BEHAVIOR OF MIGRANT SHOREBIRDS IN PLAYAS OF THE SOUTHERN HIGH PLAINS, TEXAS[1]

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Abstract. Playas in the Southern High Plains (SHP) are important for migrant shore-birds, but the functional role of playas to migrant shorebirds is not clearly understood. We conducted diurnal time-activity budgets on American Avocets (*Recurvirostra americana*), Long-billed Dowitchers (*Limnodromus scolopaceus*), Least Sandpipers (*Calidris minutilla*), and Western Sandpipers (*C. mauri*) in spring and fall 1993 and 1994 in 69 playas on the SHP of Texas. During both seasons, Least and Western Sandpipers spent 70–80% of their time feeding. Long-billed Dowitchers spent 77% of their time feeding in spring, but spent more time sleeping and less feeding in fall. American Avocets spent 41–50% of their time feeding and 34–40% of their time sleeping during each season. All four species spent minimal time engaged in locomotion, body maintenance, alert, and aggressive behaviors. American Avocets and Long-billed Dowitchers fed most during the midday and late periods and slept most during the early period. Least Sandpipers fed most during the early period, whereas feeding activities of Western Sandpipers remained 70–80% throughout the day. Each of these species use different behavioral strategies in response to such factors as migration distances, energetic needs, differential predation, nocturnal foraging, and diet. Playas appear to serve as important intermediate stopover sites for shorebirds during migration.

Key words: American Avocet, Least Sandpiper, Long-billed Dowitcher, playas, shore-birds, Western Sandpiper.

INTRODUCTION

Time-activity budgets allow researchers to evaluate how animal populations apportion time in response to physiological changes, environmental factors, or human disturbances. Time-activity budgets may be especially important in providing information about the ecology of migratory birds (Paulus 1988). Migratory birds typically use a variety of habitats during different periods of their annual cycle (Moore et al. 1995). However, the importance of specific habitats to migratory birds often is unknown because knowledge of the birds' behavior in those habitats often is lacking. In the case of migrant shorebirds, behavioral sampling allows researchers to determine the importance of certain habitats and may provide insight into the significance of certain activities during a critical time in the birds' annual cycle (Ashkenazie and Safriel 1979). Studies of shorebird activity patterns have focused primarily upon foraging and aggressive behav-

iors, but few have provided detailed time-activity budgets. Moreover, little is known about shorebird activity patterns during migration.

Some migrant shorebirds in interior North America require a network of intermediate stopover sites that act as "stepping stones" for the birds to continue and complete their migration (Skagen and Knopf 1993). In the Southern High Plains (SHP) of Texas, approximately 19,000 playas constitute > 90% of the wetland habitat within the region (Bolen et al. 1989). The mosaic arrangement of these wetlands may create an important network of intermediate stopover sites for migrant shorebirds; however, the functional role of playas to migrant shorebirds is not understood. Knowledge of the functional role of playas to migrant shorebirds is vital to assess the ecological needs of migrant shorebirds and to develop conservation strategies.

We evaluated the importance of playas as intermediate stopover sites to migrant shorebirds. Specifically, we examined diurnal behavior patterns of migrating American Avocets (*Recurvirostra americana*), Long-billed Dowitchers (*Limnodromus scolopaceus*), Least Sandpipers (*Calidris minutilla*), and Western Sandpipers (*C. mauri*) on playas in SHP of Texas during spring and fall migration. We selected these species be-
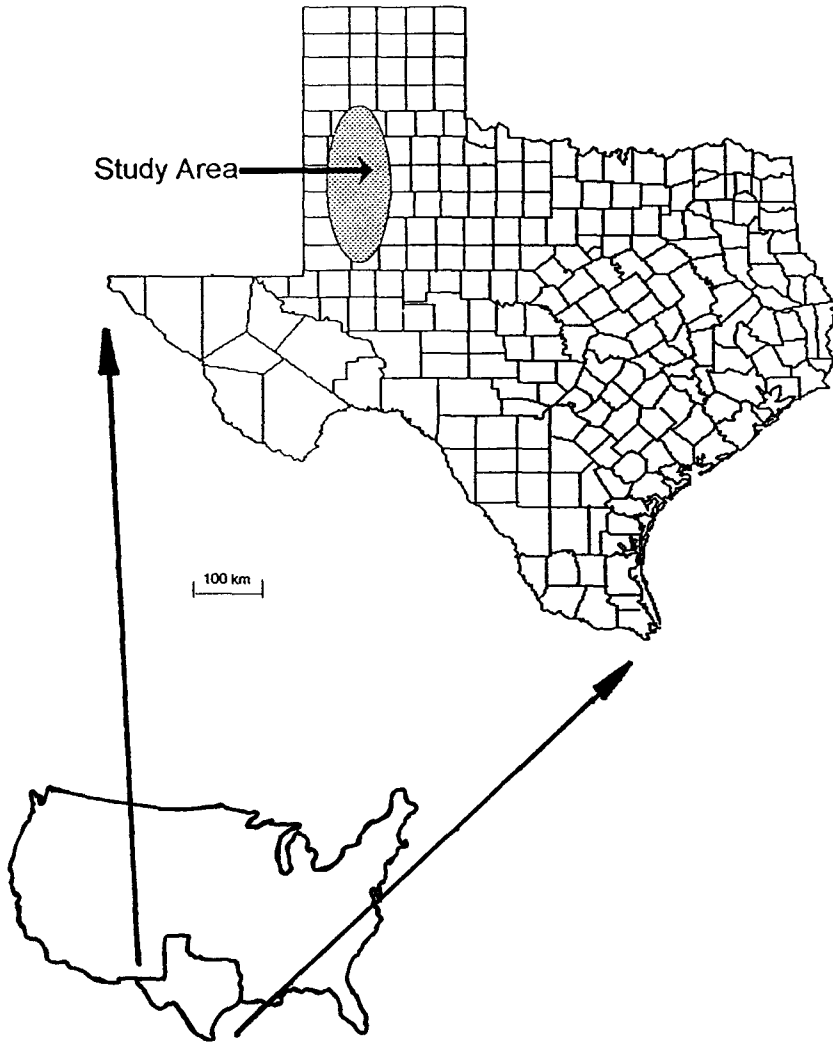
FIGURE 1.   Study area counties in the Southern High Plains of Texas.

cause they were common during both migrational periods and they represented a wide range of size classes and feeding guilds (small probers, medium probers/gleaners, larger gleaners [Helmers 1992]). Moreover, these four species provided an opportunity to assess the importance of playas among a diverse group of shorebirds that have different life history strategies.

METHODS

We conducted the study on 69 playas in Hockley, Lynn, Floyd, Hale, Castro, Dawson, Lubbock, Martin, Parmer, and Howard counties in West Texas (Fig. 1). These counties comprise > 23,000 km² of the SHP and contain 8,500–9,000 playas (Guthery et al. 1981). Average size of the 69 playas was 9.5 ha.

We used focal individual sampling (Altmann 1974) to summarize behaviors of the four species during spring (10 March–28 May 1993, 27 February–23 May 1994) and fall (21 July–28 October 1993, 24 July–29 October 1994) migration. Observations were made using a 15 × 45X spotting scope or 10 × 60X binoculars. We recorded behavioral data in three diurnal periods: early (sunrise–11:00), midday (11:01–15:00), and late (15:01–sunset) (Bergan et al. 1989). We attempted to randomly assign each species to

one of the three diurnal periods and to a particular hour within the diurnal period, but this was not always possible because shorebirds were widely dispersed. We attempted to sample an equal number of individuals of each species within each diurnal period.

We observed each bird for 5 min and dictated behaviors into a tape-recorder. We were able to collect behavioral data on all individuals that occurred in small flocks ($\leq$ 20 birds). For larger flocks ($>$ 20 birds), we randomly selected individuals in the flock by directing the spotting scope or binoculars at the flock and selecting the individual in the center of the field of view. We continued randomly selecting individuals in the flock by moving the scope or binoculars in a zig-zag pattern across the flock so that individuals in all portions of the flock were sampled (Davis et al. 1989).

We classified behaviors into six categories: feeding (pecking, probing, or scything), locomotion (walking, wading, swimming, or flying), sleeping (stationary with either the bird's bill tucked under wing and eyes closed, or neck and head held motionless), body maintenance (preening, bathing, or neck and wing stretching), alert (stationary with bird visually scanning surroundings), and aggression (chasing, pecking, or threatening another individual). We also recorded the species of individuals involved in the aggression. Behavioral classifications were based upon descriptions by Baker (1971), Burton (1972), Hamilton (1975), and Metcalfe and Furness (1986).

STATISTICAL ANALYSES

We analyzed time-activity data using multivariate analysis of variance (MANOVA) with a factorial arrangement (SYSTAT 1992). Species, season, year, and time period were independent factors in the MANOVA. We used MANOVA because the dependent variables (i.e., individual behaviors) were not independent of each other; the amount of time engaged in one activity influences the amount of time engaged in other activities. Wilks' lambda (λ) was the test criterion. All tests were considered significant at $P \leq 0.05$.

Following a significant overall MANOVA, univariate analysis of variance (ANOVA) was used to determine differences in individual behaviors of each species between seasons and among diurnal periods (Barker and Barker 1984). MANOVA was not used to examine differences in overall behavior of Long-billed Dowitchers between seasons and among diurnal periods for 1993 because of low sample size (n = 35) during fall. Therefore, we used ANOVA with a factorial arrangement to assess differences in individual Long-billed Dowitcher behaviors between seasons and among diurnal periods in 1993. If differences existed between factors, Fisher's least significant difference test was used. Comparisons were controlled for experiment-wise Type I error at $P = 0.05$. We also used chi-square test for independence to determine the influence of season on the type of aggressive encounters (intraspecific or interspecific) observed (Conover 1981). Pearson chi-square test statistic was the test criterion. Behavioral data met assumptions of normality and homogeneity (Johnson and Wickern 1988, SYSTAT 1992).

RESULTS

INTERSPECIFIC DIFFERENCES

A 4-way interaction (Wilks' λ = 0.98, $P < 0.01$) occurred in the initial behavioral analyses. Therefore, subsequent analyses were within year. In 1993, overall behavior (i.e., simultaneous behaviors) differed among species (Wilks' λ = 0.77, $P < 0.001$), but was similar between seasons (Wilks' $\lambda > 0.1$, $P = 0.45$) and among diurnal periods (Wilks' λ = 0.99, $P > 0.1$). There were no significant 2-way or 3-way interactions.

Species differed in the amount of time they spent in each of the behaviors except body maintenance (Table 1). Feeding was the dominant activity of Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers, whereas feeding and sleeping were the dominant activities of American Avocets (Fig. 2).

During 1994 there was a 3-way interaction in overall behavior (Wilks' λ = 0.96, $P < 0.001$). Overall behavior differed among species in spring (Wilks' λ = 0.78, $P < 0.001$) and fall (Wilks' λ = 0.68, $P < 0.001$). During each migrational period, the four species differed in the amount of time they spent in each behavior (Table 1).

During spring, Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers spent most of their time feeding, whereas American Avocets spent most of their time feeding and sleep-

TABLE 1. Analysis of variance tests for interspecific differences in individual behaviors among American Avocets, Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers during spring and fall migration on the Southern High Plains of Texas, 1993–1994.

Behavior	Year	Season	F^a
Feeding	1993	combined[b]	64.6
	1994	spring	41.6
	1994	fall	25.7
Locomotion	1993	combined	35.3
	1994	spring	11.8
	1994	fall	89.5
Sleeping	1993	combined	136.6
	1994	spring	50.1
	1994	fall	71.6
Body maintenance	1993	combined	1.3*
	1994	spring	3.6**
	1994	fall	8.9
Alert	1993	combined	10.2
	1994	spring	8.4
	1994	fall	15.3
Aggression	1993	combined	18.8
	1994	spring	10.4
	1994	fall	25.5

[a] 1993: df = 3, 1270; 1994: df = 3, 990 for spring; df = 3, 1303 for fall. All F-values significant at $P < 0.001$, except where noted as nonsignificant (*) or $P < 0.01$ (**).
[b] Individual behaviors in spring and fall 1993 were combined because multivariate analysis of variance conducted prior to univariate analysis of variance indicated overall behaviors were similar between seasons.

ing (Fig. 3). Feeding was the dominant behavior in the fall for Least Sandpipers and Western Sandpipers, and feeding and sleeping were the dominant behaviors for American Avocets and Long-billed Dowitchers (Fig. 3).

The number of aggressive encounters was variable among the four species (Table 2). Western Sandpipers were involved in the most aggressive encounters, whereas Long-billed Dowitchers were involved in the least. Long-billed Dowitchers (100%), American Avocets (94.9%), and Western Sandpipers (80.9%) were involved primarily in intraspecific aggressive encounters. In Least Sandpipers, intraspecific aggression accounted for 47.5% of the aggressive encounters, whereas interspecific encounters accounted for 52.5%. The type of aggressive encounter (inter- vs. intraspecific) used by each species only differed between seasons for Least Sandpipers (Table 2).

SEASONAL AND DIURNAL EFFECTS

American Avocet. In 1993, overall behavior of Avocets differed between seasons (Wilks' λ = 0.97, $P < 0.05$), but not diurnal periods (Wilks' λ = 0.98, $P > 0.1$). The 2-way interaction also

was not significant (Wilks' λ = 0.97, $P > 0.1$). Avocets spent more time in locomotion ($F_{1,610}$ = 8.6, $P = 0.004$) and aggression ($F_{1,610}$ = 5.4, $P = 0.02$) in spring than fall (Fig. 2).

In 1994 there was a 2-way (period × season) interaction (Wilks' λ = 0.96, $P = 0.001$). Overall behavior differed among diurnal periods during spring (Wilks' λ = 0.89, $P < 0.001$), but not fall (Wilks' λ = 0.96, $P > 0.1$). Avocets fed more during midday and late periods than in the early period. Sleeping was highest in the early period and lowest during midday (Table 3).

Long-billed Dowitcher. In 1993, Long-billed Dowitchers spent similar amounts of time in each behavior during each season ($P > 0.1$). Sleeping was the only behavior that differed among diurnal periods (Table 4). Dowitchers slept more during midday than during early and late periods. There was no 2-way interaction for any behavior ($P > 0.1$).

In 1994 there was a 2-way (period × season) interaction (Wilks' λ = 0.96, $P < 0.001$). During spring and fall, overall behavior of Long-billed Dowitchers differed among diurnal periods (spring: Wilks' λ = 0.93, $P < 0.01$; fall: Wilks' λ = 0.87, $P < 0.001$). In spring and fall, dowitchers fed more during midday and late periods than during the early period. Dowitchers slept more in both seasons during the early period compared with midday and late periods. During spring, body maintenance was highest during the early period and least in the midday period (Table 4).

Least Sandpiper. Overall behavior of Least Sandpipers differed between seasons (Wilks' λ = 0.91, $P = 0.001$) and among diurnal periods (Wilks' λ = 0.89, $P = 0.008$) during 1993. There was no 2-way interaction (Wilks' λ = 0.93, $P > 0.05$). Least Sandpipers spent more time feeding ($F_{1,241}$ = 8.8, $P = 0.003$) in spring than fall (Fig. 2). Locomotion ($F_{1,241}$ = 8.8, $P = 0.003$), body maintenance ($F_{1,241}$ = 4.5, $P < 0.05$), and aggressive ($F_{1,241}$ = 4.3, $P = 0.04$) behaviors were higher in fall than spring. Least Sandpipers fed more in the early period than the midday period. In contrast, sleeping was highest during midday and least during early and late periods (Table 5).

In 1994, overall behavior differed between seasons (Wilks' λ = 0.97, $P = 0.03$) and among diurnal periods (Wilks' λ = 0.91, $P < 0.001$). There was no 2-way interaction (Wilks' λ = 0.95, $P > 0.05$). Aggression was the only be-
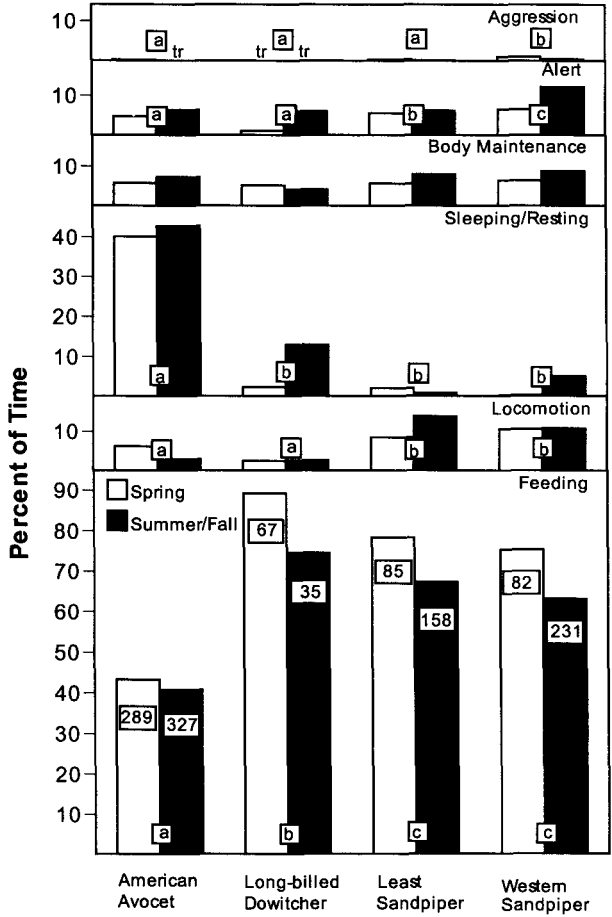
FIGURE 2.   Diurnal time-activity budget of four shorebird species during spring (10 March–28 May) and fall (21 July–28 October) migration in 38 playas on the Southern High Plains of Texas, 1993. Behaviors with the same letter within a bar graph did not differ ($P > 0.05$) among species for the year. Sample sizes are shown in the bottom bar graph. Behaviors with "tr" indicate that a bird spent trace amounts ($< 0.5\%$) of time engaged in that behavior.

havior that differed between seasons ($F_{1,402} = 6.7$, $P = 0.01$). Least Sandpipers fed more during early and midday periods than the late period. Locomotion was highest during the early period and least during midday, whereas body maintenance was higher in the late period than early and midday periods (Table 5).

Western Sandpiper. In 1993, overall behavior by Western Sandpipers did not differ between seasons (Wilks' $\lambda = 0.99$, $P > 0.1$) or among diurnal periods (Wilks' $\lambda = 0.94$, $P > 0.05$). There was no 2-way interaction (Wilks' $\lambda = 0.94$, $P > 0.05$). In 1994, there was a 2-way (period × season) interaction (Wilks' $\lambda = 0.91$, $P < 0.05$). Overall behavior did not differ

among diurnal periods for each season (spring: Wilks' $\lambda = 0.84$, $P > 0.1$; fall: Wilks' $\lambda = 0.92$, $P > 0.1$).

DISCUSSION

In playa lakes, feeding was the dominant activity of all four shorebirds during each season. Studies at other stopover sites in North America also have found that migrating shorebirds spend most of their time feeding (Wishart and Sealy 1980, Young 1989, DeLeon 1996). Because the SHP is located between the desert and mountains of New Mexico to the west and the dry (i.e., contains sparse wetland habitats) Red Rolling Plains and Edwards Plateau of Texas to the east (Bolen
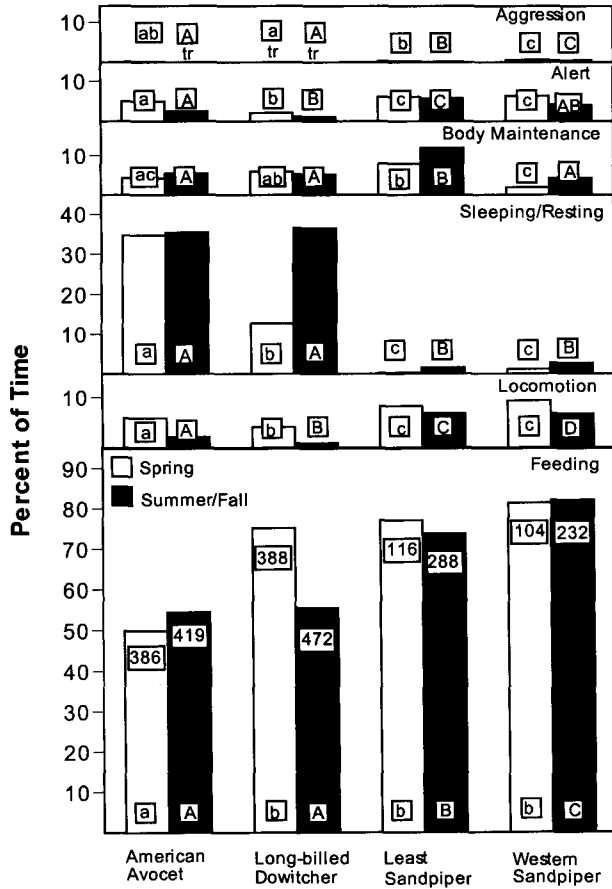
FIGURE 3. Diurnal time-activity budget of four shorebird species during spring (27 February–23 May) and fall (24 July–29 October) migration in 30 playas on Southern High Plains of Texas, 1994. Behaviors with the same lowercase letter within a bar graph did not differ ($P > 0.05$) among species for spring migration. Behaviors with the same uppercase letter within a bar graph did not differ ($P > 0.05$) among species for fall migration. Sample sizes are shown in the bottom graph. Behaviors with "tr" indicate that a bird spent trace amounts ($<$ 0.5%) of time engaged in that behavior.

et al. 1989), SHP playas likely provide a significant wetland complex between the Gulf Coast and Cheyenne Bottoms, Kansas for shorebirds to acquire needed food resources (U.S. Fish and Wildlife Service 1988). Knowledge of shorebird nutrient reserves are needed to test this assumption.

INTERSPECIFIC DIFFERENCES

In spring, Least Sandpipers, Western Sandpipers, and Long-billed Dowitchers fed more during the day than American Avocets, whereas in fall, Least and Western Sandpipers fed more than Long-billed Dowitchers and Avocets. However, we did not conduct nocturnal observations

of the four shorebird species, even though these species can feed at night (McNeil et al. 1992, Dodd and Colwell 1996). Therefore, it is possible that nocturnal foraging may have had an influence on the interspecific differences we observed during the day.

Another more likely reason for the difference in diurnal foraging between Avocets and the other three species may be related to their breeding ranges. Least Sandpipers, Western Sandpipers, and Long-billed Dowitchers breed in the sub-arctic and arctic (Richards 1988, Cooper 1994, Wilson 1994), whereas Avocets breed throughout the western U.S. including the SHP (Seyffert 1985, Robinson et al. 1997). Sub-arctic

TABLE 2. Intraspecific and interspecific aggression observed during focal individual sampling of American Avocets, Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers in 69 playas on the Southern High Plains of Texas during spring and fall migration, 1993–1994. Chi-square tests determined seasonal differences in type of aggressive encounter exhibited by each species.

Species	Season	Aggressive encounters	
		Intraspecific	Interspecific
American Avocet	Spring	27	0
	Fall	12	2
	$\chi^2_1 = 0.4, P > 0.5$		
Long-billed Dowitcher	Spring	14	0
	Fall	7	0
	$\chi^2_1 = 1.8, P > 0.1$		
Least Sandpiper	Spring	9	22
	Fall	19	9
	$\chi^2_1 = 8.9, P < 0.05$		
Western Sandpiper	Spring	88	20
	Fall	81	20
	$\chi^2_1 = 0.4, P > 0.5$		

and arctic breeding shorebirds have a narrow time window in which to lay eggs; they must lay their eggs immediately after the snow melts (O'Reilly and Wingfield 1995). This narrow window likely places greater constraints on these shorebirds than those that breed in southerly latitudes. In order to arrive early on their breeding grounds with adequate energy reserves required for reproduction, sub-arctic and arctic breeding shorebirds must spend most of their time feeding at each stopover site (O'Reilly and Wingfield 1995). Shorebirds that breed at more southerly latitudes have a wider window of time in which to successfully breed and, consequently, can migrate and forage at a more leisurely pace.

Dietary differences also may have influenced time spent foraging. In the SHP, American Avocet diets were more diverse and contained larger-sized prey than the other shorebirds (Davis 1996). Moreover, Avocets used a wider range of habitats that allowed them to potentially shift to habitats with abundant prey. As a result, Avocets may spend less time feeding because they are able to exploit abundant prey. Also, they may select prey that are energetically more profitable. For example, Avocet diets were composed of more nektonic insects such as Corixids and Notonectids and large-sized vertebrates such as larval Tiger salamanders (*Ambystoma tigrinum*) than diets of other shorebirds. Most of the nek-

tonic insects and large-sized vertebrates had higher energy content than benthic invertebrates like Chironomid larvae that occurred in diets of other shorebirds (Davis 1996).

In addition, body size differences between Least and Western Sandpipers and Avocets may contribute to observed interspecific differences in feeding activities. Goss-Custard et al. (1977) and DeLeon (1996) observed small-bodied shorebirds spending more time feeding than large-bodied shorebirds. Moreover, Pienkowski and Evans (1984) reported that the metabolic rates of shorebirds increase with decreasing body size. Consequently, small-bodied shorebirds such as Least and Western Sandpipers may spend more time feeding because of their metabolic disadvantage relative to larger-bodied shorebirds such as American Avocet (Calder 1974).

Whitfield (1985) also suggested that small-bodied shorebirds are more vulnerable to raptor predation than large-bodied shorebirds. Small-bodied shorebirds may respond to this increased vulnerability by increasing their vigilance to reduce the risk of predation (Barnard 1980). Additionally, Metcalfe (1984) noted that large shorebird species may be less vigilant because they may have fewer predators. In our study, Least and Western Sandpipers (the smaller-bodied species) were more vigilant (i.e., more time alert) than the larger Avocets.

Myers (1984) noted that aggressiveness in shorebirds varied among species and environmental conditions. Aggression that occurs during migration is associated primarily with defending or procuring foods (Recher and Recher 1969). On the SHP, all aggressive encounters were between foraging individuals. Western Sandpipers were the most aggressive, whereas Avocets and Dowitchers were least aggressive. The higher frequency of intraspecific aggression by Western Sandpipers compared to Avocets and Dowitchers may be related to flock size because intraspecific aggression among shorebirds increases as density of shorebirds within a feeding area increases (Burger et al. 1979). Western Sandpipers typically foraged in large flocks (100–200 individuals), whereas Avocets and Dowitchers typically foraged solitarily or in small groups (10–20 individuals).

SEASONAL AND DIURNAL EFFECTS

Feeding and sleeping were the only behaviors that consistently varied between seasons. Feed-

TABLE 3. Diurnal time activity budgets by migrant American Avocets within periods of the day in 69 playas on Southern High Plains of Texas during spring 1994. Time periods were early (sunrise–11:00), midday (11:01–15:00), and late (15:01–sunset). Sample sizes for time periods were $n = 120$ for early, $n = 147$ for midday, and $n = 119$ for late.

Behavior	Day time (%)			F^a
	Early	Midday	Late	
Feeding	38.8A[b]	61.1B	47.2A	9.0**
Locomotion	4.2A	7.8B	5.2AB	3.4*
Sleeping	47.3A	22.2B	37.3A	10.7**
Body maintenance	2.0A	4.5AB	6.0B	3.0*
Alert	7.4	3.7	4.2	2.8
Aggression	0.3	0.1	0.0	1.0

[a] F and P values for analysis of variance comparisons among time periods. * $P < 0.05$, ** $P < 0.001$.
[b] Means within a row denoted by the same letter are not different ($P > 0.05$).

ing was higher in spring than fall for all species except Avocets. During our study, adverse weather conditions occurred more often in spring than fall (low temperatures [< 0°C], strong winds [> 33 km hr^{-1}]; National Oceanic Atmospheric Administration 1995). These conditions increased thermoregulatory costs of smaller-bodied shorebirds because they have greater thermal conductance and poorer insulation than larger-bodied shorebirds (Kendeigh 1970, Wiersma and Piersma 1994). Adverse weather also may indirectly affect shorebirds by decreasing prey availability (prey may migrate farther below the surface to avoid low temperatures) (Burger 1984). Presumably, shorebirds respond to decreasing prey availability by increasing their feeding rates. Wishart and Sealy (1980) determined that higher feeding rates occurred in Marbled Godwits (*Limosa fedoa*) during high winds, and Goss-Custard et al. (1977) reported time spent feeding by knots (*Calidris canutus*) increased with decreasing air temperatures.

Puttick (1984) noted that seasonal fluctuations

TABLE 4. Diurnal time activity budgets by Long-billed Dowitchers within periods of the day in 69 playas on Southern High Plains of Texas during spring and fall 1993 and 1994. Time periods were early (sunrise–11:00), midday (11:01–15:00), and late (15:01–sunset). Sample sizes for time periods were early (1993: $n = 33$; 1994: $n = 142$ for spring, $n = 158$ for fall), midday (1993: $n = 39$; 1994: $n = 131$ for spring, $n = 175$ for fall), and late (1993: $n = 30$; 1994: $n = 115$ for spring, $n = 139$ for fall).

Behavior	Year	Season	Day time (%)			F^a
			Early	Midday	Late	
Feeding	1993	combined[b]	87.5	78.0	88.1	0.5
	1994	spring	66.6A[c]	77.1B	83.8B	7.8***
	1994	fall	34.7A	67.3B	64.5B	25.4
Locomotion	1993	combined	1.6	2.6	3.3	0.2
	1994	spring	3.9	4.3	4.2	0.1
	1994	fall	1.0	1.0	0.8	0.4
Sleeping	1993	combined	0.5A	14.9B	0.2A	3.5*
	1994	spring	18.8A	12.2AB	5.7B	5.5**
	1994	fall	56.9A	25.1B	27.5B	25.7***
Body maintenance	1993	combined	6.2	2.1	6.5	1.2
	1994	spring	9.0A	3.6B	4.7B	3.7*
	1994	fall	4.5	5.4	5.9	0.3
Alert	1993	combined	4.2	2.4	1.4	1.6
	1994	spring	1.7	2.8	1.7	1.7
	1994	fall	1.0	1.0	1.4	0.5
Aggression	1993	combined	0.0	0.0	0.0	—
	1994	spring	0.1	0.0	0.0	1.1
	1994	fall	0.0	0.1	0.0	1.2

[a] F and P values are analysis of variance comparisons among time periods. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[b] Individual behaviors in spring and fall 1993 were combined because behaviors were similar between seasons.
[c] Means within a row denoted by same letter are not different ($P > 0.05$).

TABLE 5. Diurnal time activity budgets by migrant Least Sandpipers within periods of the day in 69 playas on Southern High Plains of Texas during spring and fall 1993 and 1994. Time periods were early (sunrise–11: 00), midday (11:01–15:00) and late (15:01–sunset). Sample sizes for time periods were early (1993: n = 93, 1994: n = 143), midday (1993: n = 80, 1994: n = 131), and late (1993: n = 70, 1994: n = 130).

| Behavior | Year | Day time (%) | | | F^a |
		Early	Midday	Late	
Feeding	1993	76.9A[b]	65.7B	69.4AB	3.7*
	1994	80.6A	76.3A	66.8B	8.1***
Locomotion	1993	12.0	12.8	10.6	0.5
	1994	9.2A	5.7B	6.4B	10.1**
Sleeping	1993	0.0A	3.3B	0.5A	3.8*
	1994	1.6	0.8	1.3	0.3
Body maintenance	1993	5.9	8.7	9.3	0.7
	1994	4.7A	8.8A	19.4B	14.0***
Alert	1993	5.1A	9.3B	10.1B	3.6*
	1994	3.7A	8.2B	5.7AB	4.1*
Aggression	1993	0.2	0.2	0.0	1.2
	1994	0.2	0.1	0.1	1.0

[a] F and P values for analysis of variance comparisons among time periods. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[b] Means within a row denoted by same letter are not different ($P > 0.05$).

in prey abundance can influence foraging patterns of shorebirds. Invertebrate abundances during spring were lower than during fall (0.62 g m^{-2} vs. 1.21 g m^{-2}; Davis 1996). A consequence of lower invertebrate abundances in spring may be that birds must spend more time feeding to increase chances of encountering invertebrates. A similar response to declining prey abundances has been reported for Sanderlings (*C. alba*) (Maron and Myers 1985).

Feeding and sleeping activities differed most among diurnal periods. Feeding by American Avocets and Long-billed Dowitchers was highest during midday and late periods, whereas feeding by Least Sandpipers was highest during the early period. Feeding activities of Western Sandpipers remained high (70–80%) throughout the day. Possibly the combination of changing diurnal temperatures and fluctuating invertebrate availability played a role in feeding patterns. Temperatures were lowest during morning and increased throughout the day. The low temperatures during morning may affect shorebirds directly through increased thermoregulation costs and indirectly through decreased invertebrate availability (Burger 1984).

Avocets and Dowitchers may minimize feeding during morning because the combined energy demands of thermoregulation and unsuccessful feeding attempts are too high. Because of their better insulation and lower thermal conductance (Kendeigh 1970, Wiersma and Piersma 1994), the strategy for larger shorebirds such as

Avocets may be to conserve energy reserves in morning instead of incurring a negative energy balance through the combined demands of thermoregulation and less successful feeding. The concomitant increase in sleeping during morning is consistent with such a strategy. As temperatures increase through the day, thermoregulation costs decline and successful feeding should increase because invertebrate activity is increased (Chapman 1969, Johnson 1995). Least and Western Sandpipers also must respond to lower prey availability and thermoregulation costs during morning, but because of their smaller size, they have greater metabolic costs (Kendeigh 1970, Pienkowski and Evans 1984). Consequently, these species may not be able to effectively use sleeping to conserve energy because their costs during sleeping may be higher than the combined costs of thermoregulation and less successful feeding.

FUTURE RESEARCH NEEDS

The ecological importance of nocturnal habitats and behaviors requires study. Differences in behaviors between diurnal and nocturnal periods illustrate the importance of observing an animal for an entire 24-hr period (Bergan et al. 1989). Additionally, these data would allow a clearer understanding of how shorebirds allocate their time to certain behaviors in response to fluctuating environmental (temperature, precipitation, wind) and biological (bird densities, predation) conditions (McNeil et al. 1992).

Little is known about the influence of physiological factors (depleted energy reserves, thermoregulation) on the behaviors of shorebirds. Information on the influence of physiological factors will allow for a better assessment of why shorebirds allocate certain amounts of time to certain behaviors. Most of the studies on shorebird behaviors have focused upon the influence of one factor (depleted food resources) on behavior. Future research should examine the influence of several factors (thermoregulation, shorebird nutrient reserves, high metabolic rate) on the behaviors of shorebirds.

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