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## THE FORAGING BEHAVIOR OF SEMIPALMATED SANDPIPERS IN THE UPPER BAY OF FUNDY: STEREOTYPED OR PREY-SENSITIVE?<sup>1</sup>

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**Abstract:** Videotapes of migrant Semipalmated Sandpipers foraging in the upper Bay of Fundy were analyzed to test for foraging behaviors sensitive to prey density. Over a range of prey densities, both the number of steps sec<sup>-1</sup> and probes sec<sup>-1</sup> increased with increasing prey density. However, the number of steps between probes was constant over the range of prey densities observed. The average angle of directional change during foraging and the number of turns min<sup>-1</sup> were constant despite large differences in prey patchiness.

**Key words:** *Semipalmated Sandpiper*, *Calidris pusilla*, foraging behavior, stop-over area, migration, Bay of Fundy, *Corophium volutator*.

Ornithological studies have contributed much to the development of foraging theory (e.g., Tinbergen, 1967, Davies, 1977, Krebs et al., 1977, Zach and Falls, 1977). However, the foraging behavior of many birds confounds testing many predictions because birds may be difficult to observe continuously for extended periods, may take a diverse array of prey and may thwart efforts to quantify their behaviors because of their rapid movements. In this contribution,

we explore the relationship of prey density and prey patchiness (measured by coefficient of variation) on foraging behavior of Semipalmated Sandpipers (*Calidris pusilla*) which essentially prey on a single species in the upper Bay of Fundy. The high visibility and confiding nature of these shorebirds allowed us to videotape foraging behavior at close range, permitting the acquisition of data on foraging behavior that cannot be gathered for many avian species. These data are used to test predictions of the relationship of foraging behaviors to prey density and prey patchiness.

Many scolopacid sandpipers, including Semipalmated Sandpipers, undertake migrations between arctic breeding grounds and subtropical or tropical wintering areas. The distances of these migrations place extraordinary energetic demands on the birds. In addition, shorebirds have higher metabolic rates than expected based on other birds of similar mass (Kersten and Piersma 1987). It is reasonable to expect that there should be strong selective pressure to maximize food intake at stop-over areas during migration.

Semipalmated Sandpipers nest in the low- to mid-arctic (Harrington and Morrison 1979, Gratto-Trevor 1992). After nesting, the majority of central and eastern Canadian breeding birds wend their way to the upper Bay of Fundy. During an average stay of 15 days (Hicklin 1987), the sandpipers feed primarily on the abundant amphipod crustacean, *Corophium volutator* (Hicklin and Smith 1979). These sandpipers

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nearly double their weight from about 20–25 g to 40 g (Hicklin and Smith 1984) before departing on a nonstop, oceanic migration to Suriname. It is estimated that this 4,000 km flight requires 60–70 hr (Stoddard et al. 1983).

Previous research in the upper Bay of Fundy has shown that *C. pusilla* occur on intertidal flats where the abundance of *Corophium* is relatively high (Hicklin and Smith 1984, Wilson 1990, Matthews et al. 1992). Within a flat, birds are likely to forage anywhere as long as *Corophium* abundance is above a threshold density; areas below this threshold are avoided (Wilson 1990).

For individual *C. pusilla*, the only aspect of foraging behavior that has been quantified is prey capture rate as a function of prey density (Wilson 1990). In this study, we quantify a number of other foraging behaviors of *C. pusilla* which were videotaped at the height of fall migration in the upper Bay of Fundy. Analysis of these videotapes in slow-motion permitted the acquisition of data on behaviors that simply occur too quickly to quantify in field observations.

#### METHODS AND MATERIALS

The study site was located on the western shore of the Minas Basin, Bay of Fundy in the village of Avonport, Nova Scotia (Hicklin and Smith 1984). The intertidal flats have been the site of previous work on the foraging behavior of Semipalmated Sandpipers (Boates and Smith 1979, Gratto et al. 1983, Hicklin and Smith 1984, Wilson 1988, 1989, 1990). The Avonport flats are one of the most important stop-over areas for *C. pusilla* in the upper Bay during the fall migration (Hicklin and Smith 1984). Although 34 species of shorebirds may be found on the intertidal flats of the upper Bay of Fundy during fall migration (Hicklin 1987), *C. pusilla* is the most common shorebird by far, with up to 2.2 million passing through the area (Mawhinney et al. 1993). Other relatively common species are Short-billed Dowitchers (*Limnodromus griseus*), Least Sandpipers (*C. minutilla*) and Semipalmated Plovers (*Charadrius semipalmatus*).

The tidal range in the upper Bay of Fundy is the highest in the world. The tidal amplitude during neap tides is 7.5 m and during spring tides is 15 m (Dohler 1970). Because of the great tidal range, the intertidal area is expansive; nearly one-third of the bottom of the Minas Basin is intertidal (Cranford et al. 1985). At Avonport, the horizontal distance between the high and low tide marks exceeds 1 km.

The intertidal sediment varies with tidal height, becoming sandier in the lower portion of the intertidal zone. Much of the intertidal zone is dominated by the amphipod *Corophium volutator*, which builds U-shaped burrows in the top 5 cm of the sediment. Densities may exceed 100,000 m<sup>-2</sup> (Wilson 1989). *Corophium* is the major prey of many of the migratory sandpipers feeding at Avonport, including *C. pusilla*. (Hicklin and Smith 1979, Wilson 1989, 1990). Other invertebrates in the intertidal zone include the polychaetes *Pygospio elegans*, *Streblospio benedicti*, *Aglaophamus neotenus*, *Heteromastus filiformis*, and *Tharyx acutus* (Wilson 1988, 1989). Individuals of

these species are rarely eaten by *C. pusilla* (Hicklin and Smith 1979).

Three stations were established along an intertidal gradient on 3 August 1992, corresponding roughly to the upper three stations used in 1986 in a previous study (Wilson 1990). These stations were at the following tidal heights: 5.7 m, 4.9 m and 4.3 m above mean low-water; successive stations were about 300 m apart. *Corophium* densities drop precipitously below the 4.0 m mark and shorebirds avoid this area for foraging (Wilson 1990).

On 4–6 August 1992, shorebirds were videotaped at each of the stations using a Canon video camera with a 10× telephoto lens. As the tide ebbs, the foraging sandpipers follow the tideline out below the level of Station 3 and then disperse broadly to feed throughout the intertidal zone. Birds were taped at each station as each station was exposed. Once the tideline had receded past Station 3, equal time was spent videotaping at each site, moving among stations at least twice each low tide. As the tide rose, each station was videotaped until the birds were forced to move to higher ground. Therefore, we obtained videotapes of the birds feeding immediately after subaerial exposure, immediately before immersion, and at two different times during low tide exposure. All videotapes were obtained by standing at one point with the video camera mounted on a tripod. As flocks of birds flew in, they were videotaped. The birds are remarkably tame and often foraged within 4 m of the observer.

On 6 August, five core samples of the sediment were taken from each of the three stations; the cores were no closer than 5 m from each other. Each core was 10 cm in diameter and was taken to a depth of 10 cm, well below the maximum depth of *Corophium*. The sediment was sieved through a 500 µm screen. The residue with all retained organisms on the screen for each core was preserved in 10% formalin in seawater.

The residue was later washed in freshwater and then sorted under a stereomicroscope at 12×. As the sandpipers strongly select *Corophium* larger than 4 mm long (Peer et al. 1986), only *Corophium* exceeding 4 mm were counted. Differences in abundance of the large *Corophium* among the three stations were tested for significance by analysis of variance and Scheffé post hoc pair-wise contrasts (Sokal and Rohlf 1981).

The videotapes were played at slow speed to analyze foraging behavior. Most birds were not close enough to allow us to determine from the videotapes if a probe resulted in prey capture. However, several other behavior patterns could be quantified from the tapes. We recorded the number of steps sec<sup>-1</sup>, the number of probes sec<sup>-1</sup> and the number of steps between probes for 151 Semipalmated Sandpipers. Roughly equal numbers of birds were sampled from each station on each day. The video sequences used averaged 33 sec in duration (range: 4–133 sec).

Data on directional changes also were taken from the videotapes. A system was devised in which movement toward the camera was defined as south and directly away as north; these directions bore no relation to actual magnetic north. The orientation near-

TABLE 1. Abundance and coefficient of variation of large *Corophium volutator*, the primary prey item for Semipalmated Sandpipers at Avonport. Means of number per core which share the same letter are not statistically different ( $P > 0.05$ ). Each core represents 0.008 m<sup>2</sup>.  $n = 5$  for each site.

	Site 1	Site 2	Site 3
Number of prey per core ( $\bar{x} \pm SE$ )	29.4 $\pm$ 14.1 ab	53.4 $\pm$ 9.4 a	8.4 $\pm$ 7.4 b
Coefficient of variation	107%	39%	198%

est one of the eight major compass bearings (S, SW, W, NW, etc.) was recorded at the beginning of a sequence. The orientation after each change of direction was noted during a timed sequence. We then calculated the average number of changes in orientation min<sup>-1</sup>. We also determined the average of the angles of change using 45° increments for all directional changes in the sequence. For instance, a switch from N to SE was recorded as a change of 135°. Twenty birds were randomly selected from the videotape and analyzed for each of the three stations.

We tested the following predictions: (1) probe rate should increase with increasing prey density, i.e., birds should feed more intensively when walking through areas where foraging success is high, (2) step rate should decrease with increasing prey density, i.e., birds should not walk quickly through an area where foraging success is high, (3) the average number of steps between probes should decrease with increasing prey density (logically follows from predictions 1 and 2; as prey density goes up, probe rate should rise and step rate should fall), (4) the frequency of directional change should increase with increasing prey variation, measured as coefficient of variation (CV) (by turning frequently birds remain in patches where food abundance is high [Tinbergen et al., 1967, Zach and Falls, 1977]), and (5) the average angle of directional change should increase with increasing prey CV, i.e., birds should change directions more radically when prey density is patchy to restrict foraging area and take advantage of a prey patch.

## RESULTS AND DISCUSSION

Abundance data for large *Corophium*, the primary prey of the sandpipers, are given in Table 1. Prey density at Station 2 was significantly greater than at Station 3. Station 1 was intermediate, and not significantly different from either Station 2 or 3. However, the variance in density differed markedly among the three sites. The CV for Station 2 was low, indicating

fairly homogeneous prey densities. Much higher CV's were found for Station 1 and particularly Station 3.

The data on foraging behavior are given in Table 2. We first tested for block effects (effect of date). In all cases, there was no significant effect of date so all of the data were combined. The number of probes sec<sup>-1</sup> was significantly greater at Stations 1 and 2 compared to Station 3. Sandpipers had higher steps sec<sup>-1</sup> at Stations 1 and 2 than at Station 3. The number of steps between probes, however, did not vary among the three sites. The average number of changes of direction and the average angle of directional change did not differ among sites.

Over the range of prey densities in this study (Table 1), Semipalmated Sandpipers displayed a mixture of stereotyped and prey-sensitive behaviors (Table 2). We predicted that as prey abundance increased, birds should probe more frequently. This prediction was supported as the number of probes sec<sup>-1</sup> was greater at Stations 1 and 2. Our prediction that step rate would be inversely related to prey density was rejected. The sandpipers had the slowest step rate in the area with lowest prey density. We interpret this unexpected result to mean that sandpipers are relying on visual cues to choose probe sites at Station 3. In this area with low, highly variable prey density, sandpipers perhaps walk slower to allow burrows and other cues on the surface of the sediment to be seen. Additional work on the possible importance of visual cues is clearly warranted. An alternative but virtually unexplored cue might be sounds made by *Corophium* as they move within their burrows (C. L. Gratto-Trevor, pers. comm.).

We combined the two measures of foraging behavior into a composite measure, the number of steps between probes. This measure indicates an apparent stereotyped behavior. The sandpipers take roughly four steps between probes. However, this apparent constancy masks the directly proportional changes in steps sec<sup>-1</sup> and probes sec<sup>-1</sup> at the different stations;

TABLE 2. Foraging characteristics of Semipalmated Sandpipers at the three intertidal stations. Means ( $\pm SE$ ) within a row which share the same letter are not significantly different in Scheffé post hoc contrasts ( $P > 0.05$ ). For the first three behaviors,  $n = 53, 47$  and  $51$  for Stations 1, 2 and 3, respectively. The last two behaviors are based on analysis of 20 birds at each station.

Measure	Station 1		Station 2		Station 3	
Probes sec <sup>-1</sup>	0.96 $\pm$ 0.03	a	0.90 $\pm$ 0.04	a	0.79 $\pm$ 0.02	b
Steps sec <sup>-1</sup>	3.72 $\pm$ 0.11	c	3.64 $\pm$ 0.12	c	3.16 $\pm$ 0.08	d
Steps between probes	4.1 $\pm$ 0.2	e	4.2 $\pm$ 0.2	e	4.1 $\pm$ 0.2	e
Directional changes min <sup>-1</sup>	7.8 $\pm$ 0.6	f	8.3 $\pm$ 0.9	f	8.1 $\pm$ 0.8	f
Mean angle of directional change	79.5 $\pm$ 3.5	g	72.7 $\pm$ 2.8	g	82.5 $\pm$ 3.9	g

step rate and probe rate are positively correlated (Table 2).

The two measures of directional change fail to support the two predictions. No differences among sites were found for both the average number of directional changes  $\text{min}^{-1}$  and the average angle of directional change. These behaviors are therefore independent of the prey density and prey coefficient of variation seen at Avonport.

Previous work on foraging of small *Calidris* sandpipers has invoked chemoreception and touch as primary mechanisms of prey detection (Van Heezik et al. 1983). If this is so, then we would not expect the foraging speed ( $\text{steps sec}^{-1}$ ) to slow down in areas of low prey density. It seems likely that in areas where prey are relatively rare, visual cues may be used more than chemoreception or touch.

We expected that birds would switch directions more frequently and more radically (greater angles of change) when patchiness of the prey increased (Tinbergen et al. 1967, Zach and Falls 1977). We incorrectly predicted that altering the direction of movement after several successful probes would be advantageous in keeping the bird in a profitable prey patch.

Baker (1972) describes the only other study that quantified foraging behaviors of *C. pusilla* from videotapes. He quantified interprobe intervals for individual birds and showed that these intervals are strongly skewed to the low end but he did not examine the impact of prey density on interprobe intervals or other facets of foraging behavior. We believe that analysis of videotapes is a fruitful approach to the study of calidrine foraging behavior and encourage use of this technique.

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## AQUATIC COMMUNITY CHARACTERISTICS INFLUENCE THE FORAGING PATTERNS OF TREE SWALLOWS<sup>1</sup>

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**Abstract:** During periods of inclement spring weather, Tree Swallows (*Tachycineta bicolor*) were observed foraging close to the surface of a series of experimentally manipulated ponds. Censuses of foraging swallows during these periods indicated that the use of ponds for foraging was positively affected by earlier additions of nutrients and the removal of fish from the ponds. Collections of emerging insects from these ponds indicated that nutrient additions and the removal of fish greatly increased the numbers of insects emerging from those ponds. The ability of Tree Swallows to exploit local concentrations of food may be critical to their ability to return to the breeding grounds before aerial insects are reliably available.

**Key words:** *Tree Swallow*, *Tachycineta bicolor*, foraging, experimental pond communities, trophic cascade.

Tree Swallows (*Tachycineta bicolor*) are aerial insectivores that rely heavily for their food on adult stages of insects with aquatic larvae. However, individuals typically arrive on their breeding grounds in northern North America before weather conditions ensure a constant supply of aerial insects (Robertson et al. 1992, McCarty 1995). Tree Swallows have several traits that help them to survive periods of low food availability (Weatherhead et al. 1985, Stutchbury and Robertson 1990). Unlike other swallows, Tree Swallows are able to subsist for long periods of time on fruit, especially bay-berries (*Myrica* spp.), when insects are not available (Chapman 1955, Turner and Rose 1989, Place and Stiles 1992). Tree Swallows also may increase their ability to survive stressful periods by adjusting their foraging to exploit localized

food sources such as emerging aquatic insects (Dence 1946, Cohen and Dymerski 1986). The ability to exploit such local concentrations of available insects undoubtedly influences the ability of Tree Swallows to return to their breeding area early in the season. In this paper, I report observations of locally concentrated foraging activity by Tree Swallows associated with both the biotic and abiotic characteristics of the aquatic communities over which they forage. This information is significant because it shows that Tree Swallows are able to perceive and exploit small patches of abundant food and because it demonstrates an influence of aquatic community dynamics on the ecology of a terrestrial bird.

### METHODS

This study was conducted at the Cornell University Experimental Ponds Facility Unit Two, located north-east of Ithaca, New York (42°30'N, 76°27'W), during April and early May 1992. This site consists of 50, 0.1-ha artificial ponds and a 5-ha reservoir (see Hall et al. 1970 for a detailed description of the site). In 1992, 15 pairs of Tree Swallows bred at the site, and an additional 78 pairs of Tree Swallows bred at a second site, Ponds Unit One, located 2 km away. Early in the breeding season, large numbers of migrant swallows and breeding Tree Swallows from this second site forage at Ponds Unit Two.

At the time of this study, 16 of the 50 ponds were part of an experiment manipulating nutrients and animal communities. Ponds were manipulated in a 2 × 2 factorial design with four ponds per treatment combination (Morin et al. 1991, Hairston and Howarth, unpubl. data). Manipulations consisted of high phosphorus (HP) or low phosphorus (LP) additions, combined with either fish present (+F) or fish absent (−F), to create the four treatments of: HP + F; LP + F; HP − F; LP − F (Morin et al. 1991, Hairston and Howarth, unpubl. data). Ponds were fertilized with P in the form of H<sub>3</sub>PO<sub>4</sub> twice weekly during the summer of 1991, with HP ponds receiving P at a rate of 0.56 g · m<sup>−3</sup> · year<sup>−1</sup> and LP ponds receiving 0.056 g · m<sup>−3</sup> · year<sup>−1</sup>. Fish-present ponds

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