


HABITAT USE BY MIGRATING AND BREEDING SHOREBIRDS  
ON THE EASTERN COPPER RIVER DELTA, ALASKA

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THESIS

Presented to the Faculty of the University of Alaska  
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By

Stephen Michael Murphy, B.S.


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HABITAT USE BY MIGRATING AND BREEDING SHOREBIRDS  
ON THE EASTERN COPPER RIVER DELTA, ALASKA

RECOMMENDED:

  
S. F. Maclean

Robert B. ...

P. H. Mickelson

Chairman, Advisory Committee

P. H. Mickelson

Chairman, Program in Wildlife and Fisheries

John B. ...

Director, Division of Life Sciences

APPROVED:

Vice Chancellor for Research and Advanced Study

Date

## ABSTRACT

This study examines the phenology, species composition, relative abundance, patterns of habitat use, and resource partitioning by migrating and breeding shorebirds on the eastern Copper River Delta. The peak of spring migration in 1978 occurred on 11 May, several days later than normal. Interspecific competition for foraging space on intertidal mudflats was minimized by temporal differences in the peaks of migration of the most abundant species and by spatial segregation during feeding. Fall migration differed from spring migration in several ways: 1) different species composition, 2) lower densities of staging birds, 3) different patterns of habitat use, and 4) less habitat segregation between species.

Forty-five nests of six species of shorebirds were located along 52 km of transects. The peak of nest initiation was between 25 May and 31 May. Over 75% of the nests occurred in three habitat types, all of which were dominated by varying degrees of sedge, grass, and moss.

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## INTRODUCTION

This study examines the importance of the eastern Copper River Delta (ECRD) to migrating and breeding shorebirds. Specifically, the phenology, species composition, relative abundance, patterns of habitat use, and resource partitioning by spring and fall migrants are examined, as well as the phenology, distribution, density and habitat preferences of breeding shorebirds. This research was part of a larger project investigating all birds on the ECRD (see Mickelson et al. 1980).

While the western Copper River Delta is one of the most extensively studied coastal wetlands in Alaska (Hansen 1962; Shepherd 1965; Crow 1968; Chapman et al. 1969; Isleib and Kessel 1973; Bromley 1976; Senner 1977, 1979; Isleib 1979), little work has been done on the eastern delta. The hydrology and resulting plant communities of the eastern delta are considerably different from the western delta, and these differences are evident in the avifauna. The best documented example is the dusky Canada goose (Branta canadensis occidentalis), which nests in densities of around 60 nests per km<sup>2</sup> on the western delta (Bromley 1976) compared to 3.2 nests per km<sup>2</sup> on the eastern delta (Mickelson et al. 1980).

For migrating birds using the Pacific Flyway, the Copper River Delta is one of the few sizeable areas north of Washington State that offers suitable staging habitat. Senner (1977) described the Copper River Delta region as "an isolated break or habitat island along North America's North Pacific Coast, a region otherwise dominated by fjord-like coastal topography with limited intertidal habitats."

Because there are so few sizeable staging areas on the Gulf of Alaska coast and because of the short duration of the migratory movement, spectacular concentrations of shorebirds occur on the intertidal mudflats and offshore waters of the Copper River Delta each spring. Isleib (1979) reported concentrations in spring of up to 100,000 shorebirds per km<sup>2</sup> on the western Copper River delta, and estimated that the annual spring flight through the region is somewhere near 20 million shorebirds. Thirty-six shorebird species have been recorded on the Copper River Delta and adjacent habitats by Isleib (1979) and he regards 23 species as "regular and occurring in noticeable volumes." The duration of the spring shorebird movement is approximately five weeks, with the vast majority of birds passing through during a two week period beginning at the end of April.

Senner (1979) presented solid evidence, based on an energetics study, that the intertidal zone of the Copper River Delta and adjacent areas is critical habitat during spring migration for the two most abundant spring migrants, dunlins (Calidris alpina) and western sandpipers (C. mauri). Senner contended that these two species, and probably other shorebird populations, are dependent upon the food resources available on the intertidal mudflats during spring migration. While staging on the Copper River Delta, these birds replenish their fat reserves for the last leg of migration and for the impending energy-demanding reproductive phase of their annual cycle.

The values of acquiring data on avian habitat relationships on the ECRD are several. First, the coastal wetlands of the Gulf of Alaska are close to many development activities occurring in Alaska. The most

obvious activity, and potentially the most perilous to coastal habitat and wildlife, is the development of the petroleum industry. An accident involving one of the many oil tankers leaving the Port of Valdez, or an offshore oil rig, could have catastrophic effects on coastal ecosystems. It is of eminent importance to collect baseline information on the functional ecology of coastal systems so that, in the event of an oil spill, environmental damage can be assessed accurately and future management can proceed with a substantive knowledge of how the systems functioned in their natural state. The ECRD deserves special attention in this regard because it is part of a system that has already been identified as being of high value for migratory birds (King and Lensink 1974), commercially valuable anadromous fish (Gussey 1978), and other wildlife resources.

Secondly, the plant communities on the ECRD are undergoing rapid successional changes due to the uplift caused by the 1964 Great Alaska Earthquake. It is of considerable interest to evaluate the effects of these changes on wildlife populations.

Finally, human use of the ECRD has been increasing rapidly in recent years. Regular low level floatplane flights, frequent take-offs and landings, and airboat traffic have become conspicuous features of the human presence. While passive management has worked well in the past, it may be inadequate as disturbance levels increase in the future. Delineation of critical habitats and vulnerable periods for wildlife is a prerequisite to effective management under these conditions.

## STUDY SITE

The Copper River Delta is located between 60° and 60°30'N. latitude and 144° and 146°W. longitude. The mouth of the Copper River is approximately 50 km east of the town of Cordova (Figure 1). The 650+ km<sup>2</sup> wetland lies in the western hemlock (Tsuga heterophylla) - Sitka spruce (Picea sitchensis) coastal rainforest ecoregion of southcentral Alaska. Rugged mountains, glaciers, and a maritime climate resulting in high annual precipitation are prominent features of this region.

Reimnitz and Marshall (1965), Reimnitz (1966), and Galloway (1976) discussed the geologic history and geomorphology of the Copper River Delta. Galloway offered the most succinct physical description of the delta: "the Copper River has prograded a marine dominated fan-delta onto the deep tectonically active northern shelf of the Gulf of Alaska. The morphology and internal stratigraphy of the delta system are products of the sporadic influx of great volumes of bed load sediment into a basin characterized by a high wave, tide, and current energy flux." Thus three major factors influence the geologic setting of the delta: 1) large quantities of alluvial sediment, 2) intense marine reworking of the prograding deltaic sediments, and 3) tectonic instability.

Reimnitz (1966) calculated that the Copper River transports  $107 \times 10^6$  metric tons of sediment annually. Galloway (1976) compared Reimnitz' figures with the Mississippi River and stated that "with 1/6 the discharge, the Copper River transports 1/4 as much sediment and a greater volume of sand [than the Mississippi]."

Marine reworking of the effluent sediment load of both the Bering

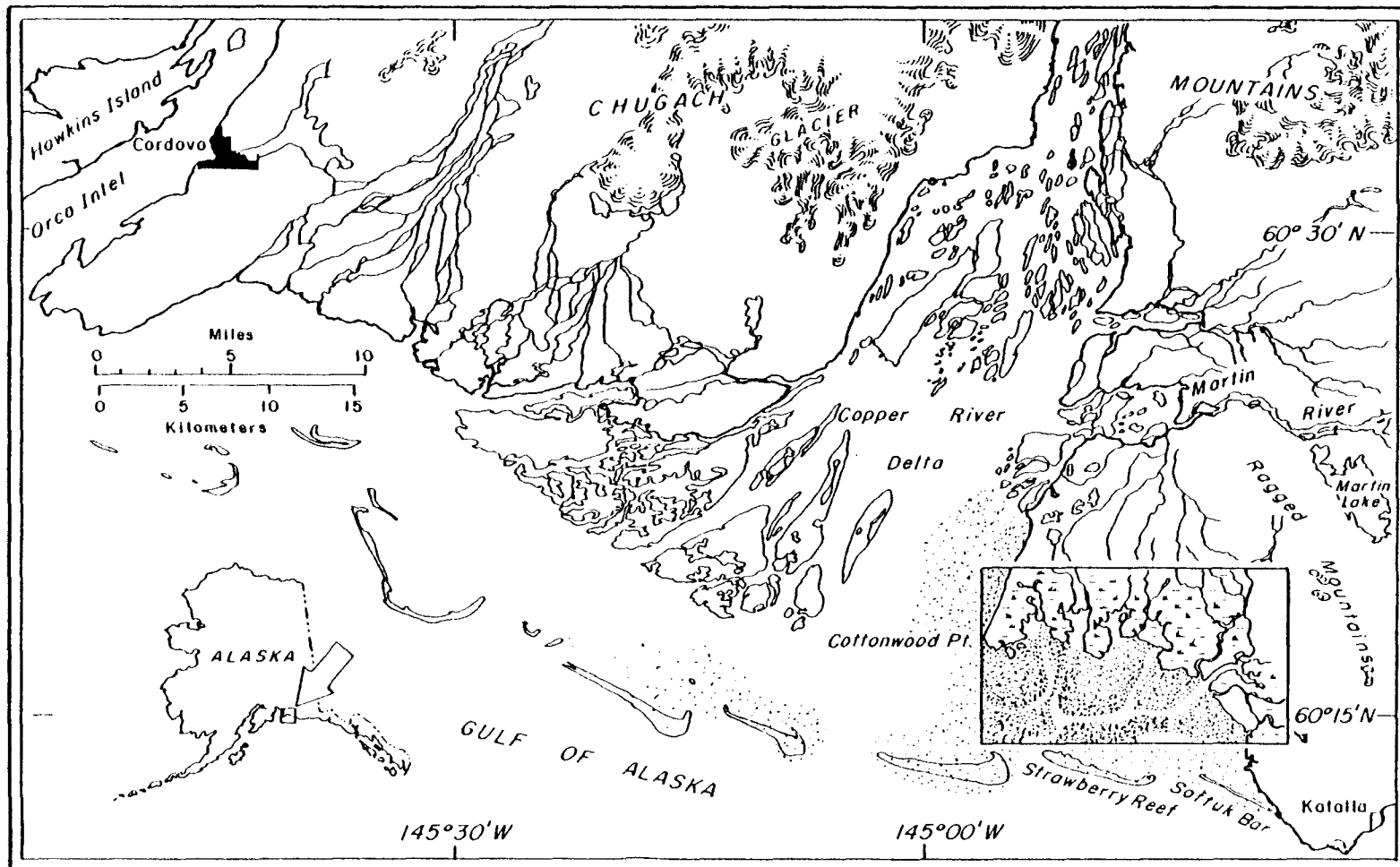


Figure 1. Location of eastern Copper River Delta study area, Alaska.

and Copper Rivers has resulted in a string of barrier islands that lie offshore from the delta margin (Figure 1). These barrier islands absorb much of the high energy waves from the Gulf of Alaska, thus creating an intertidal lagoon. The majority of the sediment load is swept to the west by westerly marine currents. This longshore transport results in a sediment plume that extends through Orca Inlet and into Prince William Sound (Galloway 1976).

Tidal influence is considerable on the Copper River Delta. Maximum tidal range in the Cordova district is 6.5 m during the highest spring tides and averages 3.5 m (U.S. Coast and Geodetic Survey, Tide Tables). This wide tidal range coupled with the prograding delta margin account for the existence of the 1000+ km<sup>2</sup> of intertidal mudflats associated with the Copper and Bering Rivers.

The Copper River Delta has a long history of seismic activity. Major tectonic uplifts, such as that caused by the Great Alaska Earthquake of 1964 (8.5 on the Richter Scale, epicenter 130 km NW of the Copper River) periodically disrupt the general trend of subsidence. Reimnitz and Marshall (1965) calculated that the gradual subsidence of the delta proceeded at a rate of 25-38 mm/yr. The 1964 earthquake interrupted this trend as the delta was uplifted between 1.8 and 3 m (Reimnitz and Marshall 1966).

Plant communities are particularly vulnerable to the violent disruptions caused by earthquakes and the more subtle changes that result from gradual subsidence. Evidence of these changes has been documented by the discovery of two buried forest horizons on the delta, dated by C-14 techniques at 750 and 1700 years old (Reimnitz 1972). At



present, shrub and spruce invasion of the uplifted supratidal marsh is occurring rapidly and a new forest community over much of the delta appears imminent in the next century, barring another cataclysmic seismic event.

#### Eastern Copper River Delta

The study site encompassed about 50 km<sup>2</sup> of the 150+ km<sup>2</sup> supratidal marsh and much of the 75+ km<sup>2</sup> intertidal mudflats and saltmarsh that collectively comprise the ECRD. The perimeter of the study area and names of sloughs and other landmarks are shown in Figure 2. For the most part, the study area was defined by natural boundaries: the Gulf of Alaska to the south, the Ragged Mountains to the east, and the main channel of the Copper River to the west. The northern boundary was defined primarily by the transition into dense shrub-dominated marsh.

There are several dominant habitat types in the study area that I classified according to Kessel (1979): 1) offshore barrier islands, 2) intertidal lagoons, 3) intertidal mud and sandflats, 4) saltgrass meadows, 5) supratidal wet meadows, 6) sloughs, 7) ponds, and 8) isolated upland habitats. The area north of the wet meadow (outside of the study area) is mostly medium shrub thicket (1.4-2.4 m high).

The barrier islands are essentially large sand dunes and the dominant vegetation is beach rye grass (Elymus arenarius). Strawberry Reef, the only barrier island I visited, also had small stands of spruce trees, alders (Alnus sinuata), and willows (Salix spp.). A fairly extensive and productive saltmarsh is developing on the inner side of this island. It differs markedly from those developing on the north

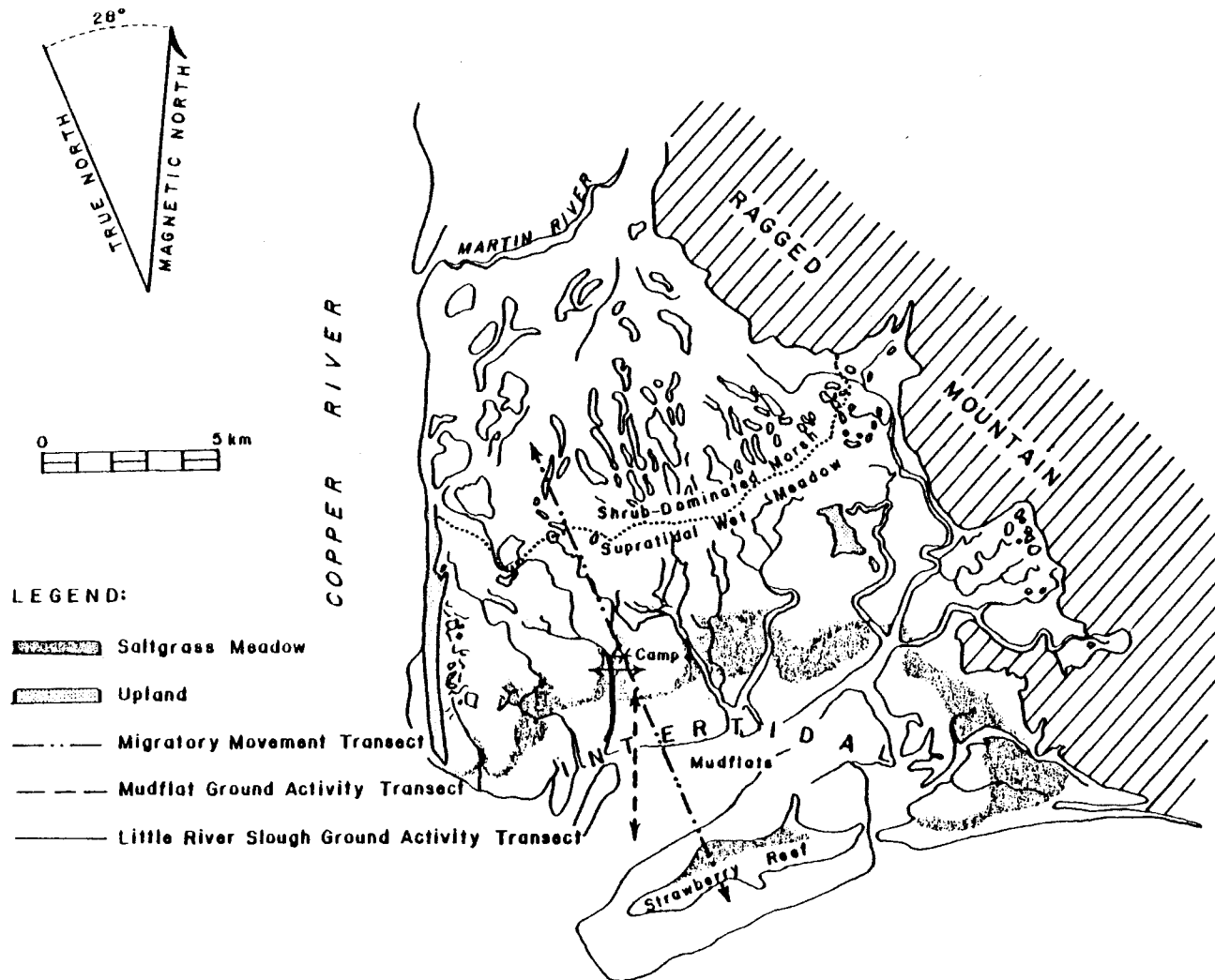


Figure 2. Major habitat types and transect locations on the eastern Copper River Delta study area, Alaska.

side of the lagoon in having several productive tidally-influenced ponds, and lush growths of saltgrass meadow vegetation.

The intertidal mudflats are inundated twice daily and support a rich infauna. Feder and Mueller (1972), Zimmerman and Merrell (1976), and Senner (1977) discussed the intertidal invertebrate fauna. Vascular vegetation is absent. At high tide this area is intertidal lagoon habitat.

The saltgrass meadow habitat on the ECRD is limited to a narrow strip along the seaward margin of the supratidal wet meadow (hereafter wet meadow). Prior to the uplift caused by the 1964 earthquake, the area under tidal influence was considerably greater. It included a large proportion of the present wet meadow, which is not now inundated even during the highest spring tides. All of the saltgrass habitat that exists now appears to have developed since the earthquake on areas that formerly were bare mudflats. The dominant pioneering plants are halophytes: alkali grass (Puccinellia spp.), plantain (Plantago maritima), and arrowgrass (Triglochin maritimum). This primary succession is relatively slow and most of the saltgrass meadow is sparsely vegetated.

The wet meadow is also in a state of transition. Areas formerly inundated by tides are now being invaded by spruce seedlings, willows, and alders, species that were not present prior to the earthquake. The best developed shrub communities are along the levees of sloughs. Most of the wet meadow is a mosaic of microhabitats dominated in different areas by sedge, moss, grass, or shrubs. In general, the wet meadow is characterized by a thick mat of mosses that are present everywhere

except pond bottoms, slough banks, and depressions that are at least seasonally flooded. Moss cover is thickest on slough levees and other well-drained areas. Shrub growth is evident throughout the wet meadow, but is generally sparse in terms of percent cover. The western portions of the study area appear better drained than the eastern portions.

An integral component of the ECRD is the extensive network of sloughs. Tidal influence is significant, but sloughs never overflow their banks except far up in the wet meadow after long periods of heavy rain. There is a conspicuous lack of ponds, and sloughs provide the majority of open water habitat. Saltgrass meadows are forming along the mouths of the sloughs and for a short distance upstream.

There are several small isolated upland habitats. Two spruce-covered rocky outcrops lie between Gus Wilson Slough and Cudahy Slough, and another lies 5 km further east. A series of sand dunes along the main channel of the Copper River supports cottonwoods (Populus balsamifera) and dense, tall alders (2.4-4.9 m high).

## METHODS

The main field camp on the ECRD was established along Little River Slough on 21 April 1978. I was active in the field from this date to 30 September 1978. Other researchers from the University of Alaska remained in the field until 18 October 1978 and returned in 1979 from 15 April to 22 October. Some of the data collected in October 1978 and during the 1979 field season (see Mickelson et al. 1980) will be presented and discussed.

### Migration

We monitored bird movements across a north-south line transect for 15 minutes every two hours during daylight, 5 a.m. - 7:15 p.m. ADST, from 23 April to 16 May and more sporadically during daylight from 22 August to 16 October. Observations were made from a 4 m high tower located approximately 50 m south of the main camp. The locations of the camp and migratory movement transect are shown in Figure 2. A minimum of two observers participated in each 15 minute count; during the peak of spring migration at least three and often four observers participated, with one person serving as a recorder.

The tower was located at the wet meadow/saltgrass meadow interface so observers looking south monitored bird movements over mudflats and open water, and observers looking north monitored bird movements over the marsh. For each observation, the following data were recorded: time of observation, species or group of birds observed (e.g., unidentified mixed flock of shorebirds), number of birds, their flight direction,

altitude, and their location with respect to topographical features (e.g., flight over vegetated marsh, mudflats, or open water).

Ground activities and patterns of habitat use by migrant shorebirds were monitored using belt transects. In spring, monitoring activities were concentrated on the intertidal mudflats, which were used by the vast majority of staging shorebirds. During fall migration patterns of habitat use by shorebirds were different, so a second ground activity transect was established on Little River Slough.

The mudflat ground activity transect was a 100 m x 2.5 km belt transect that extended from the seaward edge of the saltgrass meadow, south across the mudflats towards Strawberry Reef Island (Figure 2). The transect was marked at 100 m intervals with conduit piping sunk vertically into the substrate and painted different colors for easy recognition at a distance. After trying different techniques, I concluded that the only accurate way to sample on this transect throughout the tidal cycle was to stand adjacent to the transect and follow the tide in and out on foot. I stood approximately 100 m north of the incoming or receding tide and used a 15-40x spotting scope on a tripod to make observations. Birds were monitored over the entire length of the transect whenever possible. This was difficult when visibility was poor and at the lower tidal stages, but this problem was minimized by the tendency of the birds to stay close to the tide line. Investigator disturbance is difficult to assess; however, I feel that it was negligible since I frequently was within 10 m of birds without any apparent disruption of their activity.

For all species on the ground in the transect, I recorded their numbers, activity, location with respect to the transect segments, and spatial position relative to the tideline, tide channels, or tide pools. The position of the incoming or receding tide was constantly monitored. The activity variables were:

- 1 = feeding
- 2 = loafing (resting or inactivity)
- 3 = preening
- 4 = courtship
- 5 = copulation
- 6 = interspecific aggressive interaction
- 7 = intraspecific aggressive interaction

For the purposes of most of the data analysis, only the feeding and loafing activities were used. Preening and aggressive interactions typically occurred briefly while birds were either loafing or feeding, and courtship and copulation were rarely observed. This transect was monitored daily from 29 April to 19 May in spring, and from 25 July to 15 August in fall. Bird densities on the intertidal mudflats were too low in fall to yield useful results from this transect. Monitoring of this transect was suspended before the end of fall migration so more time could be spent monitoring the Little River Slough ground activity transect. However, time spent on the mudflats in the fall did allow me to gain insight into the species composition, relative abundance, and patterns of habitat use on the intertidal mudflats.

The Little River Slough ground activity transect was located near

the main camp and was monitored from 25 July to 29 September. Nearly all shorebird movements were up and down the north-south oriented slough, so the transect was established perpendicular to the slough (Figure 2). The transect was 100 m x 500 m and passed through three distinct habitat types: saltgrass meadow, exposed mud, and water. The amount of these three habitat types available to shorebirds varied with of the level of the tide. I monitored bird activities for 30 minutes out of every four hours. During the summer months four observation periods per day were possible, but during September only three counts per day were possible due to shorter days.

All birds in the transect were identified to species and counted. In addition, their activity, habitat type, and time spent in the transect were recorded. Tide level was recorded at the start of each count. I also monitored aerial movements of birds through the transect and recorded bird species, numbers, direction, and altitude.

During spring migration, counts of the number of shorebirds visible at 3/4 incoming tide on a 2.5 km<sup>2</sup> plot in the vicinity of the mudflat ground activity transect were made to approximate the density of birds staging on the study area. Other investigators (Storer 1951 and Recher 1966) used similar census techniques on the ebb tide. I found that the greatest concentrations of shorebirds, and hence the best time to census, occurred soon after the tide reached the 3/4 incoming stage.

#### Breeding

We searched for nests along 11 belt transects spaced at 1.6 km



intervals that corresponded to the north-south section lines of U.S. Geological Survey quadrangle maps. The 11 transects extended from the upper intertidal mudflats to the southern edge of the shrub marsh and ranged from 3 to 9 km in length. Total length of the 11 transects was 52 km. From two to six, but usually three, observers walked at evenly spaced intervals along each of the 30 m wide transects.

We plotted nest locations on the maps, placed a wooden tongue depressor along the rim of each nest, and tied a piece of bright flagging tape at least 4 m away to facilitate relocation. Information recorded at each nest site included: presence or absence of adults, stage of incubation as determined by floatation (Westerskov 1950), nest materials, vegetation type, substrate type, proximity of water and water body type, and physiographic type. We walked the 11 transects four times during the nesting and early brood-rearing periods. The same data were also collected for nests encountered off transects.

We assessed and mapped vegetation types visually by percent cover along the 11 belt transects. Hand drawn maps (scale: 13 cm = 1 km), prepared from enlarged (28x) color infrared photographs (scale: 1:60,000) taken by the National Oceanic and Atmospheric Administration on 2 October 1976, were used for this purpose. Eight vegetation types were identified and the percent cover of each vegetation type was extrapolated from 1.56 km<sup>2</sup> of transects to the 91 km<sup>2</sup> study area. We also identified six physiographic types, four substrate types, and four water body types.

## Data Analysis

To analyze data collected on the migratory movement transect we treated each set of 15 minute migration watches for each day as random samples. We then calculated the mean number per hour moving in each direction each day.

Chi-square tests were used to analyze the ground activity data. Hypotheses were tested to determine if the activity patterns of shorebirds were independent of tidal stage and the location of the birds relative to the tideline. Additional hypotheses were tested to determine if there were interspecific differences in activity patterns. To insure independence of observations only one observation for each species (the one with the greatest number of birds) was used from each observation period.

Estimates of nesting density were made by a simple extrapolation from nests found on the transects to the entire study area. Since transects were of unequal sizes (from 7.5 - 20.3 ha), a ratio estimator was used and each transect was treated as an unbiased sample. Number of nests was the variate of interest and area was the supplementary variate (see Mickelson et al. In press).

## SPRING MIGRATION

### Results

Common snipe (Capella gallinago) and greater yellowlegs (Tringa melanoleucus) were present in low numbers on the ECRD when field activities commenced on 21 April 1978. Spring migration continued until the end of May; the main passage of shorebirds occurred during the last week of April and the first two weeks of May (Figure 3). The first wave of birds arrived on 25 April when an estimated 650 birds per hour moved west across the transect line. Following this first wave, a series of peaks ensued until 16 May, after which numbers dropped dramatically. The two largest peaks in abundance occurred on 1 May (1725 birds per hour) and 11 May (3775 birds per hour). Nearly all of the shorebird sightings on the migratory movement transect were made over the intertidal mudflats.

Daily surveys of staging shorebirds on the intertidal mudflats revealed that over 99% of the shorebirds were of four species: western sandpipers, dunlins, short-billed dowitchers (Limnodromus griseus), and long-billed dowitchers (L. scolopaceous). It was usually impossible to distinguish between the two dowitcher species so they have been lumped and collectively referred to as dowitchers. Counts of these four species on an area approximately 2.5 km<sup>2</sup> were made daily at 3/4 incoming tide (Figure 4). The relative abundance of these species during spring migration was 56% western sandpipers, 27% dunlins, and 17% dowitchers. The greatest concentration of staging shorebirds occurred on 11 May when

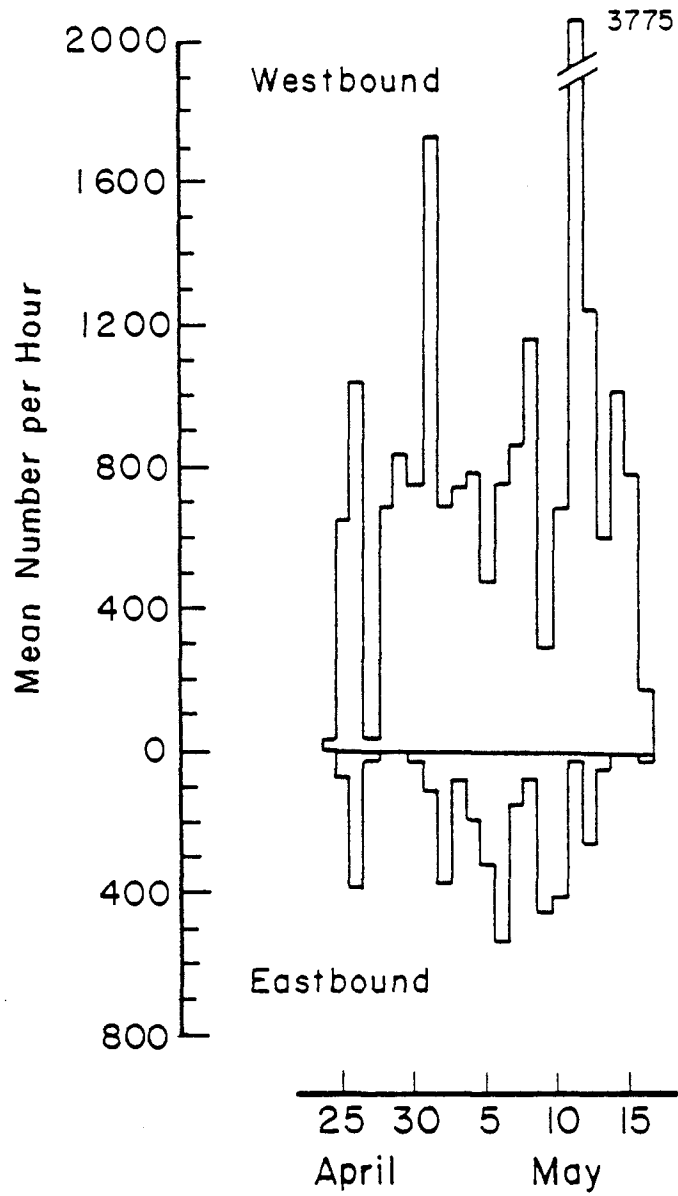


Figure 3. Mean numbers of eastbound and westbound shorebirds per hour during spring migration 1978 on the eastern Copper River Delta, Alaska.

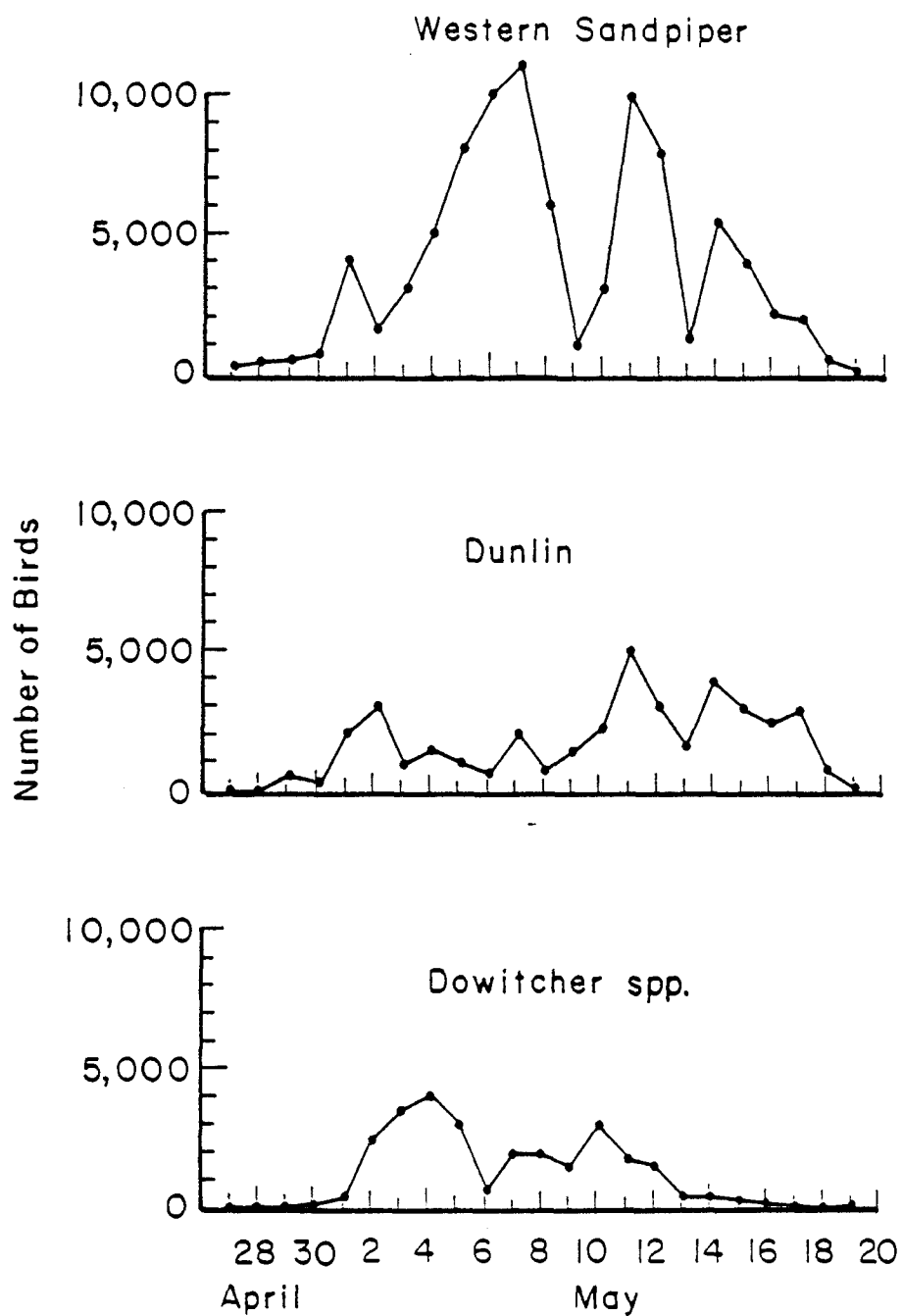


Figure 4. Number of shorebirds counted daily during spring migration 1978 at 3/4 incoming tide on approximately 2.5 km<sup>2</sup> of intertidal mudflats on the eastern Copper River Delta, Alaska.

approximately 10,000 western sandpipers, 5000 dunlins, and 1800 dowitchers were recorded on the 2.5 km<sup>2</sup> plot.

Twenty-two shorebird species were recorded during spring migration in 1978. Table 1 gives the status, phenology, and preferred habitats of spring migrant shorebirds. Species are presented approximately in the order of their relative abundance.

The activity patterns of spring migrant shorebirds staging on the intertidal mudflats were monitored from 29 April to 19 May 1978. Activity pattern, as used here, is defined as the activity of a bird and the temporal and spatial setting of the activity relative to the tide. Figure 5 gives the percentage of western sandpipers, dunlins, and dowitchers engaged in each activity at different tidal stages.

Western sandpipers were actively feeding during all tidal stages in daylight hours when the transect was monitored. A small percentage of western sandpipers loafed at 3/4 incoming tide. Dunlins and dowitchers showed a much greater tendency to loaf at high tidal stages. Dunlins began to loaf at 1/2 incoming tide and peak numbers of loafing birds occurred at 3/4 incoming tide. Dowitchers showed a similar pattern except 33% of these birds were also observed loafing at low tide.

The location of feeding and loafing birds relative to the tide is given in Table 2. Western sandpipers tended to feed and loaf greater than 10 m from the tide line. Dunlins fed primarily while on exposed mud, both within and greater than 10 m from the tide line. When loafing, dunlins were greater than 10 m from the tide line 90% of the time. Dowitchers fed mainly in water, both at the tide line and in tide

Table 1. Status, phenology, and habitat preferences of spring migrant shorebirds on the eastern Copper River Delta, Alaska in 1978.

Species	Status	Date first seen	Peak abundance	Date last seen	Primary habitat <sup>5</sup>	Secondary habitat <sup>5</sup>
Western sandpiper	A	4-27	5-7	5-20	MF	S
Dunlin	A	4-29	5-11	5-26	MF	-
Dowitcher spp.	A	4-30	5-4	5-29 <sup>3</sup>	MF	S
Least sandpiper	C	4-27	5-6	5-27 <sup>3</sup>	SGM	S
Northern phalarope	C	5-3	5-19	5-27 <sup>3</sup>	IL	S
Common snipe	C	4-21 <sup>2</sup>	-	- <sup>3</sup>	SWM	P
Whimbrel	FC	5-5	5-20	6-20 <sup>4</sup>	SWM	MF
Greater yellowlegs	FC	4-21 <sup>2</sup>	5-11	5-15 <sup>3</sup>	S	MF
Pectoral sandpiper	FC	5-7	5-21	5-30	SWM	SGM
Black-bellied plover	FC	4-30	5-19	5-25	MF	-
Semipalmated plover	FC	4-27	-	- <sup>3</sup>	SGM	S
American golden plover	UC	5-1	-	5-20	MF	-
Ruddy turnstone	UC	5-8	-	5-22	MF	-
Black turnstone	UC	5-7	-	5-8	MF	-
Spotted sandpiper	UC	5-4	-	5-7	S	-
Lesser yellowlegs	UC	4-30	-	5-20	S	MF
Red knot	R	5-10	-	5-23	S	-
Marbled godwit	R	4-30	-	5-8	MF	-
Hudsonian godwit	R	4-30	-	5-8	MF	-
Bristle-thighed curlew	R	5-19	-	5-19	MF	-
Bar-tailed godwit	CA	5-8	-	5-8	MF	-

<sup>1</sup>Status codes

A = abundant  
C = common  
FC = fairly common  
UC = uncommon  
R = rare  
CA = casual

<sup>5</sup>Habitat codes

MF = intertidal mudflat  
SGM = saltgrass meadow  
SWM = supratidal wet meadow  
IL = intertidal lagoon  
S = slough  
P = pond

<sup>2</sup>Birds already present when investigators arrived

<sup>3</sup>Local breeders, last date migrants were seen was difficult to determine

<sup>4</sup>Nonbreeding summer visitors

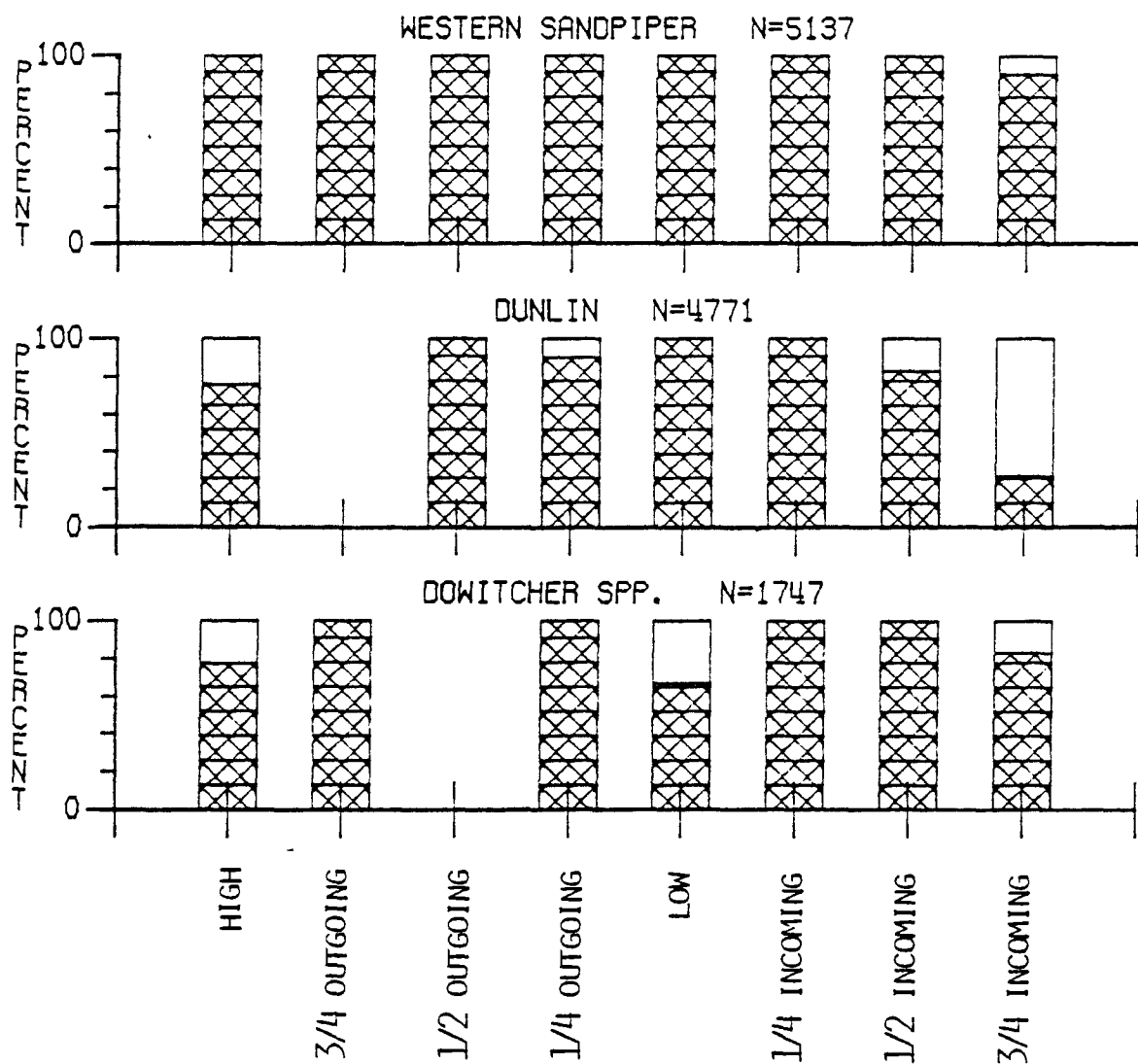


Figure 5. Percent of shorebirds engaged in feeding (shaded areas) and loafing (unshaded areas) during different tidal stages on intertidal mudflats during spring migration 1978 on the eastern Copper River Delta, Alaska.



Table 2. Location of feeding and loafing spring migrant shorebirds by percent and actual numbers (in parentheses) in four microhabitats on the intertidal mudflats on the eastern Copper River Delta, Alaska in 1978.

Location	Western sandpiper		Dunlin		Dowitcher spp.	
	feeding	loafing	feeding	loafing	feeding	loafing
In water	2 (125)	0	4 (113)	3 (54)	45 (702)	33 (64)
Tide pools	5 (275)	0	13 (352)	0	21 (329)	6 (11)
Out of water but within 10 m of tide line	20 (1023)	0	35 (934)	7 (153)	15 (235)	8 (16)
Out of water and greater than 10 m from tide line	72 (3614)	100 (100)	47 (1245)	90 (1675)	19 (289)	53 (101)
Total	99 (5037)	100 (100)	99 (2644)	100 (2127)	100 (1555)	100 (192)

pools. Most dowitchers loafed on exposed mud greater than 10 m from the tide line, although some loafed in water.

Three null hypotheses were tested for each species to determine whether activity patterns were influenced by tides. Three additional hypotheses were tested to determine whether there were interspecific differences in these activity patterns. These hypotheses and the results of the chi square analyses are given in Table 3. In all cases the null hypotheses were rejected, indicating that both activity and location of the birds were dependent on the stage of the tide and that the activities of birds were also dependent on their location. Rejection of the three hypotheses testing interspecific relationships indicated that there were both temporal and spatial differences in the activity patterns of these species.

#### Discussion

Spring migration in 1978 was late. Peak abundance of shorebirds normally occurs during the first week of May (Isleib 1979), but according to both the migratory movement transect data (Figure 3) and the mudflat ground censuses (Figure 4), the peak of shorebird abundance in 1978 occurred on 11 May. While dunlins were the only species that reached peak abundance on 11 May, cumulatively there were more shorebirds moving through and staging on the ECRD on this day than any single day. The phenology of shorebird migration on the ECRD in 1979 more closely resembled the phenology of a normal year. A peak movement of 3800 birds per hour was recorded on the migratory movement transect

Table 3. The null hypotheses and chi square statistics for shorebird ground activity patterns during spring migration 1978 on the eastern Copper River Delta, Alaska.

Species	Hypothesis	$\chi^2$	df <sup>1</sup>	p	Accept or Reject
Western sandpiper	Activity is independent of tidal stage	127.4	7	.01	Reject
	Activity is independent of location	39.1	3	.01	Reject
	Location is independent of tidal stage	2395.3	15	.01	Reject
Dunlin	Activity is independent of tidal stage	1521.1	6	.01	Reject
	Activity is independent of location	1034.1	3	.01	Reject
	Location is independent of tidal stage	3832.0	12	.01	Reject
Dowitcher spp.	Activity is independent of tidal stage	224.0	6	.01	Reject
	Activity is independent of location	120.4	3	.01	Reject
	Location is independent of tidal stage	1091.4	18	.01	Reject
All species	All species feed in the same location	3084.9	6	.01	Reject
	All species loaf in the same location	512.9	6	.01	Reject
	All species feed at the same tidal stage	1167.2	14	.01	Reject

<sup>1</sup>degrees of freedom

on 5 May 1979 (Mickelson et al. 1980).

Annual phenological variations in shorebird migration are probably best attributed to weather, both locally and along the entire Pacific Flyway. Recher (1966) stated that "It is generally accepted that the rate and duration of migratory movements [of shorebirds] are affected by prevailing climatic conditions." The arrival, duration of stay, and departure of shorebirds on the ECRD seemed to be profoundly affected by weather, especially wind. At higher tidal stages birds became restless, feeding activity tapered off, and the birds regularly "boiled up" in mixed species flocks swarming in tight but fluid formations, often alighting at the same place from which they took off. Considering the high energy demands of migration, it seems paradoxical that these birds would expend energy on an activity that gets them no closer to their breeding grounds. It is this paradox, however, that leads one to suspect that this behavior has some specific functions. Local swarming flight by shorebirds at 3/4 incoming and high tide on the ECRD had two possible conclusions. Birds either resettled on the mudflats or they quickly gained hundreds of meters of altitude and disappeared, presumably continuing their migration. It was my distinct impression that while wheeling around in all directions and at different altitudes the birds were testing migrating conditions, particularly the wind, and if conditions were favorable the birds departed. A study conducted in the midwest on migrating shorebirds (Brooks 1965) concluded that wind was "the primary or even sole weather stimulus to continuing migration for shorebirds." Another probable function of this type of behavior was

to reinforce flock bonds.

One of the more interesting aspects of migrant shorebird ecology is the question of how dense mixed species aggregations of shorebirds, with seemingly similar habitat requirements, are able to partition resources and avoid competitive exclusion. Recent studies (Recher 1966, Recher and Recher 1969, Goss-Custard 1970, Burger et al. 1977, Senner 1977, Burger et al. 1979) have demonstrated that migrant shorebirds do indeed show considerable resource overlap. A solid theoretical framework dealing with resource partitioning, niche breadth, and niche overlap in bird communities has been established (see Cody 1974), but for several reasons many of the theories, developed primarily from work with passerines, do not apply to migrating shorebirds. Shorebirds staging on intertidal mudflats are unable to partition space in the same fashion as forest and shrubland birds because intertidal mudflats lack vascular vegetation and hence foliage height diversity. In addition, the cyclic ebb and flow of the tide constantly changes the available feeding space and the diversity and availability of prey items in the intertidal zone (Burger et al. 1977). Thus theories of food and space partitioning developed in less dynamic environments do not apply well to intertidal habitats. Finally, migrant shorebird activity patterns are cued to tidal periodicity rather than diel periodicity (Burger et al. 1977); hence, habitat segregation by temporal means operates in a different manner than in terrestrial communities. These characteristics of migrant shorebird-habitat relationships must be kept in mind during any discussion of resource partitioning by these birds.

The most critical resources for staging shorebirds appear to be food and space. Several researchers have argued that space is potentially more limiting than food (Recher 1966, Burger et al. 1979). However, if a bird is denied access to space it is probably being denied access to food resources as well. An alternate approach is to regard space as a potentially limiting resource only as it relates to gaining access to food. Space for loafing birds does not appear to be limiting, as evidenced by the tendency of loafing shorebirds to form extremely dense mixed species flocks with infrequent aggressive interactions (Recher and Recher 1969, Goss-Custard 1970, Burger et al. 1979). While birds are foraging, however, aggressive interactions between individuals are much more frequent (Recher and Recher 1969, Goss-Custard 1970, Burger et al. 1979) indicating that interference competition is occurring (Pianka 1976). Food resources do not occur uniformly on intertidal habitats; rather, they occur in zones and are often patchy within those zones (Bengston and Svensson 1968, Wolff 1969). Foraging shorebirds occur in those areas where the food resources are in sufficient densities to provide enough food in a given amount of time to support their energy requirements (Wolff 1969). In addition, many species forage in large flocks because flocking facilitates predator detection (Goss-Custard 1970). However, if flock size becomes too large and dense, feeding efficiency decreases. While the actual quantity of food may not be limiting, access to the food resources is restricted and the result is competitive interactions between individuals. Whether the birds are competing for food or space becomes a circular argument

because the two are inseparable. An appropriate description of this competitive situation perhaps would be to call it competition for foraging space.

Competition for resources in short supply has led to the evolution of aggression which acts as a population spacing mechanism (Recher and Recher 1969). Since aggressive interactions require individuals to spend time and energy that might otherwise be spent procuring resources, it is always advantageous for individuals to avoid competitive interactions whenever possible (Pianka 1976). The following discussion describes mechanisms by which shorebirds avoid deleterious levels of competition for foraging space.

Birds are able to reduce or eliminate competition by either behavioral or morphological mechanisms (MacArthur and Levins 1964). Behavioral mechanisms of resource partitioning provide spatial or temporal segregation between species while segregation by morphological divergence results in differences in resource use. Seldom is any one mechanism of niche segregation a perfect predictor of the interactions between two species (Ashmole 1968). Rather, it is the cumulative difference between two species across the entire resource spectrum that determines the degree of overlap between two species.

The most effective way for two organisms or groups of organisms to avoid competition is to avoid habitat overlap completely. In the Copper River Delta region macrohabitat segregation was quite evident among spring migrant shorebirds. Of the 23 shorebird species cited by Isleib (1979) as "regular and occurring in noticeable volumes" along the north

Gulf coast in spring, only about 11 species occurred regularly and in noticeable numbers on the ECRD. Surfbirds (Aphriza virgata), red knots (Calidris canutus), ruddy turnstones (Arenaria interpres), black turnstones (A. melanocephala), sanderlings (C. alba), and red phalaropes (Phalaropus fulicarius) all occur in 10,000's or 100,000's during spring migration in the north gulf coast-Prince William Sound region (Isleib and Kessel 1973) but were uncommon, rare, or absent on the ECRD study area (Table 1). These species could have been frequenting other habitat types that were not included on the study area, such as rocky shorelines, offshore barrier islands with sandy high energy beaches, and offshore waters.

Macrohabitat segregation also occurred on the ECRD study area. For example, dunlins, western sandpipers, dowitchers, and black-bellied plovers (Pluvialis squatarola) made extensive use of the intertidal mudflats but were seldom seen in saltgrass meadow or supratidal wet meadow habitats. Conversely, least sandpipers (Calidris minutilla), common snipe, and pectoral sandpipers (Calidris melanotos) were observed using the vegetated habitats almost exclusively.

Since species with similar feeding apparatus have the greatest potential for overlap of food resources (Burton 1974), morphologically similar species that migrate at the same time predictably would use different habitats (Recher 1966). On the east coast of North America, Recher (1966) found that western and least sandpipers segregate in much the same fashion as on the ECRD: western sandpipers on the mudflats and least sandpipers in the vegetated marsh. In California however, less



marsh habitat is available so complete habitat segregation between western and least sandpipers is not possible. Under these circumstances aggressive interactions between these two species were reported to be more frequent than among any other two shorebird species.

Long-billed dowitchers, short-billed dowitchers, and common snipe constitute another group of morphologically similar species with a high potential for food overlap. On the ECRD common snipe were never observed on intertidal mudflats and thus were completely segregated from the intertidal dowitcher species. No macrohabitat segregation was evident between the two dowitcher species.

Habitat segregation within habitat types, or microhabitat segregation, was another important means by which shorebirds avoided interspecific competition. Since the vast majority of shorebirds used intertidal mudflats during spring migration, research efforts were concentrated in this habitat type in an effort to discern interspecific differences in the use of space. As previously mentioned, spatial partitioning in this habitat can only occur on a horizontal plane.

Chi square analysis of shorebird activity data revealed that for all species examined, activity was dependent on location (Table 3). In other words, birds tended to feed and loaf in different habitats. There were also species-specific microhabitat preferences for feeding birds ( $\chi^2=3084.9, df=6, p<.01$ ). Examination of feeding bird observations in Table 2 shows where each species was feeding. It is not difficult to visualize a gradient of feeding birds starting with dowitchers in the water at tideline blending into an aggregation of birds dominated by

dunlins feeding on exposed mud but in close proximity to the tide line, finally grading into a group of birds dominated by western sandpipers spread out over the mudflats well away from the receding or incoming tide.

There were also significant interspecific differences in the microhabitat preferences of loafing birds ( $\chi^2=512.9, df=5, p<.01$ ). Although the differences were statistically significant, they were not as clearcut as for feeding birds (Table 2). That is, 100% of the western sandpipers, 90% of the dunlins, and 53% of the dowitchers loafed in the same microhabitat (on exposed mud, greater than 10 m from the tide line). Goss-Custard (1970) also reported that feeding shorebirds were considerably more dispersed than loafing shorebirds.

Because of difficulties in identifying dowitchers to species, I can not present data on the microhabitat preferences of long- and short-billed dowitchers. On the occasions when I felt I was able to make positive identifications, I could not discern differences in the patterns of microhabitat use between these two species.

There is a key distinction between the levels of resource partitioning that are accomplished by macro- and microhabitat segregation. Birds which segregate by macrohabitats have virtually no resource overlap. Birds which segregate by microhabitats on intertidal mudflats, while alleviating competition for foraging space, may still be competing for the same food resources because of the transitory nature of the microhabitats. That is, although birds may not feed in the same location at the same time, they still end up feeding in the same

locations and thus compete for the same food resources.

Just as there was macro- and microhabitat segregation by migrant shorebirds, there was also large scale and small scale temporal segregation. Large scale temporal segregation reduced both inter- and intraspecific competition for foraging space and was accomplished primarily by a staggering of the peaks in abundance of the most abundant species (Figure 4). Dowitchers peaked first on 4 May, followed by western sandpipers on 7 May, and by dunlins on 11 May. Furthermore, each of these species, or species groups, had several peaks of abundance during the migratory period. The selective advantage of having slight differences in species phenologies are that no changes in feeding strategies, patterns of habitat use, or morphology are required to reduce the levels of competition for foraging space. Urner and Storer (1949), Storer (1951), and Recher (1966) have reported the same phenomenon for spring migrant shorebirds at different locations in North America.

The distribution of the abundance of staging dowitchers during spring migration is also noteworthy (Figure 4). Distinct peaks were evident on 4 May and 11 May. Isleib and Kessel (1973) described short-billed dowitchers as abundant migrants usually arriving on the Copper River Delta during the last days of April, while long-billed dowitchers were described as common migrants arriving during the first week of May. Although my data can not fully support the hypothesis, it may be that the two peaks represent the respective peak passages of the two species. If this is the case, then temporal segregation appears to

be the primary means by which these two morphologically similar species segregate during spring migration.

Once again, it should be kept in mind, that although birds are avoiding competition for foraging space, they are still exploiting the same food resources, thus competition for food is not substantially reduced by temporal segregation. It is also doubtful that temporal segregation is a fail-safe mechanism to reduce competition even for foraging space. Since the movements of migrating shorebirds are dependent on prevailing weather conditions, it seems likely that in some years birds would be forced by weather to pile up in isolated staging habitats (such as the Copper River Delta). Nonetheless, this is but one of several means by which these birds avoid competitive strife and it appears to have worked well in 1978.

Chi square analysis of ground activity data revealed that all species do not feed at the same tidal stage ( $\chi^2=1167.2, df=14, p<.01$ ) indicating that there were interspecific temporal differences in activity patterns relative to tides. Senner (1977) reported the same activity patterns among western sandpipers and dunlins at Hartney Bay (50 km west of the ECRD) as I did on the ECRD (Figure 5). Western sandpipers fed during all tidal stages while dunlins were inclined to loaf during higher tidal stages. Senner did not document the activities of dowitchers, but in this study dowitchers showed an activity pattern that was quite similar to dunlins with one anomaly; 33% of the dowitchers recorded at low tide were loafing. Goss-Custard (1970) also reported the presence of loafing birds at low tide on open mudflats but

offered no explanation why birds would loaf during a time when prey is most readily available. Perhaps the birds are satiated after feeding intensely on the ebbing tide and are forced to rest by the capacity of their digestive system. Except for this anomaly, the activity patterns of these species were readily interpretable. Dunlins and dowitchers were more likely to loaf at high tidal stages because of reduced availability of preferred prey items and foraging space. Senner's (1977) invertebrate samples at Hartney Bay revealed that the mudflats exposed during high tides were almost totally devoid of infaunal organisms. Macoma balthica, a small pelecypod that made up the bulk of the dunlins' diet at Hartney Bay, was almost totally absent in the most landward intertidal zone. Dowitchers, which also prey on infauna, are probably similarly restricted by low prey availability at high tide. Western sandpipers, on the other hand, have a more generalist feeding strategy (Recher 1966, Senner 1977). By being less selective and feeding on surface prey items, western sandpipers are able to feed at all tidal stages.

Segregation between species by behavioral mechanisms often results in species expanding, contracting, or changing their niches. While behavioral mechanisms may initially segregate species along different niche dimensions, morphological divergence is imminent as species evolve to exploit these niches with maximum efficiency (Recher 1966). The high degree of adaptive radiation, particularly of the feeding apparatus, and speciation in the Charadrii suggests that competition, displacement, and the subsequent evolution of new forms has occurred in the past, and the

widespread occurrence of morphologically similar species suggests that this process is an ongoing one. Specialization of the feeding apparatus is one of the principle means by which birds partition food resources (Schoener 1965, Holmes and Pitelka 1968, Cody 1974), and in the Charadrii it has allowed species to attain a degree of niche segregation where spatial segregation was not possible. So while species may show considerable spatial overlap, there may be little or no overlap in food resources.

Bill length, more than any other mensural character, is a good indicator of the type of feeding apparatus that a bird possesses and the mode of feeding it employs. An index based on the ratio of bill lengths of two species was developed to compare the degree of similarity between their feeding niches (Hutchinson 1959). Hutchinson (1959) hypothesized that for two species to coexist sympatrically, they must differ by a ratio of 1.2 to 1.4. So that the hypothesis pertains to migrant shorebirds I would state it as: for sympatric species to avoid interference competition they must differ by a ratio of more than 1.4. I chose a minimum bill ratio of 1.4 because that is the bill ratio of western and least sandpipers and they have been shown to engage in aggressive interactions, displacement, and other manifestations of competition while staging during migration (Recher 1966). I obtained bill measurements for all of the abundant and common spring migrants and calculated bill length ratios for each pair of species (Table 4). Of the 21 pairs of species, 6 pairs (29%) had bill length ratios of 1.4 or less. Of these 6 pairs, 5 pairs segregated by macrohabitats (Table 1),

Table 4. Bill length ratios<sup>1</sup> of abundant and common spring migrant shorebirds staging on the eastern Copper River Delta, Alaska in 1978.

	Long-billed dowitcher	Common snipe	Short-billed dowitcher	Dunlin	Western sandpiper	Northern phalarope	Least sandpiper
Long-billed dowitcher	-						
Common snipe	1.01	-					
Short-billed dowitcher	1.10	1.09	-				
Dunlin	1.57	1.56	1.42	-			
Western sandpiper	2.56	2.53	2.31	1.62	-		
Northern phalarope	2.63	2.60	2.38	1.67	1.03	-	
Least sandpiper	3.59	3.55	3.25	2.28	1.40	1.37	-

<sup>1</sup> Bill lengths taken from Palmer (1967)

the most effective means of avoiding resource overlap. The one pair that did not segregate by habitat was long-billed and short-billed dowitchers. As previously stated, these species may have segregated temporally during spring migration. Nonetheless, segregation between these two species was not complete and I feel that there are several possible explanations for this. Speciation may have occurred so recently that, although the breeding ranges of the two species are distinct, they have not yet diverged morphologically or in their patterns of habitat use during migration. It is also possible that selective pressures favoring segregation in migration are too weak to produce divergence, or that these pressures are overwhelmed by selective pressures exerted on the breeding or wintering grounds that do not promote divergence.



## FALL MIGRATION

### Results

Fall shorebird migration in 1978 on the ECRD began as early as 15 June when western sandpipers began moving through in small flocks. Migration continued for more than four months as there were several shorebird species still present on 16 October when field activities terminated.

Figure 6 gives the mean number of shorebirds per hour moving east and west past the migratory movement transect from 22 August to 14 October. There were two distinct peaks in easterly movement; the first on 1 September (290 birds per hour) was mostly dowitchers, and the second on 14 October (260 birds per hour) was almost exclusively pectoral sandpipers.

A second transect monitoring bird movements was established perpendicular to Little River Slough (Figure 2). Figure 7 gives the mean number of shorebirds moving north and south across this transect line from 25 July to 29 September. Figure 8 gives the mean number of birds per hour passing the transect for the most abundant species and species groups. Over 99% of the small shorebirds that were positively identified on the transect were least sandpipers. Other peeps recorded included western sandpipers, semipalmated sandpipers (Calidris pusilla), sanderlings, and Baird's sandpipers (C. bairdii). Other shorebird species that occurred on the transect were (in decreasing order of abundance): greater yellowlegs, lesser yellowlegs (Tringa flavipes),

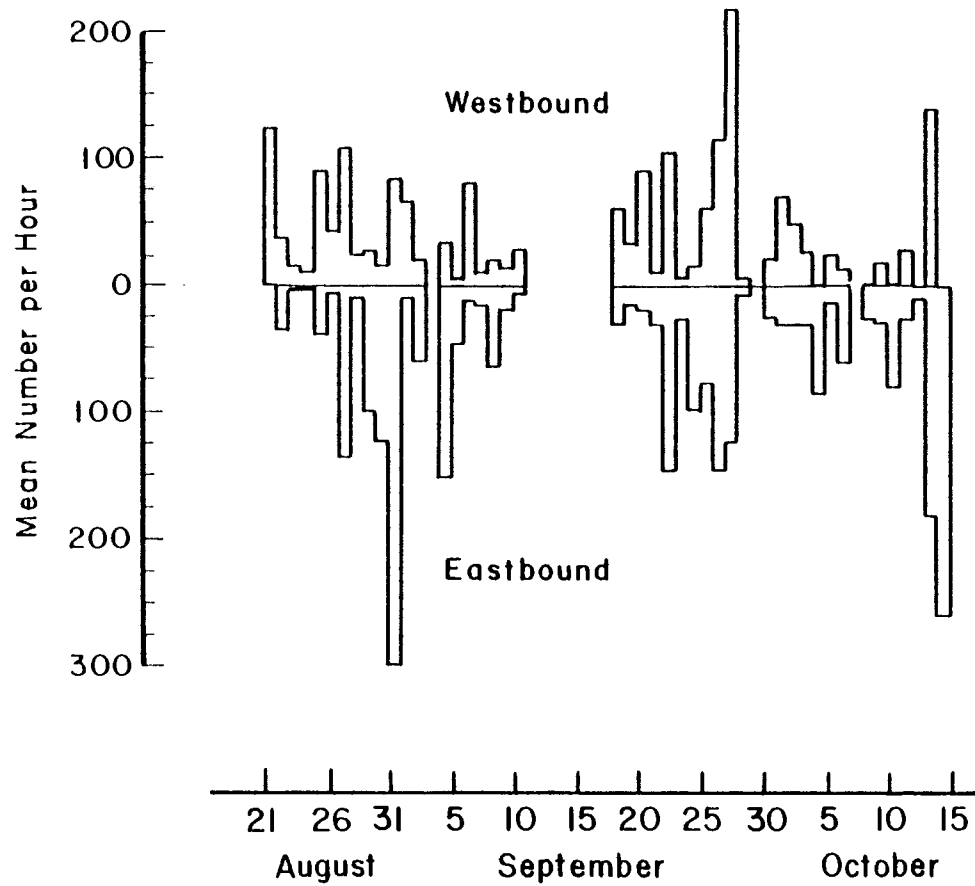


Figure 6. Mean numbers of eastbound and westbound shorebirds per hour during fall migration 1978 on the eastern Copper River Delta, Alaska.

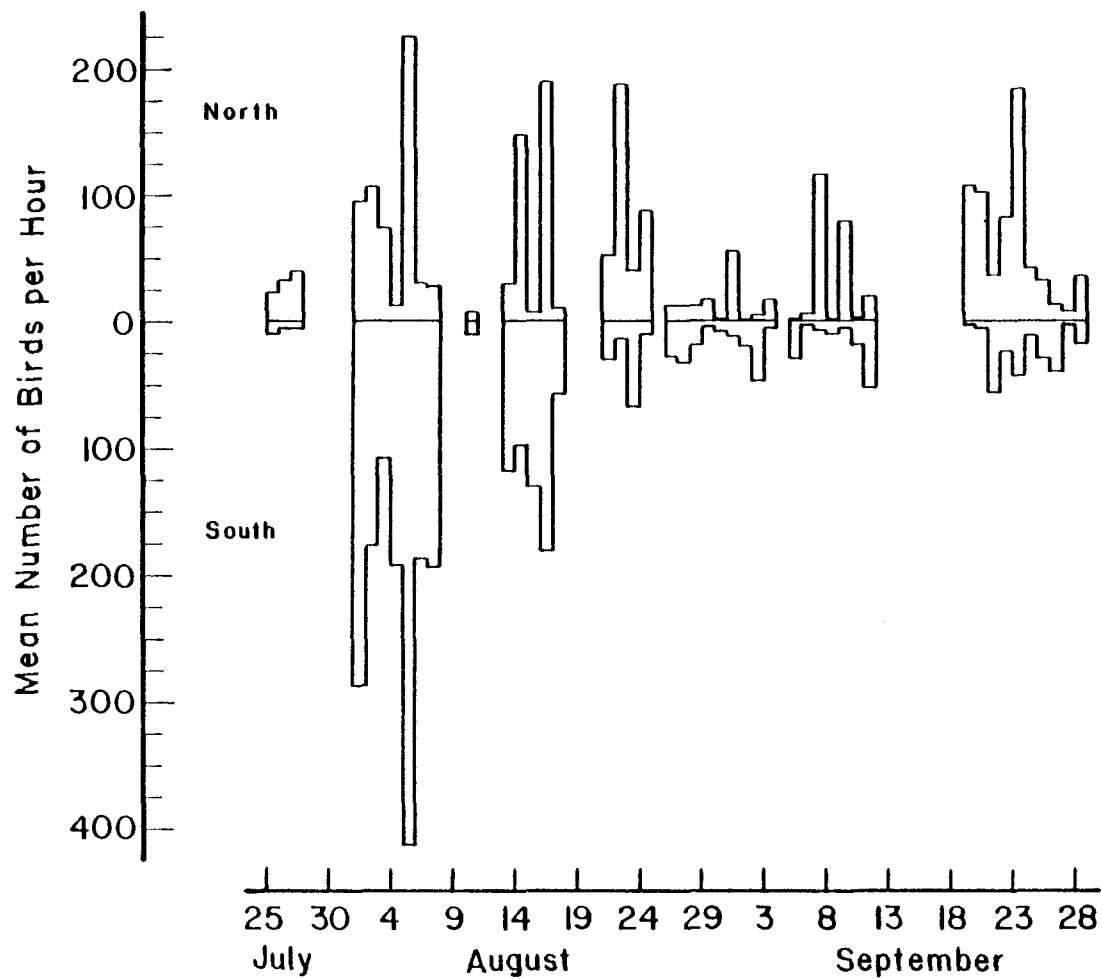


Figure 7. Mean numbers of shorebirds moving up and down Little Slough per hour during fall migration 1978 on the eastern Copper River Delta, Alaska.

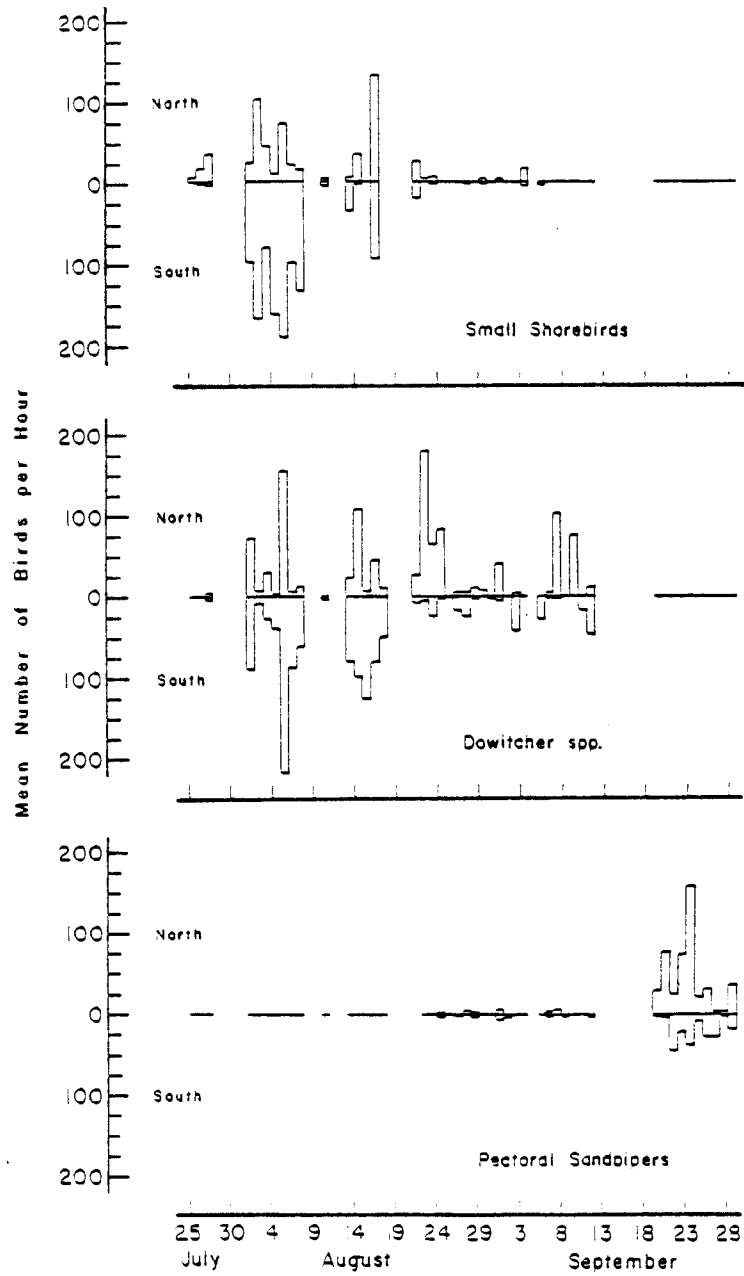


Figure 8. Mean numbers of small shorebirds, dowitchers, and pectoral sandpipers moving up and down Little River Slough per hour during fall migration 1978 on the eastern Copper River Delta, Alaska.

American golden plovers (Pluvialis dominica), northern phalaropes (Phalaropus lobatus), ruddy turnstones, common snipe, whimbrels (Numenius phaeopus), black turnstones, and dunlins. Several of these species were more abundant in other habitat types. In all, 27 shorebird species were positively identified during fall migration. Their status, phenology, and preferred habitats are given in Table 5.

The activity patterns of fall migrant shorebirds staging on Little River Slough were monitored from 25 July to 29 September along a belt transect established perpendicular to the tidally influenced slough. The transect passed through three distinct habitat types: saltgrass meadow, exposed mud, and open water. Figure 9 gives the percentage of birds engaged in feeding and loafing at each tidal stage for dowitcher spp., pectoral sandpipers, least sandpipers, lesser yellowlegs, and greater yellowlegs.

Dowitchers showed increased loafing on the incoming tide, with over 70% of the birds loafing at 3/4 incoming and high tide. As the tide receded, the dowitchers began to feed again and by 1/2 outgoing tide 98% of the birds were feeding. Lesser yellowlegs appeared to have an activity pattern similar to the dowitchers, but incomplete data at two of the tidal stages hampered interpretation. Pectoral sandpipers and least sandpipers used the slough habitat for feeding, but rarely for loafing. Greater yellowlegs showed a pattern of feeding and loafing that is difficult to interpret in terms of the tide.

Dowitchers were the only birds for which there was sufficient data to test for the independence of activity and tidal stage. The results

Table 5. Status, phenology, and habitat preferences of fall migrant shorebirds on the eastern Copper River Delta, Alaska in 1978.

Species	Status <sup>1</sup>	Date first seen	Peak abundance	Date last seen	Primary habitat <sup>4</sup>	Secondary habitat <sup>4</sup>
Dowitcher spp.	A	- <sup>2</sup>	7-15	10-16 <sup>3</sup>	S	MF
Northern phalarope	A	- <sup>2</sup>	7-14	9-21	IL	P
Pectoral sandpiper	A	9-1	10-10	10-16 <sup>3</sup>	SGM	S
Least sandpiper	A	- <sup>2</sup>	8-3	9-3	S	SGM
Greater yellowlegs	C	- <sup>2</sup>	8-21	10-16 <sup>3</sup>	S	SGM
Western sandpiper	C	6-15	7-11	9-15	MF	S
Common snipe	C	- <sup>2</sup>	9-19	10-16 <sup>3</sup>	SWM	P
Lesser yellowlegs	FC	6-24	8-28	9-29	S	SWM
Ruddy turnstone	FC	7-14	7-26	8-23	MF	S
Black-bellied plover	FC	7-6	7-26	8-16	MF	S
American golden plover	FC	8-26	9-19	10-15 <sup>3</sup>	SGM	P
Whimbrel	FC	7-11	7-18	9-21	SWM	S
Semipalmated plover	FC	- <sup>2</sup>	-	8-29	S	SGM
Dunlin	FC	10-10	10-16	10-16 <sup>3</sup>	MF	-
Black turnstone	FC	7-14	-	8-26	MF	S
Surfbird	UC	8-11	-	8-27	MF	-
Spotted sandpiper	UC	8-7	-	9-30	S	-
Red knot	UC	7-14	-	7-21	MF	-
Sharp-tailed sandpiper	UC	9-25	-	10-16 <sup>3</sup>	SWM	SGM
Semipalmated sandpiper	UC	7-10	-	8-28	S	-
Hudsonian godwit	UC	7-14	-	8-23	S	MF
Sanderling	R	9-2	-	9-22	S	-
Bristle-thighed curlew	R	8-25	-	-	-	-
Wandering tattler	R	8-25	-	-	MF	-
Saunders' sandpiper	R	9-2	-	-	S	-
Upland sandpiper	R	8-24	-	-	-	-

<sup>1</sup>Status codes  
 A = abundant  
 C = common  
 FC = fairly common  
 UC = uncommon  
 R = rare  
 CA = casual

<sup>2</sup>Local breeder, arrival of first fall migrants difficult to determine

<sup>3</sup>Still present on study area when field activities terminated

<sup>4</sup>Habitat codes  
 MF = intertidal mudflat  
 SGM = saltgrass meadow  
 SWM = supratidal wet meadow  
 IL = intertidal lagoon  
 S = slough  
 P = pond

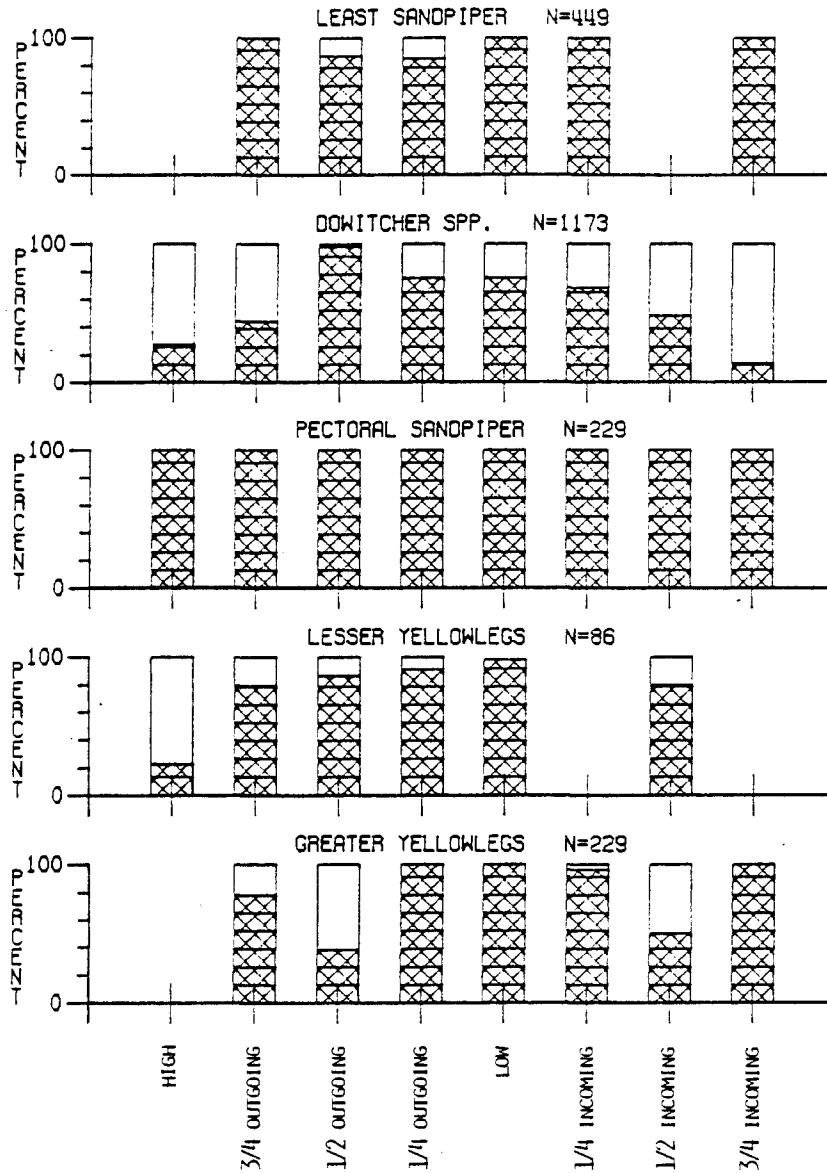


Figure 9. Percent of shorebirds engaged in feeding (shaded areas) and loafing (unshaded areas) during different tidal stages along Little River Slough during fall migration 1978 on the eastern Copper River Delta, Alaska.

of the chi square analysis ( $\chi^2=255.3, df=7, p<.01$ ) indicated that the null hypothesis ( $H_0$ : activity is independent of tidal stage) should be rejected.

The habitat types used by shorebirds feeding and loafing in the transect are given in Table 6. Exposed mud was used most extensively for feeding and loafing by all species. Greater yellowlegs, lesser yellowlegs, and dowitchers also used the open water habitat for feeding. Only pectoral sandpipers used the salt grass meadow for feeding. Dowitchers were the only species that made extensive use of the slough for loafing. They loafed primarily on exposed mud.

There were sufficient data for dowitchers, lesser yellowlegs, and greater yellowlegs to test the null hypothesis that activity is independent of the location of the bird. This hypothesis was rejected for dowitchers ( $\chi^2=26.4, df=1, p<.01$ ) indicating that dowitchers were more likely to feed in certain locations and loaf in others. The hypothesis was accepted for lesser yellowlegs ( $\chi^2=1.4, df=1, p<.01$ ) and greater yellowlegs ( $\chi^2=0.5, df=1, p<.01$ ) indicating that these species used the same habitats for feeding and loafing. Three additional null hypotheses were tested to determine if there were interspecific differences in activity patterns:

$H_0$ : All species feed in the same habitats

$H_0$ : All species loaf in the same habitats

$H_0$ : All species feed at the same tidal stages.

The first hypothesis was rejected ( $\chi^2=227.7, df=8, p<.01$ ) indicating that there were interspecific differences in preferred feeding habitats. The



Table 6. Location of feeding and loafing fall migrant shorebirds by percent and actual numbers (in parentheses) in three habitat types along Little River Slough on the eastern Copper River Delta, Alaska in 1978.

Location	<u>Least sandpiper</u>		<u>Dowitcher spp.</u>		<u>Pectoral sandpiper</u>		<u>Greater yellowlegs</u>		<u>Lesser yellowlegs</u>	
	feeding	loafing	feeding	loafing	feeding	loafing	feeding	loafing	feeding	loafing
Water	0	0	31 (232)	17 (74)	5 (14)	0	38 (29)	29 (4)	18 (11)	29 (7)
Exposed mud	99 (429)	100 (15)	69 (515)	83 (352)	53 (158)	0	60 (46)	71 (10)	82 (51)	71 (17)
Saltgrass meadow	1 (5)	0	0	0	42 (127)	0	2 (2)	0	0	0
Total	100 (434)	100 (15)	100 (747)	100 (426)	100 (299)	0	100 (77)	100 (14)	100 (62)	100 (24)

second hypothesis regarding loafing birds was accepted ( $\chi^2=6.5, df=3, p<.01$ ) indicating that species tended to loaf in the same habitats. The third hypothesis was rejected ( $\chi^2=445.2, df=28, p<.01$ ) indicating that all species did not feed during the same tidal stages.

### Discussion

Fall migration was not merely a reverse of what occurred in spring. Fall migration extended over a period of four months, whereas spring migration was completed in less than six weeks. Consequently, there were fewer birds moving through and/or staging on the ECRD at any given time during fall migration. The maximum number of shorebirds crossing the migratory movement transect per hour in fall was 290 (Figure 6) compared to 3800 in spring (Figure 3). Circumstantial evidence also suggests that layover periods for individual birds were longer in fall than in spring. This was indicated by the high percentage of birds recorded moving west across the aerial transect as well as east during fall migration (Figure 6). These were local movements by birds and they indicated that the net movement of birds through the ECRD relative to the number of birds staging on the ECRD was much lower than during spring migration.

The longer duration and general diffuse character of fall migration can be attributed to several factors. Spring migrants are on a more accelerated timetable because the impending breeding season dictates that they move over a short time span and at a rapid pace. Fall migrants are on a more relaxed timetable so birds can afford to stage

for longer periods in good habitat. In addition, the timing of migration for different species can be offset so there is virtually no temporal overlap (Table 5 and Figure 8). For example, least sandpipers started moving through in July, peaked in August, and were last seen on 3 September. By contrast, pectoral sandpipers did not occur until 1 September and were still moving through in mid-October. Many species also segregate temporally by age and sex class during fall migration (Pitelka 1950, Recher 1966, Matthiessen 1967). The passage of different cohorts of a population may be offset by weeks making the passage of the species a lengthy process (Table 5). For example, fall migration of lesser yellowlegs lasted more than three months.

Species composition and relative abundances of fall migrants also differed considerably from that recorded in spring (Tables 1 and 5). Of the four most abundant spring migrant shorebirds (western sandpipers, dunlins, short-billed dowitchers, and long-billed dowitchers), only the two dowitcher species were abundant as fall migrants. Western sandpipers, for example, constituted over 50% of the spring shorebird flight, but in fall they were merely common migrants in July and uncommon or absent during the other months of fall migration. Fall migration of dunlins was somewhat of an enigma. Isleib and Kessel (1973) listed dunlins as abundant in late July and the first week of August, common through the remainder of August until mid-September, and rare and local from mid-September until mid-October. In 1978 on the ECRD, dunlins were uncommon in July, rare in August, and absent in September. In mid-October they started showing up on the mudflats just

as field activities were being terminated. Dunlin migration in 1979 was quite similar (Mickelson et al. 1980). According to Gill and Jorgenson (1979) there were still over 30,000 dunlins staging at Nelson Lagoon on the Alaska Peninsula as late as mid-October in 1976. Possibly we terminated field activities before the main passage of dunlins. It seems likely however, that if large concentrations of dunlins passed through the Copper River Delta in late October, local birders would be aware of it.

Despite the difficulty in characterizing fall migration of dunlins, it is clear that both dunlins and western sandpipers did not use the ECRD in fall at anywhere near the levels that they did in spring. Since these two species made up over 80% of the spring migrants, the total volume of migrants was much lower in fall than in spring. Several species, notably northern phalaropes, pectoral sandpipers, ruddy turnstones, and American golden plovers, occurred in greater numbers during fall migration than during spring migration.

Another striking contrast between spring and fall migration was a change in patterns of habitat use. Fall migrants used a variety of habitats, while spring migrants were found almost exclusively on intertidal mudflats. Staging fall migrants included several species, such as dowitchers, that primarily used mudflats in spring but were found along sloughs in fall. Use of saltgrass meadow and supratidal wet meadow habitats also increased during fall migration. Birds undoubtedly exploited the habitats with the greatest food availability in both spring and fall; so there may have been a quantitative change in prey

availability in different habitat types between spring and fall that would account for the observed shift in habitat use. Fall migrants also occurred in smaller flocks, which enabled them to use small parcels of good habitat with limited crowding.

Dowitchers, the only species for which there were activity data in both spring and fall, showed similar activity patterns relative to the tide in both seasons. Birds tended to loaf during high tidal stages and feed during low tides. This relationship between dowitcher activity and tidal stage was even more clearly defined in fall (compare Figure 5 and Figure 9). For all other species there were insufficient data to test for independence of activity and tidal stage. However, least sandpipers and pectoral sandpipers seldom or never loafed in the transect; if they were present in the transect, they were feeding regardless of the tidal stage.

The activities of birds relative to habitat types yielded some interesting results. Although there were significant interspecific differences in preferred feeding habitats, all species used exposed mud as their primary feeding habitat (Table 6). Pectoral sandpipers also fed in saltgrass meadow habitat with nearly the same frequency as exposed mud. The long-legged species (dowitchers, greater yellowlegs and lesser yellowlegs) used water in the slough as their secondary feeding habitat. Least sandpipers fed exclusively on exposed mud and this constituted a shift in primary feeding habitat from spring, when they used saltgrass meadows much more extensively. This shift of feeding habitat occurred in the absence of western sandpipers that are

capable of displacing the morphologically similar but smaller least sandpipers (Recher 1966). On the east coast of North America, least sandpipers reportedly use vegetated habitats where they are sympatric with morphologically similar congeners. In California least sandpipers are able to segregate temporally from congeners during migration, and under these circumstances they used exposed mud for feeding habitat (Recher 1966). I conclude from Recher's observations and my data that exposed mud is the preferred feeding habitat of least sandpipers and they use it when not prevented by competitive interactions with dominant congeners.

The preferred microhabitats of feeding dowitchers were almost identical in both spring and fall despite the change in location of the transect. In spring, 39% of the dowitchers fed in water (at tide line and in tide pools) and 61% fed on exposed mud. In fall, 31% of the dowitcher feeding was in water and 69% fed on exposed mud.

As was the case in spring, when positive identification of individual dowitchers was made, no difference in habitat preferences between species could be discerned. Gill and Jorgenson (1979) reported that the two dowitcher species segregated by habitat during fall migration; long-billed dowitchers preferred mudflats and short-billed dowitchers preferred mixed mud/sand flats. I was unable to make this distinction between the two species.

Loafing birds showed an even greater affinity for exposed mud than feeding birds. Of all loafing shorebirds, 82% were on exposed mud. Long-legged species occasionally would loaf in water, but surprisingly

few birds loafed in the saltgrass meadow. There were no significant interspecific differences in the preferred loafing habitats between the three species that loafed in the transect.

Compared to spring, activity patterns by staging fall migrants were less structured and spatial segregation between species was less definitive. This suggests that levels of interspecific competition for foraging space were well below levels that evoke aggression and cause species displacement. Further evidence that levels of interspecific competition were low comes from bill length ratios (Table 7) and preferred habitats (Table 5) of the abundant and common fall migrants. Recall that in spring long-billed and short-billed dowitchers were the only pair of species that had bill length ratios less than 1.4 and still used the same habitat, and it was hypothesized that these species segregated temporally. In fall, there were 28 pairs of abundant and common species; 11 of these (39%) had bill length ratios less than 1.4, indicating morphological similarity. Of these 11 pairs, eight pairs used different habitats. Three species pairs, involving long-billed dowitchers, short-billed dowitchers, and greater yellowlegs, had bill length ratios of 1.1 or less, occurred in the same habitat type, and had very similar activity patterns (Table 6 and Figure 9). It was uncertain to what degree the dowitcher species segregated temporally, but it was certain that greater yellowlegs migration overlapped with one or both of the dowitcher species. When species with similar morphologies and patterns of habitat use are able to coexist without indications of competitive strife it seems safe to assume that critical resources were

Table 7. Bill length ratio<sup>1</sup> of abundant and common fall migrant shorebirds staging on the eastern Copper River Delta, Alaska in 1978.

	Long-billed dowitcher	Common snipe	Short-billed dowitcher	Greater yellowlegs	Pectoral sandpiper	Western sandpiper	Northern phalarope	Least sandpiper
Long-billed dowitcher	-							
Common snipe	1.01	-						
Short-billed dowitcher	1.10	1.09	-					
Greater yellowlegs	1.20	1.20	1.10	-				
Pectoral sandpiper	2.38	2.36	2.16	1.96	-			
Western sandpiper	2.56	2.53	2.13	2.11	1.07	-		
Northern phalarope	2.63	2.60	2.38	2.17	1.10	1.03	-	
Least sandpiper	3.59	3.55	3.25	2.96	1.51	1.40	1.37	-

<sup>1</sup> Bill lengths taken from Palmer (1967)



not limiting.

The main reasons that foraging space was not limiting can be attributed to the above mentioned segregation of the most morphologically similar species and, much more importantly, the long duration and diffuse nature of fall migration. In other words, temporal segregation of species and cohorts of species populations over the four month migratory period served to maintain densities of staging shorebirds, even in prime habitats, at low levels. In addition, food availability probably increased in fall relative to spring due to production during the summer.

While temporal differences in the migration of cohorts of a population and among the various species undoubtedly reduces competition for foraging space during fall migration, it is unlikely that these differences evolved for this purpose. Rather, many of these differences seem to be related to conditions on the breeding grounds. Holmes and Pitelka (1968) concluded that an early departure by adults of three Calidris sandpiper species provided the main relief to inter- and intraspecific competition for food on the breeding grounds. Ashkenazie and Safriel (1979) suggested that female semipalmated sandpipers desert the breeding grounds after hatching because the high energy demands of egg laying and incubation makes it necessary for them to seek out better feeding grounds as soon as possible.

Whatever the reasons for temporal segregation during fall migration, this segregation of species and cohorts of species populations does not necessarily reduce competition for food resources on the

staging grounds. A prey item consumed by a bird on 1 August may not be available to a bird on 1 September, so migrants could be still sharing a finite food resource regardless of the timing of their migration.

However, since the birds that did occur sympatrically during migration did not show overt signs of interspecific competition, it seems unlikely that food resources were limiting.

## BREEDING

### Results

Ninety-five nests of six shorebird species were found on the ECRD in 1978. Least sandpipers were the most abundant breeding shorebird species and the second most abundant breeder of all species. Only savannah sparrows (Passerculus sandwichensis) were more abundant (Mickelson et al. 1980). Northern phalaropes were the second most abundant breeding shorebird species, followed by short-billed dowitchers, common snipe, dunlins, and semipalmated plovers (Charadrius semipalmatus). The number of nests found on transects and the estimated total number and density of nests on the study area are given for each species in Table 8. Shorebirds were the most abundant species group breeding on the study area, with an estimated density of 28.5 nests/km<sup>2</sup>.

The phenology of initiation of egg laying for each species is given in Figure 10. The earliest known laying date was 14 May, an unsuccessful dunlin nest. The first known successful nests were initiated on 18 May by least sandpipers and northern phalaropes. The peak of laying for most species occurred around 31 May. The latest date of initiation of laying was 28 June by a northern phalarope. The fate of this nest was not determined. The last known successful nest was a least sandpiper nest initiated on 18 June. With four days needed to complete a clutch and approximately three weeks to incubate the eggs, the hatching period for successful nests would be 12 June to 12 July.

Clutch size and nest fate information are given in Table 9. Mean

Table 8. Number of nests found on transects, estimated total numbers, standard error, coefficient of variation, and nest density for shorebirds breeding on the eastern Copper River Delta, Alaska in 1978.

Species	Number of nests	Estimated total nests	SE	CV	Density (/km <sup>2</sup> )
Least sandpiper	22	1291	283	22	13.9
Northern phalarope	12	704	219	31	7.6
Short-billed dowitcher	5	293	129	44	3.2
Common snipe	3	176	110	63	1.9
Dunlin	2	117	85	73	1.3
Semipalmated plover	1	59	71	125	0.6

Extrapolated from 1.56 km<sup>2</sup> of belt transects to 91.5 km<sup>2</sup> study area.

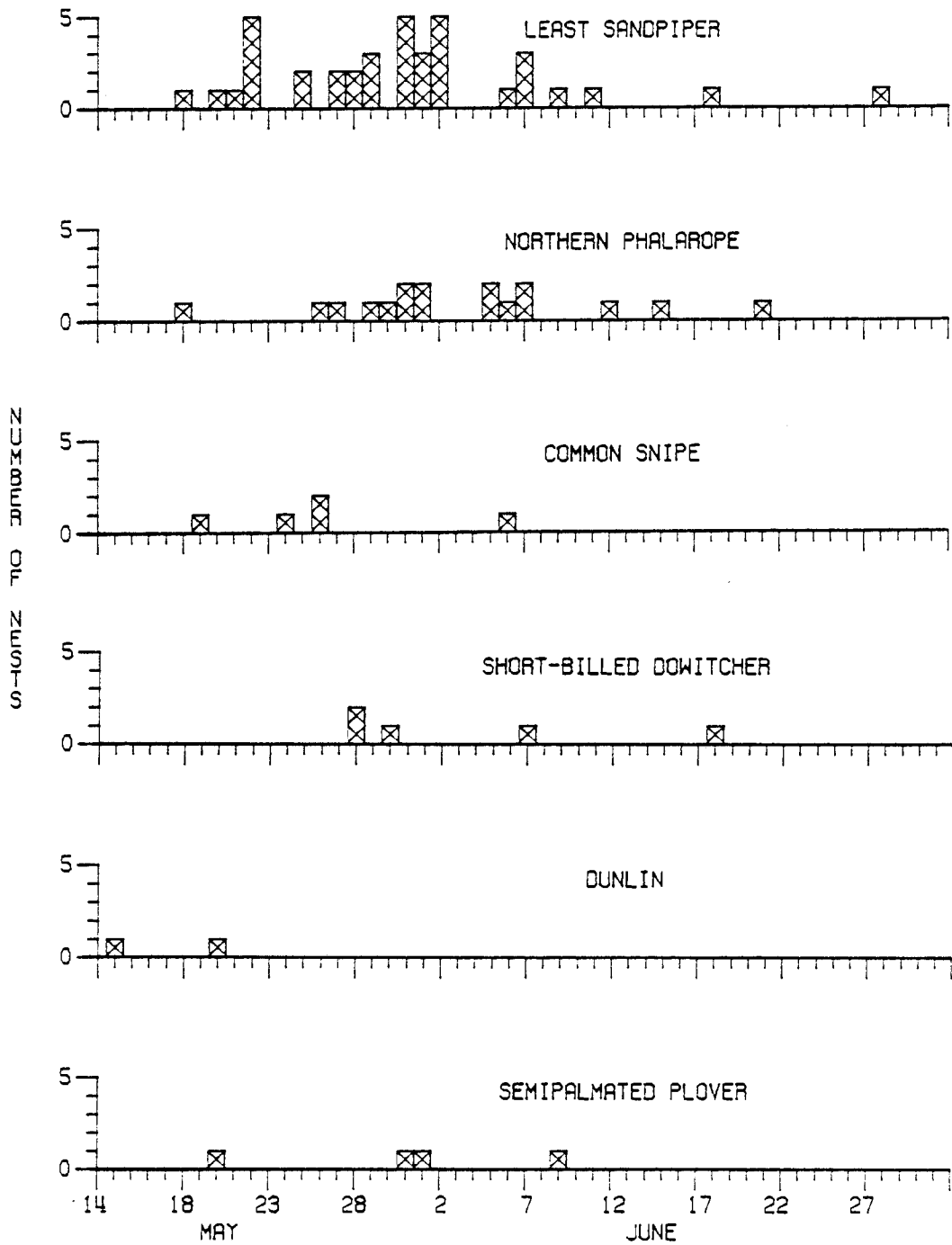


Figure 10. Phenology of initiation of egg-laying for shorebirds nesting in 1978 on the eastern Copper River Delta, Alaska.

Table 9. Number of nests, successful nests, and mean clutch size for shorebirds breeding on the eastern Copper River Delta, Alaska in 1978.

Species	Number of nests found	Number of known successful nests	Percent of known fate nests successful	Mean clutch size	SD of clutch size	Minimum-maximum clutch size
Least sandpiper	51	7	78	3.8	0.34	2-4
Northern phalarope	23	5	71	3.7	0.64	2-5
Common snipe	7	6	86	3.9	0.38	3-4
Short-billed dowitcher	7	4	57	4.0	0	4-4
Semipalmated plover	5	3	100	3.8	0.45	3-4
Dunlin	2	1	50	5.0	-	4-6

clutch size for all species was close to four, the typical size for most shorebirds (Bent 1962a, Bent 1962b). A dunlin nest that was abandoned shortly after laying had six eggs. Nest fate information was often difficult to obtain because shorebird young are nudifugous and parents remove egg shells from the nest almost immediately after hatching. However, careful inspection of the nest cup often revealed small shell fragments which indicated successful hatching. I considered a nest successful if at least one young was thought to have hatched and left the nest. All shorebird species had at least 50% nest success.

The frequency of occurrence of shorebird nests in the various physiographic, vegetation and substrate types are given in Tables 10, 11, and 12. The vegetated marsh was the physiographic type most commonly used by all species except semipalmated plovers, which preferred more sparsely vegetated types. The eight vegetation types were lumped into three groups: sedge-dominated types, moss-dominated types, and shrub-dominated types. More detailed information on the species composition and percent area covered by each vegetation type is given in Appendix I. Eighty-two percent of all shorebird nests occurred in moss-dominated vegetation types, which accounted for approximately 53% of the plant cover on the study area. Sedge-dominated vegetation types covered approximately 22% of the study area and attracted 11% of the nesting shorebirds. Shrub-dominated types covered 25% of the study area but attracted only 7% of the breeders. Moss and vegetative mat were the two most common substrates at nest sites for all species except semipalmated plovers which preferred to nest on bare ground.

Table 10. Percent and actual number (in parentheses) of shorebird nests occurring in different physiographic types on the eastern Copper River Delta, Alaska in 1978.

Species	Physiographic type					
	Shoreline of pond	Top of slough bank-vegetated	Mid-slough bank (steep)-vegetated	Mudflat-old intertidal grassbanks	Mudflat of slough	Vegetated marsh
Least sandpiper	- -	3.9 (2)	3.9 (2)	- -	9.8 (5)	82.4 (42)
Northern phalarope	8.6 (2)	4.3 (1)	- -	8.7 (2)	- -	75 (18)
Common snipe	- -	- -	- -	- -	- -	100 (7)
Short-billed dowitcher	- -	- -	- -	- -	14.3 (1)	85.7 (6)
Semipalmated plover	- -	- -	20.0 (1)	60.0 (3)	20.0 (1)	- -
Dunlin	- -	- -	50.0 (1)	- -	- -	50 (1)



Table 11. Percent and actual number (in parentheses) of shorebird nests occurring on different vegetation types on the eastern Copper River Delta, Alaska in 1978.

Species	Vegetation types						
	Sedge-dominated			Moss-dominated		Shrub-dominated	
	Sparse sedges or grasses with > 50% bare ground	Moderate sedges, grasses, and/or rushes with > 10% but < 50% bare ground	Dense sedges, grasses and/or rushes	Moss with sedges, grasses, and/or rushes and forbs	Moss hummocks with grasses, sedges, forbs, and sparse shrubs	Moderate density shrubs with grasses, sedges, forbs and thin moss	Clumped locally dense shrubs with sedges, grasses, and forbs
Least sandpiper	-	2.0 (1)	2.0 (1)	29.4 (15)	62.7 (32)	4.0 (2)	-
Northern phalarope	-	-	8.7 (2)	26.0 (6)	52.0 (12)	8.7 (2)	4.3 (1)
Common snipe	-	-	28.6 (2)	28.6 (2)	28.6 (2)	14.3 (1)	-
Short-billed dowitcher	-	-	28.6 (2)	28.6 (2)	28.6 (2)	14.3 (1)	-
Semipalmated plover	20.0 (1)	20.0 (1)	-	20 (1)	40 (2)	-	-
Dunlin	-	-	-	-	100 (2)	-	-

Table 12. Percent and actual number (in parentheses) of shorebird nests occurring on different substrate types on the eastern Copper River Delta, Alaska in 1978.

Species	Substrate type			
	Mud	Sand	Moss	Vegetation mat
Least sandpiper	2 (1)	- -	60 (25)	38 (16)
Northern phalarope	5 (1)	- -	45 (9)	50 (10)
Short-billed dowitcher	- -	- -	17 (1)	83 (5)
Common snipe	- -	- -	40 (2)	60 (3)
Semipalmated plover	67 (2)	33 (1)	- -	- -
Dunlin	- -	- -	100 (2)	- -

Measurements of proximity of nests to open water and type of water body nearest the nests are given in Table 13. Distance to open water was variable for most species, especially the ones for which there was a large sample size. Small sloughs were the water body type most frequently found closest to nests for most species except semipalmated plovers which commonly nested along large sloughs and ephemeral ponds.

#### Discussion

Of the six shorebird species found nesting on the study area, only dunlins were not known to have bred on the Copper River Delta (Isleib and Kessel 1973). The discovery of breeding dunlins constitutes a considerable range extension for the species, as they had never been recorded breeding southeast of Bristol Bay (Gabrielson and Lincoln 1959).

Estimates of total numbers and density of nests on the study area (Table 8) had varying degrees of precision and accuracy. Estimates were fairly precise, as evidenced by their relatively low coefficients of variation for least sandpipers, northern phalaropes, common snipe, and short-billed dowitchers because these species were fairly abundant and evenly distributed throughout the study area. Semipalmated plovers and dunlins, by contrast, had higher coefficients of variation for the estimates of total numbers of nests because both species occurred in low densities and the distribution of semipalmated plovers was clumped along sloughs and the margin of the intertidal zone. The accuracy of the estimates can only be evaluated intuitively. I feel that the estimates

Table 13. Distance of shorebird nests to open water and type of water body nearest to nests on the eastern Copper River Delta, Alaska in 1978.

Species	<u>Distance to open water (m)</u>			<u>Frequency of occurrence of nearest water body type (%)</u>			
	Mean	SD	Range	Pond	Small slough	Large slough	Ephemeral pond
Least sandpiper	23	24	0.3-93	2	61	9	27
Northern phalarope	21	28	0.6-100	28	67	6	-
Common snipe	13	10	0.3-30	-	60	-	40
Short-billed dowitcher	14	7	3-23	17	67	-	17
Semipalmated plover	23	19	1-45	-	-	50	50
Dunlin	5	2	3-6	-	50	-	50

were low for all the species except dunlins and semipalmated plovers. All of the shorebirds breeding on the study area except semipalmated plovers were "tight sitting" and would not flush unless approached within 2-3 m, which is considerably less than half the average distance between two observers on the 30 m wide transect. In other instances, birds left their nests and walked some distance before flushing making it difficult to locate their well-camouflaged nests. Both of these behavioral traits of shorebirds caused us to miss nests on transects and subsequently to underestimate breeding populations.

During the 1979 breeding season, the same transects were monitored and the estimated shorebird density fell from 28.5 nests/km<sup>2</sup> in 1978 to 20.5 nests/km<sup>2</sup> in 1979 (Mickelson et al. 1980). Estimates of least sandpiper and northern phalarope breeding populations declined while estimates for common snipe, short-billed dowitchers and semipalmated plovers increased. However, none of these fluctuations were statistically significant (Mann-Whitney U Test,  $p < .05$ ).

Holmes (1972) cited length of breeding season, weather, predators, and food supply as the ecological factors most likely to affect shorebird breeding success. Clearly, all of these factors except predation are related to the phenology of spring breakup. An early spring means early nest site availability (Dau and Mickelson 1979), milder temperatures, and early insect emergence (Holmes 1966). Breakup on the ECRD in 1978 was early (R.H. Bromley pers. comm.) and nest success for all shorebird species was at least 50%. Abandonment and flooding were the major causes of failed nests. Loss of nests to predators was

less than 5%, which is a very low level of predation. Most of this predation was thought to have been caused by mammals.

Although I have no direct evidence of replacement clutches or multiple clutches, it appears that some species had individuals producing more than one clutch. This assumption is based on the long duration of the nest initiation period for several species. The laying period for least sandpipers was 41 days and it seems probable that it extended this long because of renesting. Northern phalaropes have a polyandrous breeding system (Schamel and Tracy 1977) and their 34 day laying period also suggested that multiple clutches were laid. The duration of the laying period for the four other species was less than three weeks. Tuck (1972) reported that first-year breeding common snipe breed later than experienced breeders, so total synchrony of the breeding effort was not expected. Based on this, I would hypothesize that the four species with the shorter duration of laying did not have individuals that produced multiple clutches.

Nest data collected on physiographic, vegetative, and substrate types along with distance of nests to water body types constituted my measure of nest site preferences. Least sandpipers, northern phalaropes, short-billed dowitchers, and dunlins all had similar nest site preferences. These species showed a preference for nesting in the vegetated marsh and in well-drained, moss dominated vegetation types. Least sandpipers, northern phalaropes, and dunlins in particular were found almost exclusively in moss dominated vegetation types and this is consistent with what was previously known about their nest site

preferences (Palmer 1967). Common snipe and short-billed dowitchers nested in all three of the major vegetation types (Table 11) indicating that these species have more plastic nest site requirements. However, a common attribute of all of the vegetation types in which short-billed dowitchers and common snipe nests occurred was the presence of varying degree of sedge and/or moss. Sedges and moss are typical nest site characteristics for these species (Tuck 1972 and Palmer 1967).

For all of these species the distance of nests to open water (Table 13) was so variable that it is doubtful that this was an important component of nest site selection. Also, I feel that it was coincidental that all of the species that nested in the vegetated marsh had nests closest to small sloughs (Table 13) since small sloughs were by far the most common water body type in the vegetated marsh.

Semipalmated plovers were the only species that showed considerable contrast in nest site preferences from the other shorebirds. Semipalmated plovers preferred to nest on bare substrates (Table 12) along slough banks or old intertidal grassbanks (Table 10). Palmer (1967) stated that these birds nest in "dry situations," and cited a diverse list of habitat types. I found semipalmated plover nests in a variety of vegetation types, but always on well-drained bare substrates. Distance to open water was not an important factor in nest site selection. However, all nests occurred along either large sloughs or ephemeral ponds where well-drained bare ground was readily available. Available nesting habitat was more limiting for breeding semipalmated plovers than for any of the species nesting in the vegetated marsh.

## SUMMARY AND CONCLUSIONS

The major passage of spring migrant shorebirds occurred between 25 April and 15 May 1978, with the peak occurring on 11 May, about one week later than normal. Western sandpipers, dunlins, short-billed dowitchers, and long-billed dowitchers were the most abundant spring migrant shorebirds, and all of these species staged on the intertidal mudflats almost exclusively. These species had slightly different phenologies and patterns of habitat use, and it was hypothesized that these differences helped to segregate species temporally and spatially in order to partition resources and reduce levels of competition for foraging space. Morphological differences in feeding apparatus also contributed to resource partitioning; birds with similar bill lengths used different habitats.

The most abundant fall migrants were short-billed dowitchers, least sandpipers, pectoral sandpipers, northern phalaropes, and long-billed dowitchers. The majority of fall migrant western sandpipers and dunlins apparently used a different migratory route than in spring, and they did not stop on the eastern Copper River Delta. Since these two species made up over 80% of the spring shorebird flight, the total volume of shorebirds migrating through the ECRD in fall was considerably lower than in spring. This, coupled with the long duration of the fall movement (more than 4 months), served to maintain low densities of birds on the staging grounds throughout the migratory period. It was hypothesized that low densities of fall migrants along with temporal segregation of species resulted in low levels of interspecific



competition for foraging space. In addition, spatial and temporal segregation between sympatric species was less clearly defined than in spring, and there was a greater degree of habitat overlap of morphologically similar species. Even though fall migration was more diffuse and less spectacular than spring migration, it would be misleading to minimize the importance of the ECRD to fall migrants because for several species the number of total bird days spent on the ECRD in fall may have exceeded that of spring.

In light of the large volume of spring and fall migrants that stage in the Copper River Delta region (Senner 1977, Isleib 1979) and the isolated "habitat island" nature of the region, the area must be considered of paramount importance for shorebird populations using the Pacific Flyway. The ECRD is an integral component of this system. Levels of use of the ECRD by staging migrants were commensurate with those of other areas that have been demonstrated to be of high, if not critical, value for migrating shorebirds (Senner 1977, 1979). The greatest threat to the welfare of these birds is degradation of the intertidal habitats on which they depend for food resources. Since the Copper River Delta is under the protective stewardship of the U.S. Forest Service it is unlikely that unsound land use decisions will be implemented. Rather, the greatest threat of habitat degradation is from marine pollution that could alter or destroy the intertidal invertebrate fauna. In the Gulf of Alaska-Prince William Sound region there has been a proliferation of oil tanker traffic and offshore oil rigs in recent years and the potential for marine pollution from these sources is

increasing. Studies conducted on the effects of oil pollution on intertidal invertebrates have revealed that many species, such as Macoma balthica, which are important shorebird food sources, are extremely vulnerable to hydrocarbon contamination (Feder et al. 1976). An untimely oil spill or chronic contamination of the marine system could have devastating effects on migratory shorebirds if contaminants were to reach the intertidal habitats of the Copper River Delta. If this bleak scenario were to become a reality, it should be a high priority to protect the intertidal habitats to the greatest possible extent.

For breeding birds the scene shifted from intertidal habitats to supratidal habitats, principally the vegetated marsh. Ninety-five nests of six shorebird species were located during the course of the breeding season. Forty-five nests were located on the 1.56 km<sup>2</sup> of transects and from these nests densities and total number of nests were extrapolated to the 91.5 km<sup>2</sup> of breeding habitat on the study area. The most abundant breeding shorebirds were least sandpipers (13.9 nests/km<sup>2</sup>) followed by northern phalaropes (7.6 nests/km<sup>2</sup>), short-billed dowitchers (3.2 nests/km<sup>2</sup>), common snipe (1.9 nests/km<sup>2</sup>), dunlins (1.3 nests/km<sup>2</sup>), and semipalmated plovers (0.6 nests/km<sup>2</sup>). The discovery of breeding dunlins extends the known breeding range of this species.

Eggs in successful nests were laid between 18 May and 18 June and nesting success for all six shorebird species was greater than 50%. The high nesting success of several species may have been due to the fact that it was an early spring.

Eighty-two percent of all shorebird nests were located in the

vegetated marsh in moss-dominated vegetation types. Another 11% were located in sedge-dominated vegetation types. The semipalmated plover was the only species that had the majority of its nests located outside of the vegetated marsh. They most frequently nested along large sloughs and ephemeral ponds on bare substrates.

Breeding birds would be largely unaffected by contamination of intertidal habitats by marine pollutants since nesting occurs in supratidal habitats. However, if current plant succession trends continue on the ECRD, changes in breeding shorebird populations undoubtedly will occur. Comparison of pre-earthquake aerial photographs taken in 1959, aerial photographs taken in 1974, and our ground observation in 1978 revealed that shrub- and moss-dominated vegetation types are increasing, while sedge-dominated types are diminishing. In the short run, species like least sandpipers and northern phalaropes that are well adapted to breeding on moss hummocks will probably continue to have breeding success on the ECRD. Species such as short-billed dowitchers and common snipe that require sedges for nesting and brood rearing habitat will probably show the first signs of decline. However, I think that the moss-dominated areas are merely a seral stage that will largely be replaced by shrubs and spruce trees. Before the turn of the century I suspect that the shorebird species currently breeding on the ECRD will be in sharp decline and that a new avifauna, probably mostly passerines, will inherit the area.

Appendix I. Species composition and percent area covered of major vegetation types on the eastern Copper River Delta, Alaska in 1978.

Vegetation type	Dominant species	Area covered (Z)
Sparse sedges or grasses with >50% bare ground	<u>Triglochin maritimum</u> , <u>Puccinellia</u> spp., <u>Carex Ramenskii</u> , <u>C. Lyngbyael</u> , <u>Plantago maritima</u> , <u>Potentilla Egedii</u>	3.48
Moderate sedges, grasses or rushes with >10% but <50% bare ground	<u>Carex Ramenskii</u> , <u>C. Lyngbyael</u> , <u>Deschampsia caespitosa</u> , <u>Juncus arcticus</u> , <u>Potentilla Egedii</u>	4.39
Dense sedges, grasses and/or rushes	<u>Carex Lyngbyael</u> , <u>Calamagrostis canadensis</u> , <u>Eleocharis palustris</u> , <u>Deschampsia caespitosa</u>	12.72
Moss with sedges, grasses and/or rushes with forbs	moss, <u>Carex Lyngbyael</u> , <u>Calamagrostis canadensis</u> , <u>Poa emimens</u> , <u>Equisetum arvense</u> , <u>Eriophorum angustifolium</u> , <u>Potentilla Egedii</u>	8.55
Moss hummocks with grasses, sedges, forbs and sparse shrubs	Moss, <u>Carex Lyngbyael</u> , <u>Calamagrostis canadensis</u> , <u>Poa emimens</u> , <u>Equisetum arvense</u> , <u>Picea sitchensis</u> , <u>Alnus sinuata</u> , <u>Salix</u> spp.	41.86
Moderate density shrubs with grasses, sedges, forbs, and thin moss	<u>Myrica gale</u> , <u>Salix</u> spp., <u>Alnus sinuata</u> , <u>Picea sitchensis</u> , <u>Calamagrostis canadensis</u> , <u>Carex Lyngbyael</u> , <u>Deschampsia beringensis</u> , <u>Festuca rubra</u> , moss	
Clumped, locally dense shrubs with sedges, grasses, and forbs	<u>Myrica gale</u> , <u>Salix</u> spp., <u>Picea sitchensis</u> , <u>Alnus sinuata</u> , <u>Calamagrostis canadensis</u> , <u>Carex Lyngbyael</u> , <u>Deschampsia beringensis</u>	4.42

<sup>1</sup> Plant names according to Hulten (1968)

<sup>2</sup> 5.5% of study area is covered by open water

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