765	84.5
Semipalmated Sandpiper	28.1	34.9	0.597	27.2
Northern Phalarope	35.2	67.4	0.837	76.7
Semipalmated Plover	48.1	54.9	0.845	39.7
Dunlin	57.7	68.1	0.909	64.1
Stilt Sandpiper	59.5	64.5	0.756	36.4
Lesser Yellowlegs	89.4	65.6	0.864	42.9
Short-billed Dowitcher	106.3	47.5	0.847	19.9
Golden Plover	152.8	50.7	0.832	29.5
Hudsonian Godwit	243.1	36.0	0.799	24.3

[a] $H = H'/H_{max}$, $H' = -\Sigma p_i \ln p_i$, p_i = proportion of food in i^{th} category.

[b] Area under the histogram of available food covered by plus and minus one standard deviation from each species mean food size, expressed as a percentage of the total area.

[c] Body weight vs. coefficient of variation, Spearman $r_s = 0.44$, $P > 0.05$ (1-tailed). Body weight vs. diversity, Spearman $r_s = 0.27$, $P > 0.05$ (1-tailed). Body weight vs. % of total area utilized, Spearman $r_s = 0.64$, $P < 0.05$ (1-tailed).

food size and bird body size (table 3). As many of the histograms of utilization are irregular, I used three measures of central tendency—mean, median, and mode—as indices of average prey size for the correlations. Bird body size is the average weight of 10 individuals of each species. All three measures of central tendency in food size correlate significantly ($P < 0.05$) with bird body weight (Spearman rank correlation, Siegel 1956). Larger-bodied birds consume larger prey.

SIZES OF AVAILABLE FOODS, SELECTIVITY, AND BODY WEIGHT

Baker and Baker (1973) suggested that in addition to consuming larger food items, large shorebirds also may be more selective with regard to prey size. Two approaches to measuring selectivity of a predator may be distinguished. First, if the food resources available to a predator are not known, some simple measure of variability in diet is a statement of selectivity. For example, in the present study, I calculated coefficients of variation for length of prey used by each of the 10 shorebird species (table 4). The rank order of these coefficients was not significantly correlated with body size (Spearman $r_s = 0.44$, $P > 0.05$). Similarly, no significant correlation was found (Spearman $r_s = 0.27$, $P > 0.05$) using an estimate of diversity of prey lengths (H'/H_{max}, $H' = -\Sigma p_i \ln p_i$, table 4).

A second approach to examining selectivity combines knowledge of variability of stomach contents and the frequency distribution of available resources (fig. 3). To illustrate how these two factors interact, I show five hypothetical circumstances in which three species with known diet variability are arrayed along a resource continuum (fig. 4). I assume that the predators are fine-grained and contact prey in proportion to their occurrence. In case 1, stomach contents of species A, B, and C all are identically variable. Because of distribution of food resources, species B is the most selective as an individual of the species must pass over many prey items before finding those of the right size. For the same reason in case 2, with stomach contents equally variable, C is the most selective. Case 3 shows C as the most selective on the basis of stomach contents as well as on the probability of encountering an appropriately-sized food item. In case 4, all sizes of food are equally abundant, and C again is more selective on the basis of stomach contents. In case 5, A is most selective on stomach contents, but C may be more selective in terms of the probability of encountering food of appropriate sizes. The areas under A, B, and C, provide the basis for a comparison of selectivity.

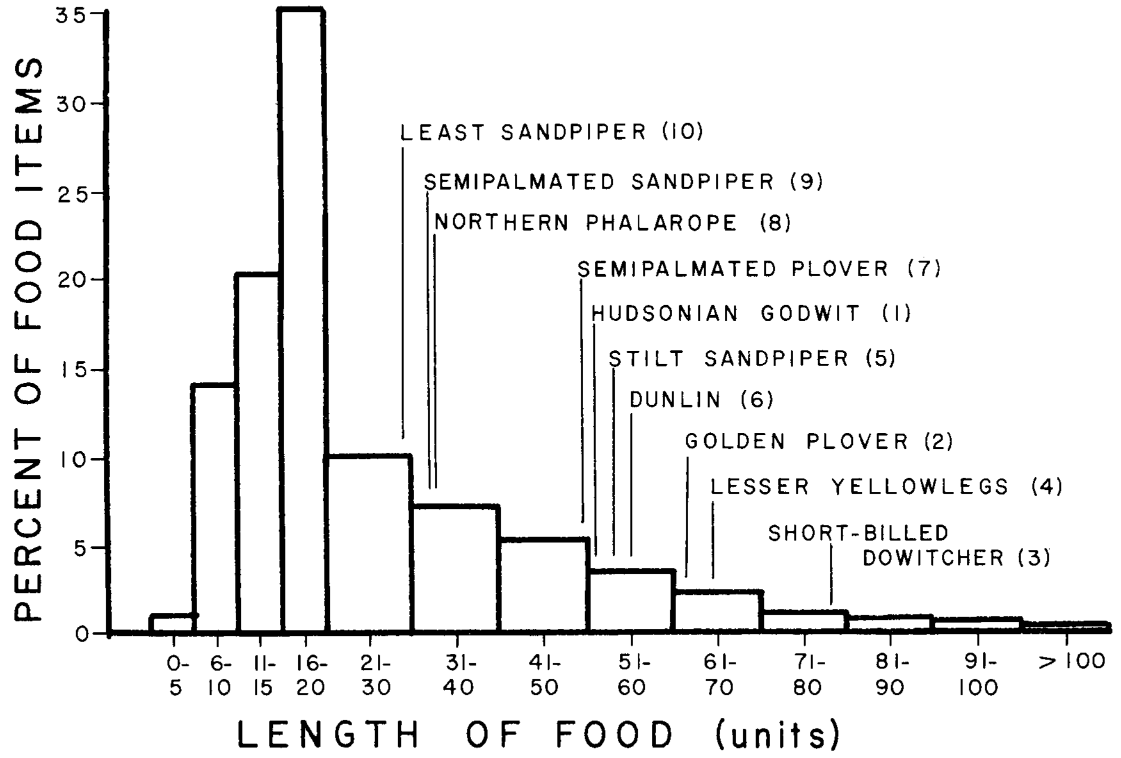

FIGURE 3. Size-frequency histograms of food available to ten species of shorebirds. The mean size of food eaten by shorebirds of each species is indicated by a perpendicular line. Parentheses enclose the rank body size of each bird. Each food length unit equals 0.105 mm.

These areas were estimated for each shorebird species by summing under the histogram of available food sizes (fig. 3) the area covered by one standard deviation on each side of the mean food size for that species and expressing this area as a percent of the area under the entire histogram. From these indices of selectivity, it seems that large shorebirds are more selective than small ones (table 4, Spearman $r_s = 0.64$, $P < 0.05$). The Semipalmated Sandpiper stands out as a major exception as it is selective and small-bodied.

SPECIES PACKING ON THE RESOURCE SPECTRUM

An ensemble of predators arrayed along a resource spectrum raises questions about the degree to which they overlap in feeding. Recent theoretical developments (MacArthur 1972, May and MacArthur 1972, Pianka 1974) suggest rules of species packing that may be applicable. MacArthur (1972) showed that the competition coefficient becomes significant near the value of $d = \sqrt{2\sigma}$, where d is the difference between means of prey size utilized by two species, and σ = the standard deviation of either of the predators' diets. As d increases greatly over 2σ, competition coefficients decline to small values, and vice versa. The relationship $d = \sqrt{2\sigma}$ assumes that the utilization curves are normal but holds for more general cases (MacArthur 1972). The theory also assumes equality of variances. The relationships of d and $\sqrt{2\sigma}$ for the shorebird community are examined in table 5. For any given comparison of two species of shorebirds, the variances are not equal. To try to compensate for this problem, I used $\sqrt{\sigma_1 + \sigma_2}$ instead of $\sqrt{2\sigma}$ which would force a choice between unequal variances. While it is apparent that the shorebird data do not conform perfectly to the assumptions of the theory, the application seems worthwhile. In fact, the numbers of stomachs required to get equal variances may be so high as to be prohibitive, making a truly correct application of the theory impossible, and in turn making the theory worthless for this particular situation.

With these difficulties in mind, we can see that the d values for the shorebird community are much smaller than $\sqrt{\sigma_1 + \sigma_2}$ in seven cases and larger than $\sqrt{\sigma_1 + \sigma_2}$ in two cases (table 5). Considered alone, this generally close packing of the shorebirds sug-

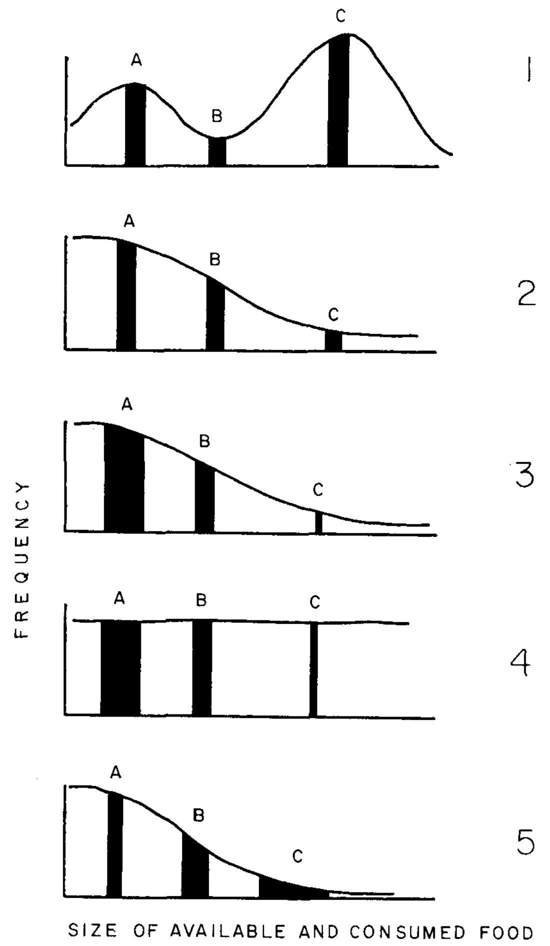

FIGURE 4. Hypothetical relationships between sizes of food available (continuous function) and sizes of food utilized (blackened areas). Three species of predators are depicted (A, B, C) under five different conditions. Width of the solid area covers one standard deviation on each side of the mean size of the food utilized.

TABLE 5. Species packing data for ten species of shorebirds.

	$\bar{Y}$[a]	σ	$\bar{Y}_{large} - \bar{Y}_{small}$ (d)	$\sqrt{\sigma_1 + \sigma_2}$
Least Sandpiper	29.3	20.2		
			— 2.8	5.6
Semipalmated Sandpiper	32.1	11.2		
			— 0.4	5.7
Northern Phalarope	32.5	21.9		
			— 17.0	7.0
Semipalmated Plover	49.5	27.2		
			— 1.5	6.7
Hudsonian Godwit	51.0	18.4		
			— 1.7	7.2
Stilt Sandpiper	52.7	34.0		
			— 2.3	8.4
Dunlin	55.0	37.5		
			— 6.4	8.3
Golden Plover	61.4	31.1		
			— 3.0	8.6
Lesser Yellowlegs	64.4	42.2		
			— 13.7	8.9
Short-billed Dowitcher	78.1	37.0		

[a] $\bar{Y}$ = mean and σ = standard deviation of food lengths in units (1 unit = 0.105 mm).

gests that competition should be severe; the theory would predict that several species should disappear from the community.

DISCUSSION

My analyses focus on size as the essential characteristic of dietary items of shorebirds. Results show that larger shorebirds consume larger food items. The relationship is not perfect, the Hudsonian Godwit being an exception. One possible explanation for this is the relatively small number of stomachs examined for this species, although the number of items is substantial. Perhaps it is simply that godwits were collected only when eating Cyclorrapha larvae; furthermore, these fly larvae may be less variable than other prey. I have no quantitative observations on habitat use by Hudsonian Godwits, but data may reveal major differences from most of the rest of the community in habitat used.

Hespenheide (1975) analyzed the interaction of prey size and identity and found that diets of two swifts and a swallow were explained partly by size preference and partly by taxonomic preference. He suggested that the taxonomic preference actually may reflect the ease with which the prey can be caught. Assessment of the interaction of prey size and identity in determining bird diets requires detailed studies of spatial and temporal patterns of prey populations and of differences in predator time budgets in different parts of the environment. Such studies are not yet available.

In their study of four *Calidris* sandpiper species at Barrow, Alaska, Holmes and Pitelka (1968) found that bill size and prey size tended to be correlated, but correlation of body size and prey size is not apparent from their data. On the other hand, both Schoener (1968) and Hespenheide (1971) described correlations between predator body weight and average prey size. It may seem surprising to those familiar with the group of shorebirds discussed here that the impressive differences in bill morphology among some of the species do not imply vast differences in diet. But, for example, I have seen Hudsonian Curlews peck tiny insects from leaf surfaces with their long drooping bills in much the same way as Least Sandpipers do. Particularly in the longer-billed species, my observations of foraging behavior of shorebirds outside the breeding season suggest that the bill is more often used in ways one would predict from its morphology, e.g., deep probing into mudflats. This observation supports the suggestion first made by Fretwell (1969) that bill morphology in finches seems more related to winter and/or migration diets.

The prediction that large-bodied shorebirds are more selective foragers than small shorebirds (Baker and Baker 1973) is supported by the somewhat crude analyses done here. Assessment of prey selection by comparing stomach contents of shorebirds and the distribution of food available may be worth pursuing in more detail. Certainly many studies of food habits of birds would benefit from some measurement of resources, however crude. One of my major assumptions here was that the predators find prey in proportion to their occurrence. This assumption seems reasonable for the shorebird community, but it may remain in doubt until we somehow get a bird's-eye view of the resource world. This may be approached most easily through experiments with species other than shorebirds. Sweep netting may mask precise patch selection behavior by the predator (see Baker 1974). To see that something else is involved in the selectivity issue, note that the Semipalmated Sandpiper, next to the smallest species, is about as selective as the Hudsonian Godwit and Golden Plover, the two largest species.

Several explanations are possible for the extreme closeness of species packing found in the shorebird community. Food is so abundant on the tundra during the main part of the breeding season that competition may be relaxed and allow tighter species packing. Furthermore, each species of shorebird in the community at Churchill forages in some subset of all the microhabitats (Baker and Baker 1973). The taxa used as food, on the other hand, are more broadly distributed, occupying more microhabitats. For example, a predator can find and consume tipulid larvae in many places even though it forages in only a few microhabitats. For this reason, overlap in food size or in taxonomic categories of food consumed by shorebirds are usually poor indices of total resource partitioning. To say that competition is relaxed does not imply that it is absent. Each shorebird species is somewhat restricted in habitat use probably because it forages more efficiently in its own preferred microhabitat than in others. Although this assumption is widely held, to my knowledge it has never been proven.

SUMMARY

Food habits of ten shorebird species breeding at Churchill, Manitoba, were studied by stomach analysis. Samples of food available to foraging shorebirds were collected also. The results of stomach analysis indicated that predator body size is positively correlated with average food size. Comparison of the food eaten and the food available indicated that large shorebirds tend to be more selective foragers, on the basis of food size, than small shorebirds. In general, the ten shorebirds are exceptionally tightly packed along the food size spectrum, more than is expected theoretically. Other niche dimensions may be more important in segregating the species. Relaxed competition in an environment of abundant resources may also explain high overlap among the shorebird community.

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