

BEHAVIOR OF MIGRATING SHOREBIRDS AT NORTH DAKOTA PRAIRIE POTHOLES¹

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Abstract. We examined diurnal time-activity budgets of American Avocets (*Recurvirostra americana*), Long-billed Dowitchers (*Limnodromus scolopaceus*), Stilt Sandpipers (*Calidris himantopus*), Semipalmated Sandpipers (*C. pusilla*), and Least Sandpipers (*C. minima*) in the Prairie Pothole Region of northwestern North Dakota during spring and fall 1994 and 1995 to evaluate the importance of prairie pothole wetlands to a variety of shorebird guilds. Long-billed Dowitchers, and Stilt, Semipalmated, and Least Sandpipers spent most of their time feeding in spring and fall. American Avocets also used prairie potholes for feeding, but other activities like locomotion, body maintenance, and sleep consumed large proportions of time. Time spent in various behaviors was similar among three diurnal (early, midday, and late) time periods during spring and fall. Avocets and dowitchers slept more during midday than early or late periods. Flock size was smaller during spring than fall in both years for American Avocets, Long-billed Dowitchers, Semipalmated Sandpipers, and Least Sandpipers and in 1994 for Stilt Sandpipers. More than half of all aggressive encounters by American Avocets, Stilt Sandpipers, Semipalmated Sandpipers, and Least Sandpipers were intraspecific during feeding. Smaller flock sizes in spring may be related to avoidance of costly aggression in spring and/or the numbers of birds migrating through the region. The Prairie Pothole Region serves as a stopover for most shorebirds to acquire energy reserves during migration, and conservation efforts should focus on preserving and enhancing prairie potholes for foraging shorebirds.

Key words: American Avocet, Least Sandpiper, Long-billed Dowitcher, Prairie Pothole Region, Semipalmated Sandpiper, shorebirds, Stilt Sandpiper.

INTRODUCTION

Analysis of behavior can aid in evaluation of shorebird habitat use and other life history requirements during migration. Goss-Custard and Durell (1990) proposed that behavioral studies should be a method of determining how birds respond to environmental changes and compete for limited resources, such as diminishing habitat. Furthermore, documenting behavior within different types of habitat allows a better understanding of why those habitats are selected (Titan 1981) and provides an opportunity to evaluate the significance of regional areas to migratory birds (Streeter et al. 1993, Davis and Smith 1998a).

Many aspects of shorebird behavior have been studied in coastal wintering and breeding areas (Holmes 1966, Baker and Baker 1973, Colwell 1993), but few studies have examined the behaviors of migrant shorebirds in inland areas (Davis and Smith 1998a). Indeed, the physiolog-

ical needs of shorebirds during these different periods of the annual cycle are quite different (O'Reilly and Wingfield 1995). These needs should be manifested in different behaviors or time allotments, such as variation in time spent feeding due to different dietary requirements and quantity and quality of available prey (Davis and Smith 1998a, 1998b). Also, although coastal and inland areas share many of the same species of shorebirds, species compositions and habitat vary between coastal and inland areas (Recher and Recher 1969, Myers 1983, Davis and Smith 1998b). Therefore, these habitats also may meet different requirements for different shorebird groups and these differences may be detected in shorebird behavior.

Many shorebird species migrate between 12,000 and 25,000 km annually from wintering to breeding grounds (Myers et al. 1987). McNeil and Cadieux (1972) suggested that the energy required by an individual shorebird for a one-way migration trip is several times more than the accumulation of premigratory fat. Furthermore, Skagen and Knopf (1993) hypothesized that migrant shorebirds require a network of intermediate stopover sites between breeding and

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FIGURE 1. Aerial view of prairie pothole wetlands of northwestern North Dakota (photo courtesy of U.S. Fish and Wildlife Service, Lostwood National Wildlife Refuge).

wintering areas to successfully complete migration. The Prairie Pothole Region of the Northern Great Plains is one of the most extensive wetland complexes in North America (Cowardin et al. 1979) and serves as one of these important stopover sites. Glaciers that covered Canada during the Pleistocene moved south over the Dakotas and other states to the east. This scouring action caused by glaciers combined with the retreat and melting of ice during the Holocene produced thousands of prairie pothole wetlands (Kantrud et al. 1989).

In this study, we evaluated the behavior of migrating shorebirds in the Prairie Pothole Region to determine factors associated with the importance of these wetlands to shorebird populations. During this time, 27 total shorebird species were identified in this region. These include one Recurvirostridae, five Charadriidae including the threatened Piping Plover (*Charadrius melodus*), one Limosini, five Tringini, two Phalaropodini, one Limnodromini, one Numeniini, nine Calidridini, one Gallinagonini, and one Ardeariini (DeLeon 1996). We examined diurnal time-activity budgets of American Avocets (*Re-*

curvirostra americana), Long-billed Dowitchers (*Limnodromus scolopaceus*), Stilt Sandpipers (*Calidris himantopus*), Semipalmated Sandpipers (*C. pusilla*), and Least Sandpipers (*C. minutilla*). These five species were studied because they represent different size classes (large, medium, and small) and feeding guilds (sweepers or scythers, probers, and gleaners) (Helmers 1992) and the information attained may be applicable to the range of shorebird species that migrate through the Prairie Pothole Region.

METHODS

STUDY AREA

We conducted our study on 28 prairie wetlands of Burke, Divide, and Mountrail counties, North Dakota. Because this area contains a relatively high density of intact wetlands (Fig. 1), we chose to study shorebirds in northwestern North Dakota to identify the significance of the Prairie Pothole Region. These counties have 122 temporary wetland basins per km⁻² (16 ha of basins km⁻²), 163 seasonal wetland basins per km⁻² (68 ha of basins km⁻²), and 18 semi-permanent wet-

land basins per km⁻² (46 ha of basins km⁻²) which are all classified palustrine wetlands. Also within these counties are 3 lacustrine basins per km⁻² (74 ha of basins km⁻²) and 1 riverine basin per km⁻² (0.81 ha of basins km⁻²) (Reynolds et al. 1997). Most likely lacustrine and riverine habitats play a relatively more important role during drought years; they do provide important wetland habitat in this region. However, during this study we focused on randomly selected palustrine wetlands because they form the most available wetland habitat in the region. Size of temporary, seasonal, and semi-permanent prairie pothole wetlands (Cowardin et al. 1979) that we used ranged between 0.76 and 17.0 ha (DeLeon 1996).

The physiography of Burke, Divide, and Mountrail counties is characterized as rolling plains (Kantrud et al. 1989). However, some areas within these counties also are drift plains (see Stewart and Kantrud 1971 and Kantrud et al. 1989 for further descriptions of North Dakota prairie wetlands). The region has a semiarid climate with mean annual precipitation, including snowmelt, of 39 cm (NOAA 1994). Mean temperature for spring migration months of April through June was 11°C and for fall migration months of July through September was 17°C (Jensen 1998).

We observed the five species between 11 May and 6 June and between 13 July and 9 September in 1994, and between 24 April and 1 June and 10 July and 7 September in 1995. We used focal individual sampling (Altmann 1974) procedures to determine shorebird behaviors during 3, 4-hr diurnal periods: early (sunrise–11:00), midday (11:01–15:00), and late (15:01–sunset). We observed randomly selected birds for a maximum of 5 min using a 15–60× spotting scope or 10 × 50× binoculars. Observations were dictated into a mini-cassette recorder and timed with a digital stopwatch. We discarded observations lasting <30 sec. Generally, each species was sampled during each diurnal period. During the spring, observations of Long-billed Dowitchers were only obtained for midday and late periods in 1994 and early and midday periods in 1995.

We classified behavioral activities into six categories: feeding (actively feeding by pecking, probing, or scything), sleeping (motionless with bill tucked under wing, head and neck held stationary, or eyes closed), alert (stationary with

bird visually scanning surroundings), body maintenance (bathing, preening, or wing and neck stretching), aggression (chasing, pecking, or threatening another individual), and locomotion (wading, walking, running, swimming, or flying). Behavioral activity classifications were based on work by Baker (1971), Burton (1972), and Metcalfe and Furness (1986). Duration of aggressive encounters was not determined due to the instantaneous nature of these encounters. However, we did record frequency and species composition of aggressive encounters. Additionally, associated flock size and time of day were noted for each observed individual in an aggressive encounter. We counted birds in all cardinal compass directions from the focal individual as part of a flock. However, birds were not considered part of a flock when the distance exceeded 5 m from the last individual counted in a particular direction. We used these criteria to better record flock size and composition for each focal individual because these variables were constantly changing.

DATA ANALYSIS

We used a factorial multivariate analysis of variance (MANOVA) to assess differences in overall simultaneous behavior among time periods (early, midday, and late), between seasons (spring and fall), and between years (1994 and 1995). MANOVA was used because the dependent variables (behaviors) were not independent of each other (Davis and Smith 1998a). The focal individual was the experimental unit. If a factor (period, season, year) was significant ($P < 0.05$) in MANOVA, a factorial analysis of variance (ANOVA) was used to test the effects of independent factors on each dependent variable (feed, alert, locomotion, body maintenance, sleep). Least significant difference mean separation was used when a period effect was detected. A 2-way ANOVA was used to test the effects of year and season on flock size within a species (SAS Institute 1989). Values presented are means ± SE. We determined the influence of season on type of aggression (intraspecific or interspecific) using chi-square test for independence (Zar 1996).

RESULTS

SEASONAL AND DIURNAL EFFECTS

American Avocet. Feeding, locomotion, and body maintenance were the predominant activi-

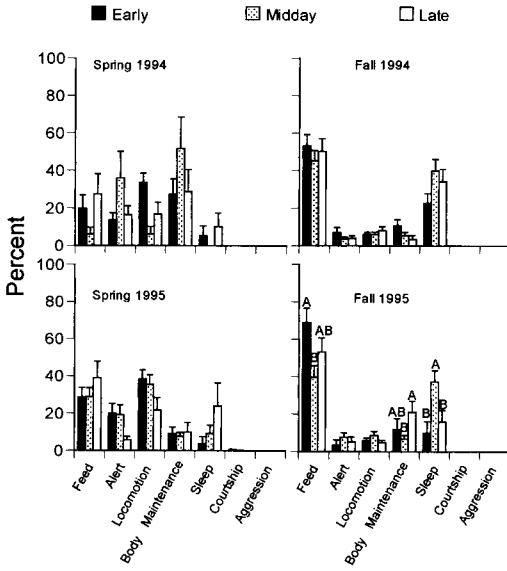


FIGURE 2. Diurnal activity budgets (mean % \pm SE) of American Avocets on prairie wetlands in northwestern North Dakota. Diurnal period means within a behavior with different letters are different ($P < 0.05$). Period means are presented within year and season because of a significant period \times season \times year interaction and a period \times season interaction in both years. Overall behavior did not differ among periods within spring 1994 (early $n = 9$, midday $n = 6$, late $n = 11$), spring 1995 (early $n = 27$, midday $n = 32$, late $n = 11$), and fall 1994 (early $n = 52$, midday $n = 58$, late $n = 42$), but differed within fall 1995 (early $n = 54$, midday $n = 51$, late $n = 33$).

ties for American Avocets ($n = 386$; Fig. 2). A significant period \times season \times year interaction (Wilks' $\lambda = 0.95$, $P = 0.05$) occurred in analysis of overall behavior. Subsequent analyses for period and season were conducted within year. However, a period \times season interaction occurred during both years (1994: Wilks' $\lambda = 0.79$, $P < 0.001$; 1995: Wilks' $\lambda = 0.89$, $P = 0.008$). Further analyses for diurnal period were conducted within year and season. Overall behavior of Avocets did not differ among the three diurnal periods during spring 1994 (Wilks' $\lambda = 0.43$, $P = 0.07$) and 1995 (Wilks' $\lambda = 0.84$, $P = 0.35$) and fall 1994 (Wilks' $\lambda = 0.91$, $P = 0.15$), but differed during fall 1995 (Wilks' $\lambda = 0.80$, $P = 0.001$).

During fall 1995, feeding ($F_{2,135} = 6.2$, $P = 0.003$), body maintenance ($F_{2,135} = 3.5$; $P = 0.03$), and sleeping ($F_{2,135} = 8.4$, $P < 0.001$) differed among periods. Time spent feeding differed between early and midday periods (Fig. 2).

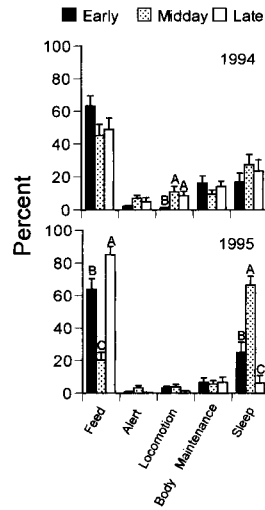


FIGURE 3. Diurnal activity budgets (mean % \pm SE) of Long-billed Dowitchers. Period means within a behavior with different letters are different ($P < 0.05$). Period means are presented within year (1994: early $n = 47$, midday $n = 41$, late $n = 34$; 1995: early $n = 44$, midday $n = 64$, late $n = 31$) because of a significant period \times year interaction. There were no seasonal differences in behavior and therefore behaviors are not separated by season.

Body maintenance differed between late and midday periods. Time sleeping was similar during early and late periods but was greatest during midday.

Long-billed Dowitchers. Feeding was the predominant activity for Long-billed Dowitchers ($n = 261$; Fig. 3). Overall behavior did not differ between seasons (Wilks' $\lambda = 0.98$, $P = 0.39$). A significant period \times year interaction occurred in analysis of overall behavior (Wilks' $\lambda = 0.87$, $P < 0.001$). Therefore, subsequent analyses for period were conducted within year. There were period differences for overall behavior in 1994 (Wilks' $\lambda = 0.83$, $P = 0.02$) and 1995 (Wilks' $\lambda = 0.75$, $P < 0.001$).

Locomotion varied among the three diurnal periods in 1994 ($F_{2,117} = 7.0$, $P = 0.001$), whereas feeding ($F_{2,134} = 19.1$, $P < 0.001$) and sleeping ($F_{2,134} = 13.9$, $P < 0.001$) varied among periods in 1995. In 1994, time spent in locomotion was lower during the early period than midday and late periods (Fig. 3). In 1995, time feeding was highest during early and late periods and lowest during midday. Sleeping was highest during midday and lowest during early and late periods.

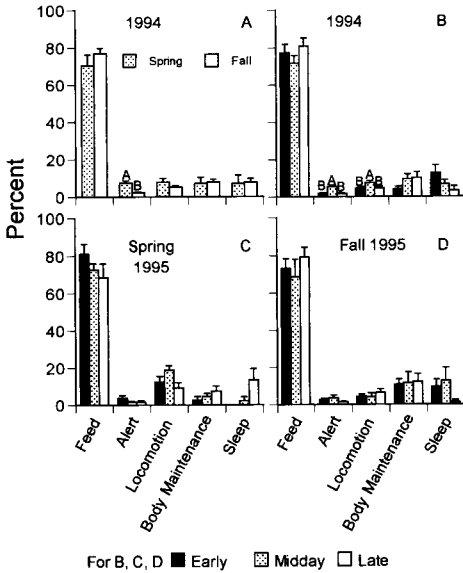


FIGURE 4. Diurnal activity budgets (mean % ± SE) of Stilt Sandpipers. Means are presented within year because of a significant period × season × year interaction. In 1994, data are separated by season (A: spring $n = 25$, fall $n = 133$) and diurnal period (B: early $n = 54$, midday $n = 62$, late $n = 42$). In 1995, data are separated within seasons (C: early $n = 14$, midday $n = 32$, late $n = 23$ and D: early $n = 44$, midday $n = 17$, late $n = 29$) because of a significant period × season interaction. Means within a behavior with different letters are different ($P < 0.05$).

Stilt Sandpipers. Stilt Sandpipers ($n = 317$) spent most of their time feeding. A significant period × season × year interaction (Wilks' $\lambda = 0.94$, $P = 0.03$) occurred in analysis of overall behavior. Subsequent analyses for period and season were conducted within year. However, because there was a significant period × season interaction (Wilks' $\lambda = 0.88$, $P = 0.04$) in 1995, further analyses of daytime effects for 1995 were conducted within season.

During 1994, overall behavior for Stilt Sandpipers differed between seasons (Wilks' $\lambda = 0.89$, $P = 0.005$) and among periods (Wilks' $\lambda = 0.81$, $P < 0.001$). Stilt Sandpipers spent more time engaged in alert activities during spring than fall ($F_{1,152} = 15.4$, $P < 0.001$) (Fig. 4). Additionally, alert ($F_{2,152} = 11.0$, $P < 0.001$) and locomotion ($F_{2,152} = 3.8$, $P = 0.03$) activities differed among diurnal periods. Time spent alert was similar during early and late periods but was highest during midday (Fig. 4). Likewise, time in locomotion was similar during early and late

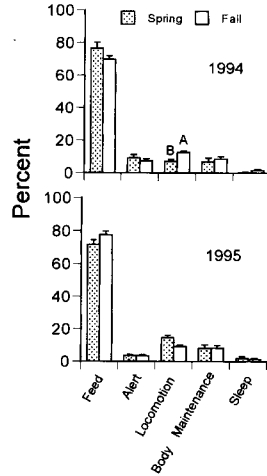


FIGURE 5. Diurnal activity budgets (mean % ± SE) of Semipalmated Sandpipers. Season means within a behavior with different letters are different ($P < 0.05$). Season means are presented within year (1994: spring $n = 48$, fall $n = 159$; 1995: spring $n = 72$, fall $n = 125$) because of a significant season × year interaction. There were no diurnal period differences in behavior and therefore behaviors are not separated by period.

periods, but higher during midday. During spring and fall 1995, none of the behaviors differed among diurnal periods (spring: Wilks' $\lambda = 0.76$, $P = 0.06$; fall: Wilks' $\lambda = 0.93$, $P = 0.8$) (Fig. 4).

Semipalmated Sandpipers. Feeding was the predominant activity of Semipalmated Sandpipers ($n = 404$; Fig. 5). Overall behavior did not differ (Wilks' $\lambda = 0.99$, $P = 0.92$) among diurnal periods. Because there was a significant season × year interaction (Wilks' $\lambda = 0.95$, $P = 0.002$), subsequent analyses comparing seasonal differences were conducted within year.

Behaviors differed between seasons (Wilks' $\lambda = 0.94$, $P = 0.03$) in 1994 with locomotion being higher during fall than spring ($F_{1,201} = 10.5$, $P = 0.001$) (Fig. 5). In 1995, overall behavior did not differ between seasons (Wilks' $\lambda = 0.95$, $P = 0.12$).

Least Sandpipers. Least Sandpipers ($n = 358$) spent most of their time feeding (Fig. 6). Overall behavior of Least Sandpipers did not differ between years (Wilks' $\lambda = 0.99$, $P = 0.44$) and seasons (Wilks' $\lambda = 0.99$, $P = 0.66$), or among periods (Wilks' $\lambda = 0.98$, $P = 0.85$).

FLOCK SIZES AND AGGRESSION

Flock sizes were similar between 1994 and 1995 for American Avocets and Long-billed Dowitch-

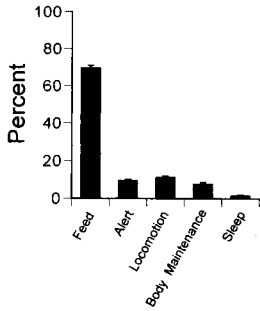


FIGURE 6. Diurnal activity budgets (mean % ± SE) of Least Sandpipers. Yearly, seasonal, and period means did not differ (all $P_s \geq 0.44$) and therefore only overall data are presented, $n = 358$.

ers, whereas flock sizes differed between years for Semipalmated and Least Sandpipers (Table 1). Mean flock size was greater during fall than spring for Avocets, dowitchers, and Semipalmated and Least Sandpipers. A significant year \times season interaction ($F_{1,313} = 10.9, P = 0.001$) occurred in analysis of flock size for Stilt Sandpipers. Therefore, we analyzed flock size within year in Stilt Sandpipers. In 1994, mean flock size for Stilt Sandpipers was greater ($F_{1,156} = 14.0, P < 0.001$) during fall ($8.76 \pm 0.58; n = 133$) than spring ($3.32 \pm 1.33; n = 25$), whereas flock size was similar ($F_{1,157} = 2.1, P = 0.15$) between spring ($12.54 \pm 1.26; n = 69$) and fall ($10.13 \pm 1.10; n = 90$) in 1995.

Number of aggressive encounters observed varied among the species (Table 2). In spring, Stilt Sandpipers, Avocets, and Semipalmated Sandpipers were involved primarily in intraspecific aggression, whereas Least Sandpipers were involved more in interspecific aggression with Semipalmated Sandpipers (Table 2). In fall, intraspecific aggression accounted for >50% of

TABLE 2. Intraspecific and interspecific aggression observed during focal individual sampling of shorebirds on prairie wetlands in northwestern North Dakota during spring and fall migration, 1994–1995. Chi-square tests determined seasonal differences in type of aggressive encounter exhibited by each species.

Species	Season	Aggressive encounters	
		Intra-specific	Inter-specific
American Avocet	Spring	111	1
	Fall	11	3
		$\chi^2_1 = 17.1, P < 0.001$	
Stilt Sandpiper	Spring	12	0
	Fall	57	11
		$\chi^2_1 = 2.3, P = 0.13$	
Semipalmated Sandpiper	Spring	66	14
	Fall	189	50
		$\chi^2_1 = 0.4, P = 0.51$	
Least Sandpiper	Spring	4	9
	Fall	87	61
		$\chi^2_1 = 3.8, P = 0.05$	

^a Long-billed Dowitchers aggressive encounters were not tested due to few observations ($n = 8$).

the aggressive encounters for each of the species. Most of the aggressive encounters for avocets (89%) occurred during spring, whereas most aggressive encounters for Long-billed Dowitchers (75%), Stilt (85%), Semipalmated (75%), and Least (92%) Sandpipers occurred during fall. Only American Avocets and Least Sandpipers showed seasonal differences in intraspecific and interspecific aggression (Table 2).

DISCUSSION

In the Prairie Pothole Region of northwestern North Dakota, feeding was the dominant behavioral activity of most shorebird species during spring and fall migrations, except for American Avocets in spring. Avocet breeding range ex-

TABLE 1. Mean (\pm SE) flock size of shorebirds during spring and fall 1994 and 1995 in northwestern North Dakota. The F -tests indicate tests between year^a and season^b. Values are means \pm SE (n). Sample size (n) refers to number of focal individuals sampled.

Species	1994		1995	
	Spring	Fall	Spring	Fall
American Avocet	4.38 \pm 0.87 (178)	6.20 \pm 0.60 (208)	1.63 \pm 0.94 (96)	8.95 \pm 0.48 (290)
Long-billed Dowitcher	10.26 \pm 1.97 (122)	13.37 \pm 3.53 (139)	7.14 \pm 3.94 (18)	16.49 \pm 0.90 (243)
Stilt Sandpiper ^c	6.04 \pm 0.96 (158)	11.34 \pm 0.70 (159)	7.93 \pm 1.02 (94)	9.45 \pm 0.60 (223)
Semipalmated Sandpiper	5.44 \pm 0.47 (207)	7.24 \pm 0.43 (197)	4.99 \pm 0.54 (120)	7.70 \pm 0.34 (284)
Least Sandpiper	3.47 \pm 0.70 (183)	5.16 \pm 0.45 (175)	2.90 \pm 0.79 (41)	5.74 \pm 0.25 (317)

^a American Avocet: $F_{1,382} = 2.97, P = 0.09$; Long-billed Dowitcher: $F_{1,257} = 0.59, P = 0.44$; Semipalmated Sandpiper: $F_{1,400} = 8.01, P = 0.005$; Least Sandpiper: $F_{1,354} = 4.10, P = 0.04$.

^b American Avocet: $F_{1,382} = 47.93, P < 0.001$; Long-billed Dowitcher: $F_{1,257} = 5.35, P = 0.02$; Semipalmated Sandpiper: $F_{1,400} = 18.24, P < 0.001$; Least Sandpiper: $F_{1,354} = 11.58, P = 0.001$.

^c Year \times Season interaction ($P = 0.001$).

tends from northern Texas to southern Saskatchewan (Richards 1988). Because we did not use marked avocets during our study, we were not able to discern between local breeders and birds that would continue farther north to breed, potentially confounding avocet comparisons to the other species. Feeding also is the predominant activity of most shorebirds at other stopover sites (Goss-Custard et al. 1977, Wishart and Sealy 1980, Davis and Smith 1998a). Because the Prairie Pothole Region is located between breeding grounds in the north and wintering grounds in the south for four of the five species (Richards 1988, Gratto-Trevor 1992, Cooper 1994), prairie potholes likely provide key resources for most migrating shorebirds.

Long-billed Dowitchers, Stilt Sandpipers, Semipalmated Sandpipers, and Least Sandpipers breed in portions of northern Canada and Alaska, north of the main avocet breeding range (Richards 1988, Gratto-Trevor 1992, Cooper 1994). Skagen and Knopf (1993) developed an index for classifying midcontinent shorebirds by migration distance—short, intermediate, and long distance migrants. They classified American Avocets (2,100 km) as short, Long-billed Dowitchers (8,900 km), Semipalmated (9,500 km), and Least Sandpipers (9,100 km) as intermediate, and Stilt Sandpipers (15,000 km) as long. Additionally, intermediate and long distance migrants have a relatively narrow time frame for nesting and must lay their eggs soon after the snow melts on the breeding grounds (O'Reilly and Wingfield 1995, Davis and Smith 1998a). This narrow window and less protracted migration (Hamilton 1959) may limit the time available for other behaviors during spring migration because species that breed in more northerly latitudes require increased feeding (Davis and Smith 1998a). Thus, it seems that feeding is predominant because long distant migrants need to replenish energy reserves to continue migration, and to store some energy for egg production and survival during the first days of arrival on the breeding grounds (Pienkowski and Evans 1984, O'Reilly and Wingfield 1995).

American Avocets budget relatively similar amounts of time to all behaviors during spring. Gibson (1978) documented a similar pattern in avocet behavior during spring in Oregon. Species which nest at more southerly latitudes may have a wider time frame in which to breed and therefore feed at a lower rate (Davis and Smith

1998a). Butler and Kaiser (1995) also hypothesized that Least Sandpipers in southwestern British Columbia contained lower energy reserves during spring than other migrant shorebirds (e.g., Long-billed Dowitchers, Stilt Sandpipers, and Semipalmated Sandpipers [Richards 1988]) because of their shorter migration distance to breeding grounds. Because avocets breed in the Prairie Pothole Region or are not far from their northern most breeding distribution (Richards 1988), their behavior may parallel Least Sandpipers and support Butler and Kaiser's (1995) hypothesis.

When flying south for the winter to places such as northern and central South America (Richards 1988), feeding at stopover sites such as the Prairie Pothole Region should be the predominant activity to acquire energy reserves that allow a successful migration. For example, based on analysis of collected specimens, White and Mitchell (1990) hypothesized that Western Sandpipers (*Calidris mauri*) and Long-billed Dowitchers acquired energy reserves during migration at stopover areas because they did not accumulate substantial fat deposits on wintering grounds on the Gulf Coast. Page and Middleton (1972) reported a similar situation for Semipalmated Sandpipers prior to southward migration on the east coast of the United States. If substantial accumulation of fat is not occurring on a wintering ground (White and Mitchell 1990) nor on a "migratory pause" south of the breeding grounds (Page and Middleton 1972), shorebirds must use "stepping stones" such as the potholes in the Prairie Pothole Region to acquire energy that aids in continuation and completion of their migration (Skagen and Knopf 1993).

Time spent feeding also may be influenced by diet. For example, avocets may require less time feeding during spring than the other species because they opportunistically feed on prey with higher energy content and opportunistically shift habitat use that may coincide with higher prey levels (DeLeon 1996, Davis and Smith 1998b).

Variation in feeding among diurnal periods for American Avocets and Long-billed Dowitchers could be due to energy deficits incurred overnight and late-day insect activity (Gibson 1978). In our study, feeding by avocets and Long-billed Dowitchers was generally highest during early and late periods. Gibson (1978) reported a similar pattern for prenesting and postbreeding avocets in Oregon. He attributed the morning peak

(early period in this study) in feeding to energy deficits incurred during the night, whereas the afternoon peak (late period in this study) coincided with insect activity and was considered the optimum time to feed. Additionally, because invertebrate availability may be less during the morning (Burger 1984), avocets and dowitchers might need to increase the amount of time spent feeding to be successful in capturing prey.

Feeding by Stilt, Semipalmated, and Least Sandpipers did not vary among periods. This could be attributed to body size because these sandpipers are smaller than dowitchers and avocets and metabolic rate generally increases as body size decreases (Pienkowski and Evans 1984). Additionally, as noted earlier, migration distance may explain the need for continuous feeding throughout the day to acquire needed energy reserves for these sandpipers. Moreover, large birds such as American Avocets fly at higher speeds and can reach greater distances than smaller birds with the same fat percentage (Alerstam 1993). Therefore, the three smaller sandpipers likely fed consistently throughout the day to meet the energy demands required for higher metabolisms (Pienkowski and Evans 1984) and for sustained intermediate and long distance flights.

Because all five species generally grouped in smaller intra- and interspecific flocks during spring than fall, the birds may have been less tolerant of each other during spring due to the onset of breeding. Others (Recher and Recher 1969, Burger et al. 1979) have reported that aggression among shorebirds increased as flock size increased. Shorebirds may avoid the energy expenditures of aggressive encounters by forming smaller flocks during spring than fall when migration is more protracted (DeLeon 1996). Additionally, shorebirds that continue farther north to breed must maximize their time feeding to meet the energy demands required for reproduction (O'Reilly and Wingfield 1995). Therefore, the potential for an energetically costly aggressive encounter may be less likely for a bird in a smaller flock than a larger one. However, for American Avocets, this explanation is complicated because they breed in the Prairie Pothole Region and therefore, flocks observed during spring may be composed of breeding pairs. Furthermore, occurrence of relatively smaller flocks in spring may be a function of the number of birds that seasonally migrate through this re-

gion as fewer birds were observed in spring than in fall (DeLeon 1996).

In the Southern Great Plains, Davis and Smith (1998a) found that Western Sandpipers, a similar sized shorebird to Semipalmated Sandpipers, had the most aggressive encounters, whereas Long-billed Dowitchers had the least. This is similar to our study. Also, similar to Davis and Smith (1998a), we found that most aggressive encounters for shorebirds were intraspecific. Aggressive encounters were greater for Stilt, Semipalmated, and Least Sandpipers during the fall when flocks were larger. However, American Avocets, which did not have higher aggression in fall, displayed an increase in aggression in spring probably related to defending a feeding and breeding territory (Hamilton 1975, Gibson 1978).

We suggest that the Prairie Pothole Region serves as a vital stopover site for many species and tens of thousands of shorebirds during spring and fall migrations (DeLeon 1996). Stopover sites in the Great Plains provide energy resources that are essential to the completion of shorebird migration. Thus, because wetland availability in the Great Plains is highly ephemeral and dynamic (Skagen and Knopf 1993), large regions must be protected. Therefore, conservationists should continue their efforts in acquiring, enhancing, and conserving wetland complexes.

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