

RELATIONSHIP BETWEEN PREY ABUNDANCE AND FORAGING SITE SELECTION BY SEMIPALMATED SANDPIPERS ON A BAY OF FUNDY MUDFLAT

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Abstract.—The effect of prey abundance on the distribution of Semipalmated Sandpipers (*Calidris pusilla*) was investigated on a mudflat in the upper Bay of Fundy, Nova Scotia, Canada. Semipalmated Sandpipers use the upper Bay as a stop-over area in fall migration, feeding primarily on the abundant amphipod crustacean, *Corophium volutator*. The abundance and demography of *Corophium* vary along the intertidal gradient. Only a weak relationship is seen between amphipod density and shorebird density. Shorebird feeding rate and foraging efficiency are equal at three of the four sites along the intertidal gradient. The shorebirds avoid the lowest site where *Corophium* is rare. The results suggest that any intertidal area exceeding a critical threshold density of *Corophium* is acceptable to Semipalmated Sandpipers. In such sites, feeding rate is likely determined by the rate of digestion of prey. Prey abundance does not limit the feeding rate at this important stop-over site.

RELACIÓN ENTRE LA ABUNDANCIA DE PRESAS Y LA SELECCIÓN DEL LUGAR DE FORRAJEÓ POR PARTE DE *CALIDRIS PUSILLA* EN UN LODAZAL DE LA BAHÍA DE FUNDY

Sinopsis.—El efecto de la abundancia de presas sobre la distribución del playero *Calidris pusilla* fue estudiado en un lodazal en la Bahía de Fundy, Canadá. Los playeros usan la bahía como parada de descanso y alimentación durante la migración otoñal, y se alimentan particularmente del anfípodo *Corophium volutator*, el cual es muy abundante. La abundancia y demografía del anfípodo varió a lo largo de un gradiente en la zona entre-mareas. Se encontró una relación poco marcada entre la densidad del anfípodo y la densidad de playeros. La eficiencia de forrajeo y proporción alimentaria de los playeros fue igual en tres de las cuatro localidades a lo largo del gradiente entre-mareas. Los playeros evitaron las localidades en donde el anfípodo era raro. Los resultados sugieren que cualquier área entre-mareas que exceda un umbral crítico en la densidad del pequeño crustáceo es aceptable para los playeros. En dichas localidades la tasa de ingestión es determinada por la rapidez con que se digiere la presa. La abundancia de la presa no limitó la tasa de alimentación del playero.

Many Nearctic scolopacid shorebirds breed in the Arctic and winter in tropical regions in the West Indies, Central America, or South America (Morrison 1984). The distance between breeding and wintering ranges demands energetically expensive migrations. In this contribution, I examine the foraging behavior of Semipalmated Sandpipers (*Calidris pusilla*) at a major staging area during the fall migration.

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Semipalmated Sandpipers breed in the high Arctic tundra (Harrington and Morrison 1979). After nesting, most of the individuals in the Central and Eastern Canadian populations migrate to the upper Bay of Fundy. During a stay of about two weeks (Hicklin and Smith 1984), the birds prey heavily upon the amphipod crustacean, *Corophium volutator*. The birds double their weight, from about 20 to 40 g, before departing on a non-stop migration to wintering grounds in South America (Hicklin and Smith 1984). This flight of 4000 km requires 60–70 h of sustained flight (Stoddard et al. 1983).

Shorebirds are known to have higher metabolic rates than expected based on other birds of similar body weight (Kersten and Piersma 1987). It is reasonable to expect that efficient foraging should be strongly selected for as the shorebirds accumulate fat for their demanding migration. In this contribution, I ask whether Semipalmated Sandpipers choose to feed in areas of highest *Corophium* density on an intertidal flat in the Bay of Fundy. Preferred prey sizes are controlled in the analysis of foraging behavior of these shorebirds. I assess the foraging efficiency of Semipalmated Sandpipers as they accumulate the necessary fat reserves to complete their fall migration.

Data were gathered to test a model of habitat selection developed by Fretwell and Lucas (1970). Their model predicts that birds must evaluate habitats on the basis of prey abundance (which has a positive effect on feeding rate) and the abundance of competitors (which has a negative effect on feeding rate). As bird density rises, feeding rate in the richest area will ultimately fall below the rate that could be realized in areas of lower prey abundance, but lower competitor abundance. The model predicts that birds must constantly assess the conflicting effects of prey abundance and competitor abundance. Feeding rate should be nearly equal across habitats with habitats of high prey abundance supporting more birds, resulting in an ideal free distribution. The model applies to those situations where prey abundance rather than prey handling times or digestion rates determine the rate of accumulation of energy.

STUDY SITE

The study area was located on the extensive intertidal mudflats near Avonport, Nova Scotia in the Minas Basin, an arm of the upper Bay of Fundy. Hicklin and Smith (1984, Figs. 1, 2) provide maps of the area. The tidal range in the upper Bay of Fundy is the highest in the world, with amplitudes varying from 7.5 m during neap tides to 15 m during spring tides (Dohler 1970). Approximately one-third of the bottom of the Minas Basin is intertidal (Amos and Joice 1977, Cranford et al. 1985). The sediments in this region are primarily fine sand, with a silt-clay fraction of about 20%; the proportion of sand increases progressively toward the low water mark (Hicklin and Smith 1984).

The dominant organism in these mudflats is the amphipod crustacean, *Corophium volutator*. These amphipods attain lengths of 8 mm and maintain U-shaped burrows in the top three centimeters of the sediment.

Corophium extend their elongate antennae from either opening of their burrows to deposit-feed (Hart 1930, Meadows and Reid 1966, Murdoch et al. 1986). Sediments composed mostly of silt and clay particles are too fine for *Corophium* (Yeo and Risk 1981); those areas are dominated by polychaete worms (Wilson 1989). At Avonport, other members of the infaunal community include the polychaete worms *Aglaophamus neotenus*, *Pygospio elegans*, *Streblospio benedicti*, *Tharyx acutus* and *Heteromastus filiformis*, but their abundance is at least an order of magnitude less than that of *Corophium*. None of these polychaete species is taken by Semipalmated Sandpipers (Hicklin and Smith 1979).

Corophium is an important prey species for a number of predators in the Minas Basin. Numerous fish species feed on *Corophium* (Dadswell et al. 1984, Gilmurray and Daborn 1981, Imrie and Daborn 1981). It is also the primary prey of a number of migratory shorebirds in North America (Hicklin and Smith 1979). Over 90% of the diet of Semipalmated Sandpipers migrating through the Minas Basin is *Corophium* (Hicklin and Smith 1984). These shorebirds show strong selection for *Corophium* greater than 4 mm in length (Peer et al. 1986). *Corophium* reaches exceptionally high densities ($>60,000/m^2$) in the summer in the Minas Basin (Gratto et al. 1983, Wilson 1988a). The high densities of this species must be a major reason Semipalmated Sandpipers use the upper Bay of Fundy as a stop-over area during their fall migration. During July and August, the upper Bay is host to approximately one million Semipalmated Sandpipers (Hicklin and Smith 1984), along with smaller numbers of several other scolopacid species (Hicklin 1987).

MATERIALS AND METHODS

To determine the distribution of foraging Semipalmated Sandpipers along an intertidal gradient, I established four stations, 200 to 300 m apart, in a linear transect perpendicular to the shoreline on the Avonport mudflats. The highest station, Site 1, was located at the +6.5 m tide mark with Site 2 at +5.7 m, Site 3 at +4.9 m and Site 4 at +4.3 m. At each site, I marked off a square area of 0.10 ha (32 m on a side) with four wooden stakes. I censused shorebird use of each of the four marked areas on six days, Aug. 6–12, 1986. Peak densities of shorebirds occur during this period (Hicklin 1987). Adjacent marked sites were close enough that both could be monitored simultaneously with a spotting scope (20–45 \times). On Aug. 6, all four sites were censused; thereafter, only two adjacent sites were monitored each day. Censuses were begun as soon as a marked area was exposed and were continued until the area was covered by the incoming tide. The number of shorebirds in each marked area was noted usually once a minute with a maximum of five minutes between consecutive observations. More frequent counts were made when birds were flying in and out of the marked areas. The number of birds at each count was plotted against the time of observation on a standardized graph. For all graphs, the abscissa spanned 300 min, the value of the maximal time of tidal emergence of Site 1. The area under this plot, determined by

digitizing the area with a graphics tablet, gives an estimate of total bird-minutes for that low tide period. Bird-minutes is an absolute measure and hence has no error term associated with it. The unit of bird-minutes rather than bird-seconds or bird-hours was chosen because the precision of the census data was on the order of minutes. Although every change in shorebird abundance in the plots could not be recorded because of the necessity of making other observations, counts were frequent enough that this method provides a more precise measure of shorebird use than simply averaging a sequence of census data (Wilson 1988b). To permit comparison of sites which differed in periods of intertidal exposure, the period of exposure of the lowest site being compared was used in the calculation of bird-minutes. For instance, in comparing Sites 1 and 2, any birds found in Site 1 before the receding tide uncovered Site 2 or after the incoming tide covered Site 2 were not used in calculating shorebird use. This procedure ensured that equal periods of time were used in the comparison of sites.

To determine prey abundance at the different sites, five 0.008 m² cores, 10 cm deep, were taken in each area on 10 Aug. The cores were sieved in the laboratory through a 250 micron screen and the retained organisms were fixed in 5% formalin. This mesh size retains even the smallest *Corophium*. The animals were later counted using a stereomicroscope. All *Corophium* in a sample were photographed on a single negative along with a metric ruler for scale. Prints of the negative were used to measure the length of every amphipod using a digitizing tablet. *Corophium* length-frequency distributions were determined for four replicates for each site. Length is a biologically meaningful measure because length and dry weight of *Corophium* are highly correlated (Boates and Smith 1979).

The relationship between prey abundance and shorebird abundance was analyzed with G-statistic analysis (Sokal and Rohlf 1981). I predicted that shorebird use should be positively correlated with prey abundance. The relative abundance of large *Corophium* (>4 mm in length) generated a proportion, which was used to predict the relative use of sites by birds, measured in bird-minutes, on a given day. For instance, if shorebird use of areas 1 and 2 were determined by the abundance of available *Corophium* at each site, one would predict that the 485 bird-minutes for Aug. 10 would be distributed in proportion to the ratio of available *Corophium* (30.7: 66.0, Table 1). Thus, the expected distribution of 187:398 (Site 1: Site 2) can be compared by calculation of G to the observed distribution of 92:493. For the Aug. 6 data, the three comparisons involved data which were partly dependent; the value of α was reduced by a factor of three to provide an overall α of 0.05.

Observations were made on the feeding rate of at least 50 birds from the three upper intertidal sites. Observations were made with a spotting scope (20–45 \times). The number of probes and the number of successful probes were counted during a measured interval of time (45–75 s). A successful probe was confirmed by observation of an amphipod in the bill and by conspicuous swallowing.

TABLE 1. Densities of *Corophium* at Avonport in August, 1986. Sites are listed in decreasing tidal height. Each mean is derived from five replicates. Density is expressed as number/0.008 m². Standard deviations (SD) are given in parentheses below the mean. Both the absolute abundance and the abundance of *Corophium* greater than four mm in length are given. Shared letters to the right of means indicate means that are not significantly different in Scheffé *post hoc* comparisons.

	Site 1	Site 2	Site 3	Site 4
Total <i>Corophium</i>	227.4 A	286.8 AB	372.8 B	61.0 C
SD	(72.55)	(66.45)	(86.90)	(43.17)
Available <i>Corophium</i> (>4 mm)	30.7 D	66.0 E	69.0 E	5.0 F
SD	(9.79)	(15.29)	(12.76)	(3.54)

RESULTS

Foraging behavior.—Semipalmated Sandpipers were observed to roost in agricultural fields when the high tide covered the mudflats. The birds returned to the flats about 2 h after high tide. The sediment from the first 200 m of the intertidal area was quite coarse, consisting primarily of gravel, and supported few infaunal organisms. This upper region was thus essentially devoid of shorebird prey and was avoided by the birds. When the tide had fallen below the gravel areas, the shorebirds followed the receding tide line out, actively pecking at the surface (not probing in the sediment). On 10 and 12 Aug., I followed the tide line out to determine what the shorebirds were taking. The shorebirds, as observed from only 5 m away, were feeding on the molted exoskeletons of *Corophium* which collected at the tide line in great numbers. I did not observe *Corophium* leaving their burrows to crawl on the surface after tidal exposure as described by Boates and Smith (1979); such crawling behavior has a semilunar rhythm (Fish and Mills 1979), probably accounting for the absence of crawling males during my observations. Few birds were actively probing at this time. The birds continued to follow the tide line for periods up to 1.5 h until the tide reached just below Site 3 (+4.9 m). Flocks then flew off up the flat to begin probing for living amphipods. The flocks flew frequently in the first 30 min after leaving the receding tide line but, thereafter, spent the majority of their time feeding. When the rising tide reached the middle portions of the flat, the shorebirds frequently flew in an agitated state and fed only infrequently. The sandpipers flocked in the upper intertidal zone without feeding until the encroaching tide forced them to fly to adjacent agricultural fields.

Prey abundance.—The results of the sampling of the mudflat community at each site are given in Table 1. Except for Site 4, the crustacean *Corophium* is the most abundant infaunal organism (Wilson, unpublished data). At Site 4, the polychaete worm, *Pygospio elegans*, is the most abundant invertebrate (122/0.008 m² core) and *Corophium* is uncommon there relative to the three higher sites.

Table 2 presents length-frequency data for *Corophium* at the different sites. Four replicates for each site are presented. These data allow one

TABLE 2. Distributions of lengths (mm) of *Corophium* at the four sites. Size-frequencies are given from four replicate cores at each site. Frequency is expressed as percentages. The line through the table separates *Corophium* into small individuals which are rarely taken by shorebirds and large individuals which are the preferred prey sizes of the shorebirds.

Length	Site 1				Site 2				Site 3				Site 4			
	A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
0-1	25	17	34	20	8	6	8	4	4	8	2	2	10	24	10	10
1-2	34	29	56	28	30	32	12	26	50	36	40	48	68	58	58	0
2-3	10	20	10	22	16	28	22	22	14	12	14	10	15	12	24	70
3-4	9	22	0	8	8	12	18	18	6	8	6	6	4	2	8	0
4-5	8	8	0	8	14	10	8	12	4	6	8	8	0	0	0	20
5-6	10	4	0	8	16	8	14	8	10	20	24	18	0	0	0	0
6-7	4	0	0	6	8	4	6	4	12	8	6	8	0	0	0	0
7-8	0	0	0	0	0	0	10	4	0	2	0	0	3	0	0	0
8-9	0	0	0	0	0	0	2	2	0	0	0	0	0	4	0	0

to assess the relative abundance of *Corophium* at each site that are acceptable prey for shorebird predators. Peer et al. (1986) have shown that Semipalmated Sandpipers rarely ingest *Corophium* less than 4 mm long. Therefore, only a proportion of the total *Corophium*, indicated in Table 1, represent available resources (Table 1). Although Sites 1 and 2 do not differ significantly in total *Corophium* abundance, Site 2 has significantly more *Corophium* which are available prey items. The analysis indicates that Sites 2 and 3 have the highest prey abundances, Site 1 is intermediate and Site 4 is poor (Table 1).

Distribution of Semipalmated Sandpipers.—Table 3 presents the abundance data (expressed in bird-minutes) for Semipalmated Sandpipers at the four sites for each daily census. For 6 Aug., three comparisons are presented, comparing shorebird use over increasing periods of time. The first comparison involves shorebird use at all four sites over the relatively short time period that the lowest site, Site 4, was exposed. A second comparison involves the upper three sites over the time that Site 3 was exposed. The final comparison involves the upper two sites over the relatively long time period of Site 2 exposure.

Table 3 also presents an analysis of the relationship between shorebird abundance and prey abundance. The ratio of available *Corophium* (Table 1) is used to generate the expected ratio of shorebird use between sites being compared. G-statistics tested the fit of the expected and observed distributions. For 6, 9, 10, 11, and 12 Aug., there is a significant difference between proportions, indicating that relative prey abundance does not predict relative shorebird abundance. On the remaining day (7 Aug.), there is no significant difference between observed and expected proportions, indicating that shorebird abundance is distributed according to prey abundance.

TABLE 3. Comparison of use of four intertidal sites by Semipalmated Sandpipers. Abundance is expressed in bird-minutes. The relative abundance of shorebirds at different sites is compared to the expected abundance predicted by the relative abundance of their principal prey, *Corophium*. G-statistics test the goodness of fit between the observed and expected distribution of shorebirds. *** = $P < 0.001$, * = $P < 0.05$, NS = not significant ($P > 0.05$).

Date	Sites	Bird-minutes	Expected	P-value
6 Aug.	1:2:3:4	620:515:347:16	272:579:605:44	***
	1:2:3	669:515:347	286:610:638	***
	1:2	735:572	418:890	***
7 Aug.	3:4	388:23	384:27	NS
9 Aug.	1:2	170:479	208:442	*
10 Aug.	1:2	92:493	187:398	***
11 Aug.	2:3	181:325	247:259	***
12 Aug.	1:2	148:460	194:414	*

Data on feeding rates at the four sites are presented in Table 4. The data reveal that neither the number of prey taken/min (ANOVA, $P > 0.20$) nor the efficiency of foraging as measured by the percentage of probes which result in prey capture (χ^2 , $P > 0.10$) differ significantly between Sites 1, 2 and 3. No data on feeding rates at Site 4 were taken because of the scarcity of birds foraging there.

DISCUSSION

This research explores habitat selection in a shorebird species with particular reference to prey abundance. The model of habitat selection in birds (Fretwell and Lucas 1970) was used to predict that Semipalmated Sandpipers in the upper Bay of Fundy should forage first in areas of highest food abundance. Subsequent arrivals should continue to select the habitat of highest food abundance until density-dependent interactions among the birds reduce the foraging efficiency in the first habitat below that which could be achieved in the habitat of second greatest food abundance. Subsequent arrivals should then select the second richest habitat until competitor density reaches a critical level at which time the third richest habitat becomes the habitat of choice. This interaction of food abundance and competitor abundance are predicted to equalize foraging efficiency in all of the suitable habitats, yielding an ideal free distribution. Habitats with high food resources should support many birds, whereas habitats with depauperate food resources should support few.

The model predicts that along a gradient of food resources in the upper Bay of Fundy, Semipalmated Sandpiper abundance should vary in proportion to prey abundance. Aggressive interactions between sandpipers were never observed during the course of this study, indicating that foraging success was not influenced by conspecific density. Virtually the only infaunal species taken by Semipalmated Sandpipers at the study site is the amphipod, *Corophium volutator* (Hicklin and Smith 1984). The abun-

TABLE 4. Feeding rate and success rate (foraging efficiency) of Semipalmated Sandpipers at the three highest intertidal stations. Feeding rate is number of *Corophium* taken per minute. Standard deviations are given below each mean. Underlined means are not significantly different in Scheffé *post hoc* comparisons. Success rate is the number of successful probes, divided by the total number of probes, expressed as a percentage. Means which are underlined are not significantly different in pair-wise χ^2 tests. Each datum represents observations on at least 50 shorebirds.

	Site 1	Site 2	Site 3
Feeding rate	15.3	16.2	14.7
	(5.76)	(4.09)	(4.74)
Success rate	33.9	36.2	44.6

dance (Table 1), size-frequency distribution (Table 2) and relative availability of prey to the size-selective shorebird predators (Table 1) vary among the four sites along the tidal gradient. A fit between prey abundance and shorebird use of study sites was found on only one of the six days of observation (Table 3). The weak relationship between prey and predator relative abundances can be understood by consideration of feeding rates (Table 4). For the three upper sites, feeding rate and feeding efficiency (proportion of successful probes) do not differ statistically. These equivalent feeding rates do not result from an interaction of food abundance and predator density as the Fretwell and Lucas (1970) model requires. In over 60 h of observation, I never observed aggressive interactions (Burger et al. 1979; Lank 1983; Goss-Custard 1977b, 1980) or threat postures (Hamilton 1959; Harrington and Groves 1977) between individual Semipalmated Sandpipers. These results indicate that the abundances of *Corophium* in Sites 1, 2, and 3 all exceed a threshold density, above which it is disadvantageous to defend feeding territories. Above this threshold density, feeding rate is not constrained by prey abundance. Given the relatively high prey densities at Sites 1, 2, and 3, there seems little benefit for Semipalmated Sandpipers to forage at Site 4, where prey densities are below the threshold density. The present data do not permit the precise determination of the threshold density. However, this density must be greater than the density of acceptable *Corophium* (>4 mm long) at Site 4 (625/m²), but less than the corresponding density for Site 1 (3838/m², Table 4). For Redshank (*Tringa totanus*) in England, Goss-Custard (1977a) showed that the relationship between *Corophium* density and Redshank feeding rate became asymptotic above densities of 2000/m².

The lack of aggressive interactions in foraging Semipalmated Sandpipers at the upper Bay of Fundy site is notable. Semipalmated Sandpipers, particularly juveniles, in Massachusetts maintained an aggressive "tail-up" posture (Drury 1961, Harrington and Groves 1977). In the lower Bay of Fundy where *Corophium* is less abundant (Gratto et al.

1983, 1984), aggressive interactions were frequently documented (Lank 1983). One would predict that food abundance in these two areas falls below the critical density, below which it is energetically advantageous to defend feeding territories (Sullivan 1986). The wealth of available food in the upper Bay of Fundy mudflats must certainly be of fundamental importance in explaining the use of the upper Bay of Fundy as a stop-over area for much of the Semipalmated Sandpiper population. As demonstrated here, the rate of feeding and, hence, the rate of fat deposition is not constrained by prey abundance. Rather, the rate of prey capture is probably determined by the capacity of the gut or rate of digestion.

Significant correlations between shorebird density and the density of their principal prey have been documented in many different intertidal areas (Bengston and Svensson 1968, Bryant 1979, Goss-Custard et al. 1977, Hicklin and Smith 1984, Wolff 1969). These studies entail geographic scales of km or more. The data from this study involve a considerably smaller scale, hundreds of m. I am able to demonstrate only a weak relationship between predator and prey density. Hicklin and Smith (1984) used the Avonport site as one of 12 sites in the upper Bay of Fundy. They show that Avonport has higher *Corophium* abundance and higher Semipalmated Sandpiper abundance than most other Minas Basin sites. However, within the Avonport site, prey density is not a good predictor of shorebird abundance (Table 2). Thus, at the level of the population or flock, Semipalmated Sandpipers in the upper Bay of Fundy frequent habitats that offer adequate numbers of prey. However, at the level of individuals, foraging location is not based on relative abundance of benthic prey and potential conspecific competitors, but rather is a dichotomous choice. Areas with prey in excess of a threshold density of prey are all satisfactory and may be chosen. Areas below the threshold density (e.g., Site 4) will be avoided. At even smaller scales, Quammen (1981) showed differential shorebird use of adjacent areas of a mudflat which differed slightly in sediment granulometry. Spatial scale must be considered in the interpretation of relationships between shorebird predators and their prey.

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