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THE IMPORTANCE OF SUBARCTIC INTERTIDAL HABITATS TO SHOREBIRDS: A STUDY OF THE CENTRAL YUKON-KUSKOKWIM DELTA, ALASKA[1]

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Abstract. A 6-year study of shorebird use of intertidal habitats of the Yukon-Kuskokwim Delta revealed this area to be one of the premiere sites for shorebirds throughout the Holarctic and worthy of designation as a Hemispheric Shorebird Reserve in the Western Hemisphere Shorebird Reserve Network. The study area, which covered 10% (300 km^2) of the delta's intertidal flats, regularly hosted 17 species of shorebirds between late April and mid-October. The greatest use was during the postbreeding period (late June–October), when Dunlins (*Calidris alpina*), Western Sandpipers (*C. mauri*), and Rock Sandpipers (*C. ptilocnemis*), each with large local nesting populations, accounted for 95% of the shorebirds recorded. Peak counts during autumn approached 300,000 birds. Considering the seasonal occurrence and turnover of populations, we estimate 1–2 million shorebirds use the central delta each year. The delta supports large fractions of the Pacific Rim or world populations of Bar-tailed Godwits (*Limosa lapponica*), Black Turnstones (*Arenaria melanocephala*), Red Knots (*C. canutus*), Western Sandpipers, Dunlins, and Rock Sandpipers. Densities of shorebirds using the central delta's four major bays and connecting coastal areas peaked at 950 shorebirds/km^2 in early September. Hazen Bay frequently hosted more than 1,200 shorebirds/km^2.

Postbreeding shorebirds used intertidal habitats in three distinct patterns according to age class. For most species (n = 7), there was a period when adults appeared first, followed by a brief interval when adults and juveniles mixed, then by a prolonged period when only juveniles remained. In the second pattern (n = 3 species), adults moved onto the intertidal flats first, were later joined by juveniles for a prolonged staging period, then migrated with them. In the third pattern (n = 3 species), only juveniles used the delta's intertidal habitat. Temporal segregation among species and age groups may minimize competition for food and thereby allow the delta to support high diversity and numbers of shorebirds.

Key words: Shorebirds; Charadriidae; Scolopacidae; Yukon-Kuskokwim Delta; Alaska; staging; migration; nesting; habitat use; intertidal; populations; hemispheric reserve.

INTRODUCTION

At temperate and southern latitudes, shorebirds are closely linked to intertidal habitats. Only recently have studies at more northern latitudes demonstrated that many species of shorebirds that use intertidal areas during the nonbreeding period also depend on similar habitats during the boreal summer (e.g., Boere 1976, Connors et al. 1979, Gill and Jorgensen 1979, Senner et al. 1981, Morrison 1984, Davidson and Pienkowski 1987, Meltofte 1987). Different species may use these northern habitats for only a few weeks or up to 4 months. Some species may spend annually up to 80% of their time on intertidal habitats. This habitat reliance must certainly have shaped the evolution of their population structures, migration strategies, molt schedules, and social systems (Burger 1984).

Worldwide, intertidal areas are suffering alteration or destruction at an alarming rate (Senner and Howe 1984, Davidson and Pienkowski 1987, Smit et al. 1987). To protect areas that support major populations of shorebirds, we must understand how shorebirds use these habitats during all phases of the annual cycle (Myers et al. 1987b). The delta of the Yukon and Kuskokwim rivers forms one of the largest intertidal expanses in North America (Dupré 1979, Thorsteinson et al. 1989). This area is known for its rich shorebird breeding grounds (Holmes 1970, 1972; Pitelka 1979), but little is published about its use by shorebirds outside the breeding season (Gill and Handel 1981, Handel and Dau 1988).

Between 1977 and 1982 we used ground and aerial censuses to assess how shorebirds seasonally used the central Yukon-Kuskokwim Delta's

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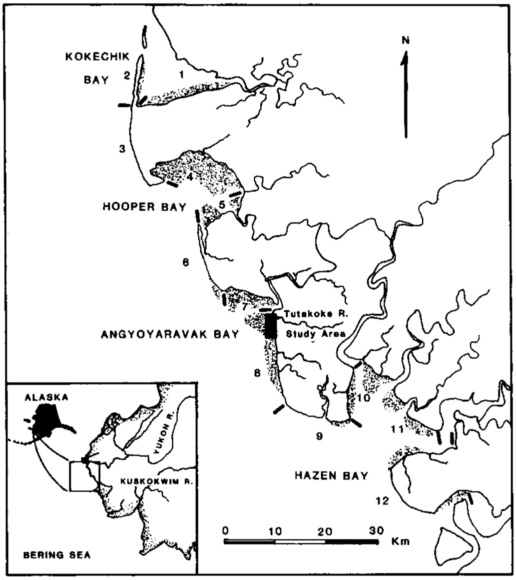

FIGURE 1. The central Yukon-Kuskokwim River Delta showing the four major bays, the Tutakoke River study area, and the 12 areas censused during aerial surveys. The shading depicts the approximate distribution of intertidal habitats exposed at mean lower low water (MLLW).

intertidal habitats. The immediate objectives of our study were to determine the relative numbers of each species using the area and to describe their spatial and temporal patterns of occurrence. Our ultimate objective was to assess the regional and global importance of this area to shorebird populations.

STUDY AREA

We conducted our study along the central coast of the Yukon-Kuskokwim Delta (Fig. 1). The entire delta includes 80,000 km² of low tundra communities (Dupré 1979), 4,100 km of shoreline broken by 22 large river mouths and 13 bays, and about 3,100 km² of unvegetated intertidal flats (King and Dau 1981). The intertidal flats are generally composed of fine silts, especially at the mouths of the major rivers, but also include extensive areas of more sandy silts and occasionally large sand bars. Adjacent to the extensive intertidal flats are about 9,200 km² of wet sedge and grass meadows that lie between the normal high-tide line and the storm-tide line (Jackson 1972, King and Dau 1981, Tande and Jennings 1986). Tides along the coast of the central delta are semidiurnal with a mean range of 2.1 m (U.S. Department of Commerce 1987).

METHODS

GROUND SURVEYS

Our census area was at the mouth of the Tutakoke River (Fig. 1) and included 90 ha of intertidal flats and 72 ha of adjoining vegetated habitat composed of about 20% salt grass meadow and 80% wet sedge meadow. Between 30 April and 15 September 1979 we systematically censused from a 4-m tower all shorebirds using the 162-ha area. We censused every other day during spring (30 April–22 May; 12 census days), and every fourth day during the nesting season (24 May–11 June; 5 census days) and postbreeding period (15 June–15 September; 23 census days).

Counts were conducted five times each census day except during midseason (24 May–19 July) when use by shorebirds was lowest and only three counts per day were done. During each census day, counts were scheduled at about equal intervals throughout the daylight period, which spanned 16 hr on 30 April, 19.8 hr at summer solstice, and 13 hr on 15 September. For each count a single observer using a 20–60× spotting scope scanned the study plot and recorded the number, habitat, behavior, and, when possible, age of all birds detected.

To determine densities of nesting shorebirds on the Tutakoke study area, 14 strip transects were censused from 14–16 June 1982 during the period of peak clutch completion (Gill and Handel, unpubl.). Transects were 30 m wide, averaged 720 m (±90 SE, range = 240–1,280) long, and were spaced 100 m apart after random placement of the initial transect. Two observers dragged a 30-m rope between them and counted all shorebirds that flushed from or flew over the census strip. Nests were counted as representing a pair of birds, individuals were counted as singles, and the total was halved to estimate the number of nesting pairs. Among the species breeding on the area, non-nesting individuals were a negligible factor in calculating nesting densities (Gill and Handel, pers. observ.).

General observations on seasonal occurrence, numbers, and ages of shorebirds using Angyoyaravak Bay (Fig. 1) were recorded on a total of 940 person-days: 27 June–5 July 1977; 3 May–12 September 1978; 22 April–19 September and 2 October 1979; 2 May–6 July, 1 August–22 Sep-

TABLE 1. Length of shoreline (km) and area (km^2) of intertidal flats within each census area.

Bay	Census area	Shoreline		Intertidal	
		km	%	km^2	%
Kokechik Bay	1	21.7	9.9	21.0	6.9
	2	20.3	9.2	3.5	1.2
(connecting area)	3	17.2	7.8	1.9	0.6
Hooper Bay	4	32.1	14.6	36.4	12.0
	5	12.1	5.5	15.9	5.2
(connecting area)	6	15.0	6.8	10.8	3.6
Angyoyaravak Bay	7	15.3	7.0	40.3	13.3
	8	16.1	7.3	87.7	28.8
Hazen Bay	9	15.0	6.8	14.9	4.9
	10	10.5	4.8	5.3	1.7
	11	21.6	9.8	56.3	18.5
	12	23.2	10.5	10.0	3.3
	Total	220.0	100.0	304.0	100.0

tember, and 3 October 1980; 26 May–28 June 1981; and 7 June–5 July 1982.

AERIAL SURVEYS

We established 12 census areas that encompassed four major bays and about 10% of the delta's entire intertidal habitat (Fig. 1, Table 1). Eleven aerial surveys were conducted during the postbreeding period between early July and early October over 5 years (1 in 1977, 2 in 1978, 5 in 1979, 2 in 1980, and 1 in 1981). Eight of the surveys covered all 12 census areas. Two observers recorded all birds seen from a single-engine float plane (Cessna 180 or 185) flown 50 m above ground at about 160 km/hr ground speed. The surveys were flown during high tide (mean height 2.2 ± 0.1 m above MLLW = mean lower low water) along a single flight line about 200 m inshore of the water's edge, where most birds were concentrated at roosts. "Figure S" patterns were flown over any expanses of intertidal flats that remained exposed.

MEASUREMENTS OF HABITAT

Area of intertidal flats and length of shoreline were measured from U.S. Geological Survey (USGS) topographic maps (scale 1:63,360) with an electronic digitizing planimeter. We also monitored tides at Angyoyaravak Bay during 1980, mapped the actual intertidal area exposed at MLLW on Bureau of Land Management color-infrared photographs (scale 1:60,000), and determined that it was about 11% less than that depicted on USGS maps. For the three other bays we assumed a similar 11% decrease in the area planimetered from the maps, but we realize these values are approximations. The Yukon-Kuskokwim Delta is dynamic; ice scour, sediment deposition, and erosion continually change the amount of intertidal habitat (Thorsteinson et al. 1989).

DATA ANALYSIS AND INTERPRETATION

Statistical analyses followed Sokal and Rohlf (1981), using the SPSS^X (SPSS 1983) software package. Values are presented as mean ± standard error of the mean unless stated otherwise. We compared relative use of vegetated coastal habitats and adjacent intertidal areas during each season with a paired *t*-test of the mean daily densities of shorebirds in each habitat during ground counts. Seasonal changes in relative use of each habitat were tested with ANOVA. Using Pearson's correlations, we tested relationships between the number of shorebirds using bays and connecting coastlines at high tides during aerial surveys and the amount of intertidal flats and length of shoreline available at MLLW. Differences were tested statistically at a significance level of $P < 0.05$.

We took several precautions to assure that our results were a valid characterization of how shorebirds use coastal habitats on the delta. We could not ground-truth our aerial estimates because almost all areas were inaccessible to us. To minimize errors in estimating the size of large flocks during aerial surveys (see, e.g., Prater 1979, Kersten et al. 1981, Garnett and Carruthers 1982), we always used the same two experienced observers, circled over large flocks to allow a consensus on their size, and used our experience in counting large flocks from the ground to refine techniques of estimation from the air.

Because identifying small sandpipers from the air is so difficult, we usually lumped all small *Calidris* sandpipers as "small sandpipers." Within Angyoyaravak Bay we monitored seasonal changes in the occurrence of these sandpipers with extensive ground censuses. We consider projections of these proportions to the other three major bays reasonable.

Neither aerial nor ground counts can be used to calculate actual densities of shorebirds. Even though the aerial surveys were flown near the time of high tide when the majority of birds were at coastal roosts, sometimes significant numbers of certain species were roosting inland beyond our survey coverage. This caution also applies to ground counts in that only a fraction of the available tidal flats was surveyed and use of the upper intertidal areas may not have been representative of shorebird use of more outlying intertidal areas during an entire feeding cycle. In addition, detectability of shorebirds using vegetated habitats on the ground census area varied with body size, behavior, and height of vegetation. Our reported densities of shorebirds were in all cases conservative or minimum estimates; no visibility correction factor or adjustment to the data was applied to increase numbers of birds seen during counts.

RESULTS

SEASONAL OCCURRENCE AT THE TUTAKOKE RIVER

Spring migration (30 April–22 May). About 20,000 shorebirds of 13 species were recorded at the Tutakoke River study site during 60 ground censuses on 12 days in spring 1979 (Table 2). Peak arrival occurred from 4–16 May for most species that nested on the Yukon-Kuskokwim Delta that year. Shorebirds occurred on 93% of the counts and averaged 336 ± 152 birds per count per day. Most numerous were Red Knots (*Calidris canutus*), Rock Sandpipers (*C. ptilocnemis*), Dunlins (*C. alpina*), and Black Turnstones (*Arenaria melanocephala*), collectively accounting for 94% of all the sightings recorded. Both Dunlins and Black Turnstones, which occurred on 92% and 77% of the counts, respectively, were common nesting species on the study area. The Rock Sandpiper occurred on 52% of the counts and nested uncommonly on tundra beginning 3–5 km inland. The Red Knot was the only major species that occurred on the area in spring that did not nest on the greater delta. Red Knots were recorded on only 15% of the counts, occurring sporadically in large flocks between 10 and 22 May. Although the largest number recorded on any single count during 1979 was 6,800 birds, larger numbers of knots used the area in years with later springs. On the evening high tide of 21 May 1980 we recorded an estimated 110,000 Red Knots (in flocks of 25,000, 40,000, and 45,000) roosting along the coast and just inland of the Tutakoke study site.

Nesting period (24 May–11 June). Five species were recorded during this period; all but the Bar-tailed Godwit (*Limosa lapponica*) nested commonly on the study area (Table 2). Shorebirds were recorded on all 14 counts and averaged 44 ± 3 individuals per count per day. Black Turnstones and Dunlins occurred on all counts and represented 64% and 29%, respectively, of all shorebirds recorded during this period; but these figures also reflected the decreasing detectability of the smaller shorebirds with increasing distance from the observation tower. Nesting densities based on strip transects indicated an average of 2.5 (±0.4) pairs of shorebirds per hectare. The nesting density of Dunlins (1.1 ± 0.2 pairs/ha) was about twice that of Red-necked Phalaropes (*Phalaropus lobatus*) and Black Turnstones (0.6 ± 0.2 and 0.6 ± 0.1 pairs/ha, respectively). The nesting density of Semipalmated Sandpipers (*Calidris pusilla*) was only 0.2 ± 0.1 pairs/ha. Red Phalaropes (*P. fulicaria*) also nested on the study area but in such low densities that they were not recorded on the transects.

Postbreeding (15 June–15 September). Fifteen species totaling 96,573 birds were recorded during this period (Table 2). Birds were seen on all 98 counts and averaged 862 ± 245 individuals per count per day, more than twice that recorded during spring migration. Two species, Dunlins and Western Sandpipers (*C. mauri*), accounted for 65% and 24%, respectively, of all birds censused. Dunlins were seen on 93% of the counts, averaged 555 ± 182 birds per count per day, and occurred in flocks of up to 7,000 birds during late August. Western Sandpipers were seen on 58% of the counts and averaged 204 ± 172 birds per count per day. The largest number of Western Sandpipers recorded on the Tutakoke census area was 8,520 on 21 July. Black Turnstones and Rock

TABLE 2. Seasonal occurrence of shorebirds recorded on ground censuses at the Tutakoke River study area during 1979.[a]

Species	Spring migration (30 April–22 May)			Nesting (24 May–11 June)			Postbreeding (15 June–15 September)		
	Total birds	% counts with birds	$\bar{x} \pm$ SE birds/count/day	Total birds	% counts with birds	$\bar{x} \pm$ SE birds/count/day	Total birds	% counts with birds	$\bar{x} \pm$ SE birds/count/day
Pluvialis squatarola	24	6.7	0.4 ± 0.3				66	15.3	0.7 ± 0.3
P. dominica							176	23.5	1.6 ± 0.8
Limosa lapponica	209	10.0	3.5 ± 3.4	4	14.3	0.3 ± 0.2	421	22.4	4.3 ± 1.9
Arenaria interpres	6	6.7	0.1 ± 0.06				7	5.1	0.06 ± 0.03
A. melanocephala	1,717	76.7	28.6 ± 7.4	393	100.0	28.6 ± 4.0	649	22.4	9.4 ± 4.0
Calidris canutus	10,834	15.0	180.6 ± 149.8				196	9.2	1.9 ± 4.8
C. pusilla	25	11.7	0.4 ± 0.3	20	42.9	1.3 ± 0.9	7	4.1	0.1 ± 0.07
C. mauri	71	6.7	1.2 ± 0.9				22,706	58.2	203.8 ± 171.8
C. bairdii	4	5.0	0.07 ± 0.07						
C. melanotus							10	2.0	0.1 ± 0.08
C. acuminata							40	7.1	0.4 ± 0.2
C. ptilocnemis	4,617	51.7	77.0 ± 35.0				2,136	34.7	18.7 ± 8.6
C. alpina	1,891	91.7	31.5 ± 8.3	176	100.0	12.0 ± 3.1	62,547	92.9	554.6 ± 181.7
Calidris sp.	700	1.7	11.7 ± 11.7				7,155	7.1	62.2 ± 51.9
Limnodromus scolopaceus	11	10.0	0.2 ± 0.1				108	10.2	0.9 ± 0.5
Phalaropus lobatus	72	35.0	1.2 ± 0.5	24	57.1	1.6 ± 0.5	348	36.7	3.4 ± 1.6
P. fulicaria	5	3.3	0.1 ± 0.08				1	1.0	0.01 ± 0.01
Total	20,186	93.3%	336 ± 152	617	100.0	44 ± 3	96,573	100.0	862 ± 245

[a] Spring migration: n = 60 counts over 12 days; nesting: n = 14 counts over 5 days; postbreeding: n = 98 counts over 23 days.

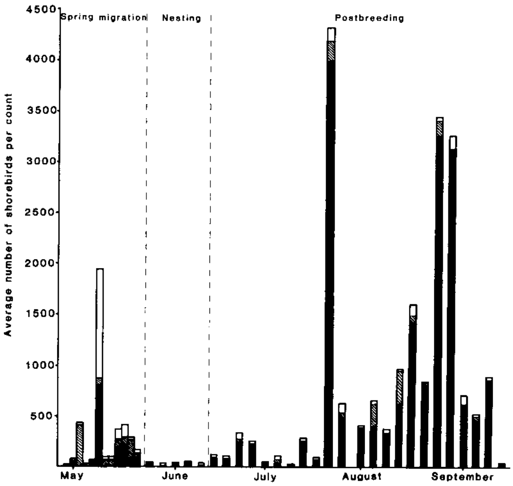

FIGURE 2. Numbers of all shorebirds using intertidal habitats (solid), using vegetated habitats (diagonal), or flying (open) during ground counts at the Tutakoke River study site, 1979.

Sandpipers were also common on the area during this period, but their overall numbers represented less than 3% of the total shorebirds recorded during autumn. The only species that frequently occurred in the area that we did not record on the ground censuses was the Greater Yellowlegs (*Tringa melanoleuca*), which occurred primarily during late summer on vegetated habitats away from the immediate coast.

HABITAT USE AT THE TUTAKOKE RIVER

Spring migration (30 April–22 May). During ground censuses of the Tutakoke River study site in spring, approximately equal numbers of shorebirds were recorded using intertidal (35.5%) and vegetated (28.8%) habitats. An equally large proportion (35.7%) was recorded flying through the area (Fig. 2). Densities of shorebirds using mudflats during the 12 census days averaged 1.3 ± 0.7 birds/ha, equalling densities of shorebirds using vegetated habitats (1.3 ± 0.5 birds/ha). Among the five principal species that used the area in spring, Dunlins and Black Turnstones, which nested on the study area, and Rock Sandpipers, which nested inland, primarily used vegetated habitats while Red Knots and Bar-tailed Godwits were more often observed in intertidal habitats (Fig. 3).

Nesting period (24 May–11 June). Half (49.9%) of the shorebirds recorded on the Tutakoke River study area during the nesting period were using vegetated habitats, a third (33.4%) were on intertidal habitats, and the remainder (16.7%) were flying over. Average densities on each habitat for the five census days of this period were lower, but not significantly so, than those recorded in spring, and densities on vegetated areas (0.29 ± 0.06 birds/ha) did not differ significantly from densities on intertidal habitats (0.18 ± 0.05 birds/ha).

Postbreeding (15 June–15 September). After the nesting period a marked shift occurred in habitat use from vegetated to intertidal areas (Fig. 2). Among the almost 100,000 shorebirds counted on 23 census days, 89.7% were on intertidal habitats whereas only 6.8% were on vegetated habitats and 3.5% were in flight. During this period, densities on intertidal areas increased to 8.6 ± 2.6 birds/ha, significantly higher than densities on intertidal areas during the spring and nesting periods ($P < 0.05$), and more than 10 times greater than densities of shorebirds on vegetated habitats during the postbreeding period (0.8 ± 0.3 birds/ha, $P < 0.01$).

Use of intertidal habitats was dominated by Dunlins (5.6 ± 2.0 birds/ha), Western Sandpipers (2.0 ± 1.8 birds/ha), and Rock Sandpipers (0.2 ± 0.1 birds/ha), all of which fed and roosted on nearshore intertidal flats. Vegetated areas were used primarily by small numbers of Dunlins (0.5 ± 0.2 birds/ha) and Western Sandpipers (0.2 ± 0.1 birds/ha) for roosting. Smaller numbers of Red-necked Phalaropes, Black Turnstones, Long-billed Dowitchers (*Limnodromus scolopaceus*), Sharp-tailed Sandpipers (*Calidris acuminata*), and a few other species also fed in coastal vegetated habitats (Fig. 3).

AGE-RELATED USE OF INTERTIDAL HABITATS

Shorebirds used intertidal habitats in three distinct patterns according to age class (Fig. 4). The most common pattern, exhibited by seven species, involved an initial period in which adults used intertidal areas alone followed by a brief period after nesting in which adults and juveniles occurred together, and then by a more prolonged period in which only juveniles occurred (Fig. 4, top). This basic pattern did vary. Western Sandpipers and Red Knots occurred on intertidal habitats during spring migration but were absent until June, when failed breeders began returning to the area. In contrast, the Black Turnstone, which nested along the coast, used intertidal habitats

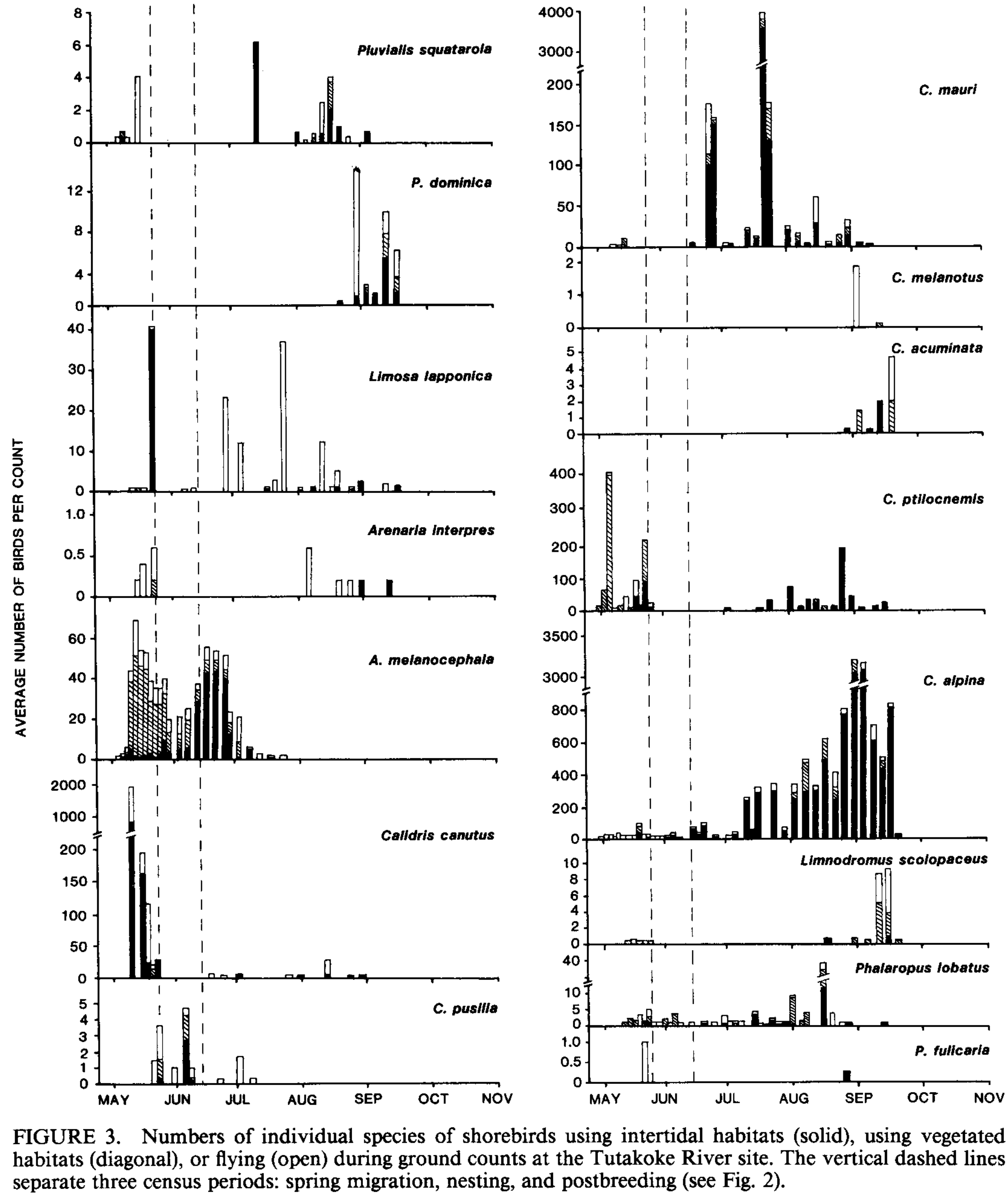

FIGURE 3. Numbers of individual species of shorebirds using intertidal habitats (solid), using vegetated habitats (diagonal), or flying (open) during ground counts at the Tutakoke River site. The vertical dashed lines separate three census periods: spring migration, nesting, and postbreeding (see Fig. 2).

in at least small numbers continuously between spring and fall migration. The remaining four species of this group did not begin to use the area until the postbreeding period (Fig. 4).

The second pattern, exhibited by Bar-tailed Godwits, Dunlins, and Rock Sandpipers, involved an initial period of use exclusively by adults followed by a prolonged period of use by both adults and juveniles (Fig. 4, middle). All three species used intertidal areas during spring. Dunlins, which nested in adjacent vegetated habitats, continued to use intertidal habitats during summer in small numbers whereas Rock Sandpipers and Bar-tailed Godwits, which both nested inland, were absent from or occurred only sporadically on intertidal flats during most of the

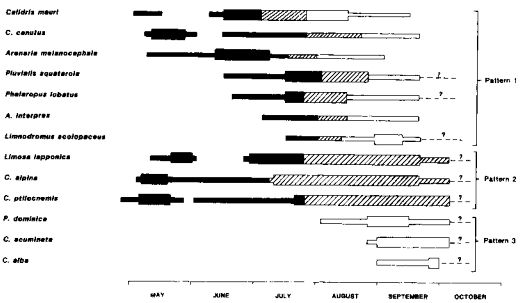

FIGURE 4. Three major age-related patterns of seasonal use of intertidal habitats by shorebirds on the central Yukon-Kuskokwim Delta (solid = adults only, diagonal = both adults and juveniles, open = juveniles only). Depending on the onset of freezing conditions in fall, some species may remain on the delta into mid-October. Wider bars indicate typical periods of greatest use for each species.

nesting period. Use of intertidal areas by all three species increased dramatically during the postbreeding period. Their numbers remained high until departure in late September and early October.

The final pattern of age-related habitat use involved the Lesser Golden-Plover (*Pluvialis dominica*), Sharp-tailed Sandpiper, and Sanderling (*Calidris alba*), none of which nested on the outer Yukon Delta. Only juveniles were recorded using intertidal habitats, and they occurred from August through early October (Fig. 4, bottom).

DISTRIBUTION AND ABUNDANCE ON THE CENTRAL DELTA

Seasonal occurrence. Among eight aerial surveys that covered all census areas of the central Yukon-Kuskokwim Delta during the postbreeding period, a mean of 167,375 ± 33,936 shorebirds was recorded (Table 3). Densities averaged 761 ± 154/km of shoreline and 551 ± 112/km^2 of intertidal area. Numbers of shorebirds started building in early July, peaked in August or early September, and remained high through late September (Table 2). Surveys during early October revealed an abrupt departure by shorebirds from the delta, with only about 20,000 birds remaining. Although timing of build-up was consistent from year to year, the total number of shorebirds and the timing of peak occurrence each fall were more variable, with almost 300,000 counted in early September of both 1978 and 1980 but only 190,000 recorded during late August 1979 (Table 3).

Small sandpipers, primarily Dunlins, Western Sandpipers, and Rock Sandpipers, accounted for 95.2% of all shorebirds recorded during 11 aerial surveys (Table 3). Bar-tailed Godwits and Red Knots accounted for 4.5%, and an additional 10 species comprised the remaining 0.3%.

Although the total number of small sandpipers remained high throughout August and September each year, the relative abundance of the major species changed. During ground censuses at the Tutakoke area in early July 1979, Western Sandpipers comprised most (88.9%) of the small sandpipers recorded, with only a few Dunlins (11.0%), and fewer Rock Sandpipers present (Table 4). In early August, however, Dunlins (83.2%) far outnumbered Western Sandpipers (9.2%), and Rock Sandpiper numbers increased. During September, the last Western Sandpipers departed and almost all (>95%) of the remaining sandpipers were Dunlins (Table 4). A single ground count at Tutakoke on 3 October 1980 after a mass departure revealed that the majority (72%) of the 4,000 sandpipers remaining were Rock Sandpipers, with only a few Dunlins present (28%).

When we applied these data on species composition from ground counts at Tutakoke to data from aerial surveys, we estimated that numbers of Western Sandpipers along the entire central delta in 1979 dropped from about 50,000 on 12 July to about 20,000 on 2 August and to less than 1,000 on 27 August. Dunlins, in contrast, increased from about 6,000 on 12 July to about 180,000, which were present on both 2 and 27 August, and dropped to about 140,000 by 20 September. During the 4 October 1980 aerial survey, we estimated that no Western Sandpipers and fewer than 5,000 Dunlins remained on the central delta.

Rock Sandpipers used the central delta between mid-July and mid-October in much lower numbers than Dunlins or Western Sandpipers. However, extrapolation of a central delta population based on ground censuses at Tutakoke is unreliable because Rock Sandpipers generally roosted along cut-bank habitats that were not uniformly distributed among bays of the central delta. The occurrence of Rock Sandpipers at the Tutakoke site was very sporadic and extrapolations from censuses there would have resulted in central delta population estimates of less than 100 birds on 12 July, about 17,000 on 2 August, 5,000 on 27 August, and 2,000 on 20 September

TABLE 3. Numbers of shorebirds recorded on aerial surveys (arranged seasonally) of the central Yukon-Kuskokwim Delta, Alaska, 1977–1981.

Species	Survey date: 7 Jul[a] 1977	12 Jul 1979	16 Jul[a] 1978	2 Aug 1979	27 Aug 1979	6 Sep 1978	7 Sep 1980	20 Sep 1979	30 Sep 1979	3 Oct[a] 1981	4 Oct 1980	Total no.	(%)
Small sandpipers[b]	4,759	59,076	32,615	217,085	180,216	264,997	272,683	141,437	124,523	23,709	16,402	1,337,502	(95.2)
Limosa lapponica	0	5,843	2,086	518	6,962	14,510	14,659	10,971	4,875	420	1,020	61,864	(4.4)
Calidris canutus	65	710	856	25	3	59	0	0	0	0	0	1,718	(0.1)
Pluvialis squatarola	0	635	18	40	26	85	45	7	0	0	0	856	(<0.1)
P. dominica	0	1	2	3	7	109	12	18	36	147	0	335	(<0.1)
Limnodromus scolopaceus	4	0	0	0	0	110	0	0	200	0	0	314	(<0.1)
Phalaropus lobatus	0	20	0	65	0	0	0	0	0	0	0	85	(<0.1)
Arenaria melanocephala	58	0	11	1	0	0	0	0	0	0	0	70	(<0.1)
Numenius phaeopus	0	0	45	0	0	0	0	0	0	0	0	45	(<0.1)
Calidris alba	0	0	0	0	0	0	0	1	34	0	0	35	(<0.1)
C. acuminata	0	0	0	0	0	8	0	0	0	0	0	8	(<0.1)
Arenaria interpres	0	0	0	0	0	1	0	0	0	0	0	1	(<0.1)
Heteroscelus incanus	0	0	0	0	0	0	0	0	1	0	0	1	(<0.1)
Unidentified large shorebirds	0	0	717	500	0	0	0	0	0	0	0	1,217	(<0.1)
Unidentified medium shorebirds	0	0	0	0	2	450	0	0	0	0	10	462	(<0.1)
Total numbers	4,886	66,285	36,350	218,237	187,216	280,329	287,399	152,434	129,669	24,276	17,432	1,404,513	(100.0)

[a] The following census areas (see Fig. 1) were not surveyed on these dates: 7 July 1977 (#1, 2, 10, 11, 12); 16 July 1978 (#1, 2, 3); 3 October 1981 (#1, 2, 3, 4, 5).
[b] *Calidris alpina, C. mauri, C. ptilocnemis,* and *C. pusilla.* See text for discussion of relative numbers and temporal occurrence of each species.

TABLE 4. Seasonal species composition of small sandpipers recorded using intertidal habitats in the postbreeding period during ground censuses of the Tutakoke River study area in 1979 and 1980.

	1–21 Jul 1979	25 Jul–14 Aug 1979	18 Aug–7 Sep 1979	11–15 Sep 1979	4 Oct 1980
Calidris alpina	11.0%	83.2%	96.9%	98.8%	28.0%
C. mauri	88.9%	9.2%	0.3%	0.0%	0.0%
C. ptilocnemis	0.1%	7.6%	2.8%	1.2%	72.0%
Total no. sightings	21,120	10,602	42,257	4,337	4,000
Total no. censuses	22	25	30	9	1

during 1979, and about 12,000 on 4 October 1980 (Tables 3, 4). Since we counted about 9,000 Rock Sandpipers on 9 September 1979 during a boat survey of roost sites just along the northern portion of Angyoyaravak Bay (census area 7), our best estimate is that numbers of postbreeding Rock Sandpipers on the central delta peaked at about 20,000 birds during late August and early September.

Relative use of bays. During the eight complete aerial surveys of the four major bays and connecting coastlines, Hazen Bay supported the greatest number of shorebirds (42% of total), followed by Angyoyaravak Bay (35%), Hooper Bay (16%), and Kokechik Bay (6%). Connecting census areas 3 and 6 accounted for the remaining 1%. The percentage of total birds using each bay and connecting shoreline was strongly correlated with the amount of intertidal flats exposed at MLLW ($r = 0.86$, $P < 0.001$) and less so with the length of its shoreline ($r = 0.66$, $P < 0.001$). There was no significant correlation between the length of shoreline and the amount of intertidal flats of the four bays and connecting shorelines ($r = 0.50$, $P = 0.32$).

Over the entire study area, densities peaked in early September at 945 birds/km^2 of intertidal flats available at MLLW. Hazen Bay, however, supported not only the highest density but also the greatest number of shorebirds during five of the eight surveys, hosting peak numbers of 156,800 birds, or 1,813 birds/km^2 in early September (Table 5). Through most of the season, densities in Hazen Bay were often double those found in other bays but by late September its relative use had fallen sharply (Table 5). Use of the other three bays varied much more throughout the season, with peak densities ranging from 729 birds/km^2 in Kokechik Bay to 1,167 birds/km^2 in Hooper Bay. On almost all surveys the two connecting coastal areas (3 and 6) supported densities far below those found within the bays themselves (Table 5).

DISCUSSION

SEASONAL IMPORTANCE OF YUKON-KUSKOKWIM DELTA

Spring migration. Intertidal habitats of the central Yukon-Kuskokwim Delta are used by shorebirds during the entire ice-free period (late April–October) and provide resources that appear to be critical to several populations for migration, molt, and reproduction. Marked seasonal differences in species composition and numbers reflect not only differences in the availability of other foraging areas along migration routes but also differences among species in their molt and migration strategies.

The large influx of more than 100,000 Red Knots to the Tutakoke study area in 1980 might have been an anomalous result of the very late spring and heavy snow conditions that year, or it may represent the typical migration pattern for the central delta. The largest single count of Red Knots recorded previously in Alaska in spring was of 40,000 birds on 11 May 1975 on the Copper River Delta (Kessel and Gibson 1978), where an estimated 100,000 migrants occur in mid-May each year (M. E. Isleib *in* Kessel 1989).

We are not certain to what breeding population the Red Knots staging on the Yukon-Kuskokwim Delta belong or where their wintering grounds are. Kessel (1989) surmises that these migrants nest on the Seward Peninsula, along the Chukchi Sea coast of Alaska, and possibly in northeastern Siberia and on Wrangel Island in the Soviet Union. The AOU (1957) formally recognizes only two races of Red Knot (*Calidris canutus canutus* and *C. c. rufa*), but at least two additional races (*C. c. islandica* and *C. c. rogersi*) are widely accepted among shorebird authorities (Cramp and Simmons 1983). Much confusion

TABLE 5. Densities of shorebirds (numbers per km^2 of intertidal at MLLW) on major bays and connecting coastlines during eight complete aerial surveys of the central Yukon-Kuskokwim Delta, 1977–1980.

Census area	Census date							
	12 Jul 1979	2 Aug 1979	27 Aug 1979	6 Sep 1978	7 Sep 1980	20 Sep 1979	30 Sep 1979	4 Oct 1980
Kokechik Bay	119	147	475	670	623	579	729	16
Area 3	7	2	9	94	106	1	13	0
Hooper Bay	150	360	397	618	1,167	763	467	76
Area 6	3	0	0	188	324	437	324	52
Angyoyaravak Bay	139	677	531	567	784	477	466	50
Hazen Bay	436	1,262	1,003	1,813	1,237	377	279	71
Total	218	718	616	922	945	501	427	57

persists, however, regarding the subspecific status of knots breeding in this region and the discreteness of various nesting and wintering areas (see Conover 1943; AOU 1957; Portenko 1972; Cramp and Simmons 1983; Roselaar 1983; Tomkovich 1987; Barter et al. 1988; M. Stishov, pers. comm.; R.I.G. Morrison, in litt.). In the Pacific Ocean region, birds winter primarily in Australia and New Zealand (Lane 1987) and along the coast of the Americas between southern California and Tierra del Fuego, where they are rare north of Peru (AOU 1983, Morrison and Ross 1989).

The number of knots wintering in Australasia has been estimated at 160,000–200,000 birds (Barter et al. 1988), while Harrington (1982) has estimated about 150,000 Red Knots winter in South America. Recent surveys along the South American coast recorded only about 53,000 birds on the eastern side of Tierra del Fuego, about 23,000 farther north along the Atlantic Coast, and a few thousand along the Pacific Coast (Morrison and Myers 1987; Morrison and Ross 1989; Myers, in litt.). An additional 10,000 knots winter along Florida's west coast and a few smaller groups winter along the Texas coast (Harrington 1982). Banding studies of these Atlantic and Gulf Coast populations have shown that they breed primarily near Hudson Bay in the Canadian Arctic and belong to the race *C. c. rufa* (Harrington 1982). These are presumed to be distinct from knots occurring in Alaska (Conover 1943, AOU 1957, Portenko 1972, Roselaar 1983, Tomkovich 1987).

Whether Red Knots staging on the Yukon-Kuskokwim Delta belong to the Australasian Flyway population or another as yet unidentified Pacific Flyway population, concentrations of more than 100,000 birds in spring on our study area constitute a significant fraction of the entire Pacific population. Even though the numbers of knots using the central delta as a spring stopover may vary each year, intertidal habitats there may provide food critical for those birds to complete migration and replenish fat and protein reserves for reproduction (Davidson and Evans 1988). Reliance on a few critical staging areas during spring typifies the migration pattern of this species as evidenced by studies of the central Canadian Arctic population (Harrington 1983) and the central Siberian population (Dick et al. 1987). Such a strategy, however, makes the Red Knot particularly vulnerable to any disturbance of critical staging areas.

Moderate numbers of migrant Rock Sandpipers and Dunlins and occasional flocks of Bar-tailed Godwits also forage with Red Knots on ice-free intertidal habitats of the central delta each spring. Godwits and Dunlins are common nesters on adjacent tundra and meadows (Gabrielson and Lincoln 1959, Holmes 1970, Holmes and Black 1973) and Rock Sandpipers nest in low densities in more upland and inland habitats of the delta (Gabrielson and Lincoln 1959; Gill and Handel, unpubl.). We do not know if the birds using intertidal habitats in spring are local nesters or birds availing of feeding opportunities before moving to more northern breeding grounds. We suspect most are local nesters, but birds from other populations may also be involved. For example, Dunlins belonging to the population that nests in northern Alaska and Siberia (*C. a. sakhalina* = *C. a. arcticola*, Browning 1977; Tomkovich 1986) have been collected during late May on the Seward Peninsula, just north of the Yukon-Kuskokwim Delta. These birds were presumably migrants (Senner et al. 1981) from wintering grounds in eastern Asia (MacLean and Holmes 1971).

Nesting. Use of intertidal habitats by shorebirds on the Yukon-Kuskokwim Delta during the nesting period is minimal, but it is important to species breeding along the coast. Most notable among these is the Black Turnstone, which has a nesting distribution concentrated within a 2-km-wide band along the coast of the central delta (Handel and Gill, unpubl.). Availability of food on intertidal habitats is postulated to be an important determinant of territorial spacing for those turnstones nesting on adjacent meadows (Handel 1982). Ultimately, because of the dense nesting concentration adjacent to intertidal habitats, availability of these food resources may also have a significant effect on the behavior and social system of this species. Holmes (1970) provided evidence that territorial spacing in Dunlin populations has evolved in relation to food abundance in early summer and Pitelka et al. (1974) argued that different social organizations of calidridine sandpipers, in general, have evolved primarily in response to variations in the abundance and dependability of food resources.

Postbreeding. Intertidal habitats of the central delta are used for a prolonged period and by a diverse group of shorebirds after breeding. They are of prime importance to species that nest locally, particularly Dunlins, Western Sandpipers, and Rock Sandpipers, which accounted for the great majority (95%) of birds recorded using intertidal areas. Predominance of these species is not unexpected since their nesting densities on adjacent vegetated habitats of the Yukon-Kuskokwim Delta are among the highest reported for these species throughout the Holarctic (e.g., this study; Holmes 1966, 1970, 1971; cf. Morozov and Tomkovich 1980; Tomkovich and Morozov 1980; Tomkovich 1982; Cramp and Simmons 1983; Meltofte 1985).

The central delta is also used during the postbreeding period by populations of these three species and other shorebirds that have come from remote breeding areas. For example, Dunlins that we color-banded during the postbreeding period at the Tutakoke study site were subsequently recovered along both the Pacific Coast of North America and Asia. The race *C. a. pacifica* nests on the Yukon-Kuskokwim Delta and winters in North America (Todd 1953, AOU 1957), while *C. a. sakhalina* reportedly nests throughout northern Alaska and eastern Siberia and winters along coastal Asia (Norton 1971, MacLean and Holmes 1971). The problem of which races of Dunlins use the Yukon-Kuskokwim Delta has become potentially more complex based on recent taxonomic studies that have proposed several new forms within Beringia (see also Browning 1977, Tomkovich 1986, Nechaev and Tomkovich 1987).

The timing of movements of Dunlins in northwestern Alaska also suggests that at least two races move to the Yukon-Kuskokwim Delta to complete molt before migrating to Asia. Adult Dunlins depart breeding areas at Barrow (*C. a. sakhalina*) in northern Alaska in late July and almost all are gone by early September; departure of juveniles occurs in late August and "precipitately" before 1 September (Holmes 1966, p. 26). Southward along the coast at Icy Cape (70°N) numbers of Dunlins peak from early to mid-August (Lehnhausen and Quinlan 1981) and in the Kotzebue Sound, Seward Peninsula, and Norton Sound regions (64°–67°N) during late August (Connors and Risebrough 1978, Shields and Peyton 1979, Woodby and Divoky 1983, Kessel 1989), some 2 weeks before they first peak on the Yukon-Kuskokwim Delta.

Rock Sandpipers nesting on the Chukotski Peninsula of eastern Siberia (*C. ptilocnemis tschuktschorum*) also come to the central delta in large numbers to molt in late August and September, based on one band recovery and several sightings of uniquely color-banded birds (Gill and Handel, unpubl.; P. Tomkovich, in litt.). In addition, Rock Sandpipers that we color-banded on the central delta in late August were subsequently found nesting on St. Matthew Island in the northern Bering Sea, 400 km WSW of our study site (Gill and Handel, unpubl.). This nesting population has been assigned to the race *C. p. ptilocnemis* (Conover 1944, AOU 1957) and is thought to be distinct from the population that breeds on the delta (*C. p. tschuktschorum*). Staging areas on the central delta are used for completing molt before the birds move to wintering areas, which are still poorly defined for the two groups but which may include overlapping portions of the Pacific Coast of North America from southwestern Alaska to northwestern California and possibly the coast of the Chukotski Peninsula in Siberia (AOU 1957). We do not know what the relative subspecific composition was of the estimated 20,000 Rock Sandpipers that staged on the central delta nor do we know what proportion of each nesting population regularly occurs there.

Although we estimated that the number of Western Sandpipers staging on the central Yukon-Kuskokwim Delta peaked at about 50,000 individuals during July, we could not determine the total numbers that staged there during the postbreeding period because we did not know the rate of turnover. However, adult and juvenile Western Sandpipers move from nesting areas on adjacent tundra to coastal and riverine intertidal habitats of the delta on a staggered departure schedule (Holmes 1972). These movements were evident from our ground censuses, which showed that numbers of adults peaked sharply in late June and juveniles peaked sharply in late July. If these movements on the delta are indicative of turnover rates found for Western Sandpipers at other autumn staging sites along the Pacific Flyway, which averaged 3 days (Butler et al. 1987, Butler and Kaiser 1988), the total numbers of Western Sandpipers using the central delta each year may be close to 700,000 birds.

Furthermore, since the main nesting concentration of Western Sandpipers occurs on the central Yukon-Kuskokwim Delta (Holmes 1972), those that stage on the delta's intertidal habitats during southward migration likely constitute a significant fraction of the world population of this species. We do not know whether Western Sandpipers that nest farther north in Alaska or in eastern Siberia also pass through the delta during migration. Senner and Martinez (1982) suggest that the most northern breeders may migrate southward across interior North America en route to wintering areas in the southern United States, Central America, and northern South America.

The Bar-tailed Godwit is the only other shorebird to rely heavily on intertidal habitats during the postbreeding period. The number of godwits using the area was probably underestimated on the aerial surveys because most godwits roosted several kilometers inland at high tide and then overflew the ground census area to feed far out on the mudflats as the tide receded. The timing of movements in fall, however, suggests that a major component of the Pacific godwit population (*Limosa lapponica baueri*) stages on the delta to molt and build reserves prior to their transoceanic migration. Migrant godwits appear on wintering grounds in Australasia as early as August but most do not arrive until October (Skinner 1983, Close and McCrie 1986, Lane 1987). Numbers of godwits on the Seward Peninsula and other areas north of the delta peak in mid-August and decline sharply by early September (Shields and Peyton 1979, Kessel 1989) when numbers peak on the central delta. Most of the godwits have left the delta by mid-September, at which time they peak on lagoons of the north-central Alaska Peninsula before final southward departure at the end of September (Gill and Jorgensen 1979, Gill et al. 1981).

COMPARISON WITH OTHER AREAS

Densities of postbreeding shorebirds using intertidal habitats of the central Yukon-Kuskokwim Delta are among the highest in the world with peaks in early September of more than 900 shorebirds/km^2 and over 1,800/km^2 in Hazen Bay alone. By comparison, during the third week of August, Connors et al. (1979) found peak densities of about 250 shorebirds/km^2 in littoral areas near Barrow, Alaska, where intertidal habitats are meager and mostly occur in a narrow strip along the shoreline; this figure excludes Red Phalaropes, which are abundant and forage in nearshore waters along the beach. South of Barrow in late August, peak densities approached 900 shorebirds/km^2 near Wales, where more typical intertidal habitat occurs (Connors and Risebrough 1978). South of the Yukon-Kuskokwim Delta at Nelson Lagoon on the Alaska Peninsula, densities peaked at about 1,200 shorebirds/km^2 in late September (Gill and Jorgensen 1979, Gill and Handel 1981, Gill et al. 1981).

The most important staging area along the Atlantic Coast of North America is the Bay of Fundy (350 km^2 of intertidal flats), where peak densities exceeding 1,600 shorebirds/km^2, primarily Semipalmated Sandpipers, have been recorded in late July (Hicklin 1987). Peak densities in fall of slightly less than 250 shorebirds/km^2 have been recorded on the Fraser River Delta (200 km^2) of southern British Columbia (Butler and Campbell 1987, Butler et al. 1987, Butler and Kaiser 1988). Densities of shorebirds on land areas (tidal flats, marshes, and salt ponds) of San Francisco Bay totalled about 300 birds/km^2 during late fall (Bollman et al. 1970), but recent more rigorous surveys suggest densities may at times be much higher (Page and Stenzel, unpubl.).

Throughout the Palearctic the one area most resembling the central Yukon-Kuskokwim Delta for extent of intertidal habitat, seasonal availability to shorebirds, and numbers and diversity of species using the area, is Europe's Wadden Sea (53°N). It differs from the Yukon-Kuskokwim Delta primarily in that most of its shorebirds are migrants and not locally nesting birds. Nonetheless, the area is recognized as having some of the most critical shorebird habitats in Europe (Prater 1981, Smit 1981). Over the German, Dutch, and Danish portions of the Wadden Sea, long-term studies have consistently revealed peak autumn densities of about 600, 525, and 915 shorebirds/km², respectively, in intertidal habitat (Smit 1981, Smit and Wolff 1981, Laursen and Frikke 1984, Prokosch 1984, Wolff and Smit 1984).

RECOGNITION OF HEMISPHERIC IMPORTANCE

Shorebirds are linked to a chain of sites throughout their annual cycle. Disruption or elimination of a single key area threatens the entire system and the birds that depend on it (Myers et al. 1987a). The fundamental basis for conserving and managing habitat for shorebirds is the knowledge of critical sites. Through the Western Hemisphere Shorebird Reserve Network (Myers et al. 1987a, 1987b; Myers, in litt.), guidelines have been developed for identifying sites important to migratory shorebirds. Four reserve categories are recognized: hemispheric sites (those supporting >500,000 birds annually or >30% of a species' flyway population), international sites (100,000 birds or 15% of a species' flyway population), regional sites (20,000 birds or 5% of a species' flyway population), and endangered species sites (critical to the survival of an endangered species; no minimum number of birds required).

Our study showed that the central delta supported peak numbers of about 300,000 shorebirds during two of the three years. The total number of individuals using the area was many times greater than the peak number recorded because of migration timing and turnover within certain populations, particularly Western Sandpipers. Given these factors, we estimate that the central delta supports 1–2 million shorebirds each year. Thus, based on overall numbers of shorebirds, the central Yukon-Kuskokwim Delta easily qualifies as a site of hemispheric importance and therefore also merits inclusion under the Ramsar Convention (Smart 1987) as a site of international importance as waterbird habitat.

The central delta also qualifies for hemispheric designation based on the proportion of the Pacific Flyway populations of several species. The breeding distribution of both the Western Sandpiper and Black Turnstone is concentrated on the central delta (Holmes 1972, Gill and Handel 1981, Handel 1982) and we estimate that about 35–50% and 90% of their respective flyway populations use the central delta's intertidal habitats after the breeding season (Gill and Handel, unpubl.). In years with late spring conditions when Red Knots stop en route to their northern breeding grounds, the number of birds that use the central delta sometimes exceeds 30% of the flyway population.

The entire Yukon-Kuskokwim Delta encompasses 10 times the amount of intertidal flats found on its central portion. We know from other limited aerial surveys conducted during our study that shorebirds use intertidal areas along the entire coast of the delta, but that certain areas appear much more attractive to shorebirds than others. In general, the active north delta appears to be used least by shorebirds while areas immediately north and south of our study area appear to be similar to the central delta. The extensive intertidal flats west and north of the mouth of the Kuskokwim River may host greater numbers and higher densities of shorebirds than the central delta (B. McCaffery, in litt.). As a whole, however, the greater Yukon-Kuskokwim Delta hosts the majority of the Pacific Flyway populations of Dunlins (*C. a. pacifica*) and Rock Sandpipers (*C. p. tschuktschorum*), the Pacific Rim population of Bar-tailed Godwits (*L. l. baueri*), and the majority of the world population of Western Sandpipers and Black Turnstones.

CONCLUSIONS

The central Yukon-Kuskokwim Delta is clearly one of the most heavily used intertidal areas in the world. For its shorebird diversity, numbers, and densities it warrants designation as a Hemispheric Shorebird Reserve. Not only is it important for locally nesting species, many representing the majority of flyway populations, but it also draws important components of more northern breeding populations. The key to how the delta is able to support such variety and numbers of birds probably lies in the complex pattern by which the species subdivide food resources both temporally and spatially. Rapid turnover of individuals and differential timing of migration by various age and sex components of populations of some species, such as Western Sandpipers, allow staggered use of rich benthos to fuel the earliest stages of their southward migration. This early, intensive use is balanced by the strategy of other species, notably the Dunlin, for which the delta provides longer-term resources for both molt and migration. Exclusive use of the delta by juveniles of some species probably reflects a mechanism to reduce competition with adults on other staging grounds rather than their inability to complete the migratory flight or their investigation of random sites along the migration route, as Pienkowski and Evans (1984) suggest for some species. Further studies will elucidate the complex ecological factors that allow the Yukon-Kuskokwim Delta's intertidal habitats to support such high diversity and large numbers of shorebirds.

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