FORAGING STRATEGIES AND NICHE DYNAMICS OF COEXISTING SHOREBIRDS AT STOPOVER SITES IN THE SOUTHERN GREAT PLAINS

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ABSTRACT.—Shorebirds encounter variable and unpredictable food resources at stopover sites during migration through interior North America. We studied foraging strategies and niche dynamics of American Avocets (*Recurvirostra americana*), Long-billed Dowitchers (*Limnodromus scolopaceus*), Least Sandpipers (*Calidris minutilla*), and Western Sandpipers (*C. mauri*) at stopover sites in 60 playa lakes of the southern Great Plains. Those species were selected because they are common in our study area during migration and represent a wide range of morphological classes. Overall foraging niches (linear combination of diet diversity, prey size, foraging-method diversity, and water depth) of avocets and dowitchers were segregated from each other and from Least and Western sandpipers. Overall foraging niches of Least and Western sandpipers were similar. Examination of single niche dimensions showed that avocets and dowitchers consumed larger prey and foraged in deeper water than did Least and Western sandpipers. Within the range of prey sizes consumed by the four individual species, all species selected small prey (0.1–5.0 mm). Preference of relatively small prey by avocets and dowitchers was likely a function of small prey being more abundant in playas than large prey (>10 mm). However, selection of small prey by Least and Western sandpipers was likely a function of lower handling costs associated with small prey. Abundance of prey items in diets of each species was not correlated with nutritional and energetic quality of prey items, but abundance of prey in the diet was correlated with abundance of prey in playa lakes. That suggests that all four shorebird species adopt an opportunistic foraging strategy during migration. Use of opportunism is likely critical for shorebirds to continue migration and arrive on breeding grounds in good condition. *Received 8 April 1999, accepted 27 November 2000.*

DURING THEIR MIGRATION through the interior of North America, shorebirds use a variety of wetlands as stopover sites to replenish energy and nutrient reserves (Farmer and Parent 1997, Skagen 1997, Davis and Smith 1998a). Because of the dynamic nature of these wetlands (i.e. highly variable water regimes), migrant shorebirds encounter variable and unpredictable food resources (i.e. predominantly invertebrates) at stopover sites (Skagen and Oman 1996, Davis and Smith 1998a). In response to those unpredictable food resources, shorebirds should forage opportunistically to successfully complete their migration (Skagen and Knopf 1994, Skagen 1997, Davis and Smith 1998a). The term "opportunistic foraging," as we use it here, simply refers to shorebirds consuming prey in proportion to availability.

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Previous studies on opportunistic foraging in shorebirds focused on the quantity of available prey items and prey sizes, or both (Couch 1966, Recher 1966, Holmes and Pitelka 1968, Thomas and Dartnell 1971, Lewis 1983, Lifjeld 1984). However, quality (e.g. gross energy, percentage fat, protein) of available prey items should also be considered when examining migrant shorebird foraging strategies because nutrient reserves are critical for survival and reproduction (Myers et al. 1979, Maron and Myers 1985). To our knowledge, no studies have examined shorebird foraging strategies in terms of how shorebirds select prey relative to the quality and quantity of available prey.

Because shorebirds frequently occur in mixed-species flocks and generally rely on variable food resources that may become depleted (Duffy et al. 1981, Schneider and Harrington 1981), niche segregation of breeding (Holmes and Pitelka 1968, Baker and Baker 1973), wintering (Baker and Baker 1973), and migrating (Recher 1966, Lifjeld 1984, Eldridge 1987, Sen-

ner et al. 1989) shorebirds have received con-
siderable attention. Those studies have primar-
ily focused on a single niche dimension (e.g.
prey-size selection, microhabitat use [water
depth]) as a measure of niche segregation
among shorebirds. Although niche segregation
is often explained by a single dimension in
some shorebird species, an examination of sev-
eral dimensions (i.e. multidimensional ap-
proach) may provide a more realistic represen-
tation of shorebird niche dynamics during
migration because individual niche dimensions
seldom act in isolation from other dimensions
(Weins 1989, Brown 1995). As more stopover
sites are lost and degraded (resulting in mi-
grant shorebirds being concentrated on lower
quality sites), information on the dynamics of
shorebird community structure will be essen-
tial for developing shorebird conservation
strategies (Davis and Smith 1998a).

Here, we report patterns in foraging niches of
coexisting migrant shorebirds and describe
foraging strategies used by migrant shorebirds.
We hypothesized that the foraging niches of co-
existing shorebirds at stopover sites differed
and that migrant shorebirds used opportunis-
tic foraging during their stay at stopover sites.
We studied four aspects of the foraging niche
(diet, prey size, feeding method, and foraging
microhabitat) of American Avocets (*Recurviros-
tra americana*), Long-billed Dowitchers (*Limnod-
romus scolopaceus*), and Least (*Calidris minutilla*)
and Western (*C. mauri*) sandpipers. We selected
those four shorebird species because they were
common during spring and fall on our study
area and they represented a wide range of an-
atomical features. Thus, we could evaluate for-
aging niches of anatomically similar (Least and
Western sandpipers) and anatomically dissim-
ilar (Least and Western sandpipers, Long-
billed Dowitchers, and American Avocets)
shorebirds.

METHODS

Study area.—The study was conducted in the Playa
Lakes Region (PLR) of the southern Great Plains in
western Texas. The PLR consists of >25,000 playa
lake wetlands (hereafter "playas") that provide most
of the wetland habitat for the region (Osterkamp and
Wood 1987). Playas serve as a major inland stopover
site for migrating shorebirds (Davis and Smith
1998a). During their stay in the PLR, shorebirds
spend most of their diurnal time feeding on inver-

tebrates (Davis and Smith 1998a, b). Because inver-
tebrate community structure is playa-specific and
invertebrate abundances are variable and unpredict-
able within playas (Davis and Smith 1998a), playas
provide a gradient of different invertebrate abun-
dances required to evaluate foraging strategies of mi-
grant shorebirds.

The study was conducted on 60 playas between
32°30' and 34°41'N and between 101°09' and
102°30'W in Castro, Lamb, Floyd, Hale, Hockley,
Lubbock, Lynn, Dawson, Martin, Crosby, and Parm-
er counties, Texas, during spring (late February to
late May) and fall (late July to late October) migration
1993 and 1994. We selected playas on the basis of
whether they had available shorebird habitat (i.e. oc-
currence of sparse vegetation and mudflat and shal-
low water depths), and whether they were in the
counties of the study (Davis and Smith 1998a). In-
formation about shorebird use of playas and habitat
conditions was obtained from weekly shorebird sur-
veys conducted in the PLR during spring and fall
1993 and 1994 (Davis 1996). At the beginning of each
migration period, we randomly selected 20 playas
from the group of 60 playas for data collection. Be-
cause playas typically dried before the end of the mi-
gration period, we replaced dried playas with ran-
domly selected playas from the group of 60 playas.

The 11 counties in our study area constitute more
than 25,000 km² of the PLR, which is one of the most
intensively cultivated regions in the Western Hemi-
sphere (Bolen et al. 1989). The climate in the PLR is
dry steppe with hot summers and mild winters. Av-
erage annual precipitation is 48 cm, with most oc-
curring between May and September (National Oce-
anic and Atmospheric Administration 1995).

Diet.—Shorebirds were randomly collected from
flocks after being observed feeding for ≥15 min (Da-
vis and Smith 1998a). Esophageal contents were re-
moved immediately and placed in 80% ethanol. We
identified invertebrates to family or order level using
Merritt and Cummins (1984) and Pennak (1989). In-
vertebrates were counted, measured, dried to con-
stant mass at 65°C, and weighed. Each prey item was
assigned to 1 of 6 size categories: 0.1–5.0 (size cate-
gory A), 5.1–10.0 (size category B), 10.1–15.0 (size
category C), 15.1–20.0 (size category D), 20.1–25.0
(size category E), and ≥25.1 mm (size category F).
We selected those size categories because they rep-
resent a size gradient of small to large prey that al-
lowed us to compare prey-size selection among
small (Least and Western sandpipers), medium
(Long-billed Dowitcher), and large (American Avo-
cet) shorebird species. Data from esophageal sam-
ples were summarized as aggregate percent dry
mass (Prevett et al. 1979). Diet compositions of the
four species are reported in Davis and Smith (1998a).

We calculated diet diversities for each species us-
ing the reciprocal of Simpson's index (Begon et al.
1990):

$$B = 1/\Sigma p_i^2$$

where p_i is the proportion of the ith prey category (i.e. percent dry mass for each prey category [family or order level]) in the diet of a given individual. The number of prey categories for each diet diversity calculation ranged from 1 (i.e. an individual's diet was composed exclusively of 1 prey category [e.g. Chironomidae]) to 10 (e.g. an individual's diet was composed of 10 separate prey categories). We used the reciprocal of Simpson's index because it is more sensitive to changes in the more abundant (i.e. important) prey categories in the diet, as opposed to Shannon-Weiner index, which is most sensitive to changes in less-abundant (i.e. rare) prey categories in the diet (Krebs 1989). The value of B ranges from 1 to n, where n is the number of prey categories in the diet. If the proportions of all prey categories are equal, then $B = n$, whereas if 1 prey category accounts for the greatest proportion of the diet and other prey categories account for only trace amounts, then $B \approx 1$ (Hespenheide 1975). Diets that were composed exclusively of unidentifiable animal matter (i.e. prey items could not be determined beyond animal matter) were not included. For the diets that were included in the calculations, unidentifiable animal matter exclusively occurred in 18 of 154 avocet diets, 11 of 156 dowitcher diets, 13 of 150 Least Sandpiper diets, and 15 of 160 Western Sandpiper diets, and constituted <10% of the diet (by mass) for those individuals.

Feeding method.—We used focal individual sampling (Altmann 1974) to record the feeding methods used by each shorebird species. We used a 15 × 45 spotting scope or 10 × 60 binoculars to observe each individual shorebird. Observations of each individual lasted 5 min, during which all feeding methods were dictated into a tape recorder with the durations of each method timed with a digital stopwatch. Although we were able to collect behavioral data on some of the birds we collected for diet analysis, often times it was difficult relocating those birds prior to collection (i.e. we lost sight of focal individuals when collecting birds in flocks). Therefore, we collected behavioral data from a random sample of each species during spring and fall. Behavioral data were collected by directing the spotting scope or binoculars at a flock and selecting the individual in the center of the field of view (Davis and Smith 1998b). We continued randomly selecting individuals in the flock by moving the spotting scope or binoculars in a zig-zag motion so that individuals in all portions of the flock were sampled (Davis et al. 1989). Feeding methods were recorded as pecking (bill penetrated the substrate or water surface less than one-fourth the total length of the bill), probing (bill penetrated the substrate or water surface greater than one-fourth the total length of the bill), and scything (bill is moved across the substrate or water surface in a sweeping motion) (Baker and Baker 1973, Hamilton 1975).

We calculated feeding-method diversities for each species using the reciprocal of Simpson's index (Begon et al. 1990). For this calculation, p_i is the proportion of the ith feeding method (i.e. percent of time engaged in a feeding method) of a given individual.

Foraging microhabitat.—We measured water depths within foraging areas of each shorebird that we collected. Foraging areas were delineated from the point where the shorebirds were first observed foraging to the point where they were collected. We then established a transect that transversed the foraging area. We recorded five water-depth measurements from randomly selected points along the transect. While collecting the feeding-method data, we also determined amount of time each species spent in the following foraging microhabitats: exposed mudflat (moist to wet mud with no standing water), shallow water (edge of mudflat to <4 cm), moderate water (4–16 cm), and deep water (>16 cm). For determination of time spent in each foraging microhabitat, water depths were estimated relative to the length of each shorebird's leg (Baker 1971).

Invertebrate availability.—After each shorebird collection, we collected invertebrates from the mudflat, benthos, and water column within the foraging area. We collected ten 5 × 10 cm core samples (Swanson 1983) for benthic invertebrates. We used a water-column (volume: 0–2,000 ml) sampler (Swanson 1978) and 24 h activity traps (Murkin et al. 1994) to collect nektonic invertebrates. Five water-column samples and five activity-trap samples were collected from foraging areas that had water depths >5 cm. Water-column and activity-trap samples could not be collected at water depths <5 cm. Core, water-column, and activity-trap samples were washed through 0.5 and 2.0 mm sieves, and invertebrates were removed and preserved in 80% ethanol. Invertebrates were identified to family or order level according to published descriptions (Merritt and Cummins 1984, Pennak 1989), measured, assigned to the appropriate size category, dried to constant mass at 65°C, and weighed.

Niche overlap.—Niche overlap between each of the four species for each niche dimension (i.e. diet, prey size, feeding method, and foraging microhabitat) was determined using Schoener's (1968) equation:

$$O_{xy} = 1 - 0.5 \; \Sigma \mid p_{xh} - p_{yh} \mid,$$

where p_x and p_y are the proportions of hth niche category for species x and y. The value of O ranges from 0 (no overlap) to 1 (complete overlap). For calculation of niche overlap, we used aggregate percent dry mass of each prey item in the diet for diet overlap, proportion of prey sizes within each size category for prey-size overlap, proportion of time spent in foraging microhabitats for foraging-microhabitat over-

lap, and proportion of time spent engaged in feeding methods for feeding-method overlap.

Foraging strategy.—We determined energy content and nutritional quality (protein and fat) of invertebrate foods. That allowed us to determine whether shorebirds were selecting invertebrate foods on the basis of food quality or food abundance. We collected invertebrates from the benthos and water column of 20 playas during spring and fall 1993 and 1994. Invertebrates were placed in plastic bags and stored frozen until analyzed. Frozen samples of invertebrates were later thawed, sorted, and identified to taxonomic groupings. Each taxonomic grouping was oven-dried at 65°C to a constant mass and ground to a homogeneous mixture in a Wiley mill. We pooled each taxonomic grouping across years, seasons, and playas because of the amount (0.5 g) needed to determine energy and nutrient content.

We determined gross energy (kilocalories per gram), percent protein, and percent fat with duplicate 0.5 g subsamples for each taxonomic group that had a sufficient biomass. When duplicate analyses differed by >10%, we reanalyzed the samples (Haukos and Smith 1995). We averaged results of duplicate samples prior to statistical analyses.

We determined gross energy with a Parr series 1241 adiabatic O-bomb calorimeter under 27 atm of pressure. Percent N was determined using macro-Kjeldahl analysis and multiplied by 6.25 to estimate percent crude protein (Robbins 1983). Percent fat was determined by lipid extraction with diethyl ether for 16 h in a Soxhlet apparatus (Dobush et al. 1985).

Data analysis.—We used MANOVA with a factorial arrangement to determine foraging niche separation (diet diversity, prey size, water depth, and feeding-method diversity) of the four species. Species and season were the independent factors in the MANOVA, whereas diet diversity, prey size, water depth, and feeding-method diversity were the dependent factors. We used MANOVA because it allows separation of the four species on the basis of a linear combination of dependent factors. We used Wilks' lambda as the MANOVA test criterion. Following a significant ($P \leq 0.05$) overall MANOVA, we separated the linear combination of factors with multivariate techniques (Harris 1975). Univariate ANOVA was used to determine differences in individual dependent factors among species when MANOVA was significant (Barker and Barker 1984). If differences ($P \leq 0.05$) existed within factors, Fisher's least significant difference test was used.

We determined shorebird prey-size selection using compositional analysis (Aebischer et al. 1993). We used compositional analysis because prey-size proportions are not independent (i.e. all prey-size categories sum to 1). We constructed log ratios by dividing the proportional use and availability for each of the prey-size categories by the proportional use and availability of the "F" size category and transform-

ing the resulting ratios to logarithms (Aebischer et al. 1993). All zero values were replaced with 0.0001 (a value less than the lowest nonzero use or availability proportions) to calculate logarithms (Aebischer et al. 1993). We then calculated the differences from each paired use and availability log ratio (e.g. use of size category "A" log ratio—availability of size category "A" log ratio). We used MANOVA to test whether the differences between use and availability log ratios were different than zero (Johnson and Wichern 1988). Following a significant MANOVA (i.e. prey-size selection was nonrandom), ranks were assigned to each prey-size category. We used t-tests to determine differences among ranks for the prey- size categories of each species (Aebischer et al. 1993).

We used Pearson correlation coefficients (r) to describe the degree of association among abundance of a prey item in the diet (aggregate percent dry mass) of each species during each season with each of the following factors: prey abundance in the environment (grams per square meter), energy value of prey items (kilocalories per gram), protein content of prey items (percent protein), and fat content of prey items (percent fat). All statistical tests were conducted using SYSTAT version 5.

RESULTS

Overall foraging niche.—A species × season interaction (Wilks' λ = 0.883; F = 6.48; df = 12 and 1,611; $P < 0.001$) occurred, separating the overall foraging niche (i.e. linear combination of the four niche dimensions measured) among the four species. Therefore, we separated overall foraging niche within seasons. In spring and fall, overall foraging niche space differed among the four species (spring: Wilks' λ = 0.282; F = 41.95; df = 12 and 820; $P < 0.001$; fall: Wilks' λ = 0.294; F = 38.36; df = 12 and 783; $P < 0.001$). Multivariate separation indicated that the four species were segregated similarly along a multidimensional niche space in both seasons (Table 1). The niches of American Avocets and Long-billed Dowitchers were segregated from each other and from Least and Western sandpipers, whereas Least and Western sandpipers occupied similar foraging niches.

Single niche dimensions and overlaps.—Diet diversities were different among the four species in spring (F = 5.88; df = 3 and 313; P = 0.001), but not in fall (F = 1.85; df = 3 and 299; P = 0.139). In spring, American Avocets and Long-billed Dowitchers exhibited similar diet diversities, and Least and Western sandpipers exhibited similar diet diversities (Table 2). Except

TABLE 1. Multivariate separation of multidimensional foraging niche space of American Avocets (spring: $n = 73$, fall: $n = 81$), Long-billed Dowitchers (spring: $n = 92$, fall: $n = 64$), Least Sandpipers (spring: $n = 84$, fall: $n = 66$), and Western Sandpipers (spring: $n = 68$, fall: $n = 92$) in the Playa Lakes Region of Texas during spring and fall in 1993 and 1994. Multivariate separation was based on a linear combination of diet, prey size, feeding-method, and foraging-microhabitat niche dimensions (represented by diet diversity, prey size, feeding-method diversity, and water depth) for each species.[a]

Multivariate separation of shorebird niche space	
Spring	Fall
American Avocet A[b]	American Avocet A
Long-billed Dowitcher B	Long-billed Dowitcher B
Least Sandpiper C	Least Sandpiper C
Western Sandpiper C	Western Sandpiper C

[a] Canonical loadings for dependent variables within each season were: 0.332 (prey size), 0.863 (foraging microhabitat), −0.187 (diet), and −0.464 (feeding method) for spring and 0.278 (prey size), 0.919 (foraging microhabitat), −0.040 (diet), and −0.324 (feeding method) for fall.

[b] Species with same letter within columns are not different ($P > 0.05$).

for Least and Western sandpipers, which exhibited a relatively high diet overlap ($O = 0.80$) in spring, all species pairs exhibited moderate diet overlaps during both seasons ($O = 0.41–0.68$; Table 3).

Prey size differed among the four species in spring ($F = 33.55$; df = 3 and 313; $P < 0.001$) and fall ($F = 16.48$; df = 3 and 299; $P < 0.001$). In spring, Long-billed Dowitchers consumed the largest prey, whereas American Avocets

TABLE 3. Diet, prey-size, foraging-microhabitat, and feeding-method niche overlaps[a] among American Avocets (AA), Long-billed Dowitchers (LB), Least Sandpipers (LS), and Western Sandpipers (WS) in the Playa Lakes Region of Texas during spring and fall in 1993 and 1994.

		Niche overlap	
Niche dimension	Species	Spring	Fall
Diet	AA-LB	0.68	0.54
	AA-LS	0.62	0.44
	AA-WS	0.59	0.41
	LB-LS	0.66	0.50
	LB-WS	0.67	0.50
	LS-WS	0.80	0.57
Prey-size	AA-LB	0.69	0.78
	AA-LS	0.87	0.63
	AA-WS	0.69	0.62
	LB-LS	0.58	0.85
	LB-WS	0.40	0.84
	LS-WS	0.82	0.97
Foraging-microhabitat	AA-LB	0.72	0.68
	AA-LS	0.23	0.12
	AA-WS	0.23	0.28
	LB-LS	0.51	0.44
	LB-WS	0.51	0.44
	LS-WS	0.76	0.89
Feeding-method	AA-LB	0.00	0.00
	AA-LS	0.06	0.04
	AA-WS	0.06	0.04
	LB-LS	0.10	0.10
	LB-WS	0.38	0.21
	LS-WS	0.72	0.89

[a] Niche overlaps were determined by Schoener's equation (1968). Determination of spring niche overlaps was based on 73 American Avocets, 92 Long-billed Dowitchers, 84 Least Sandpipers, and 68 Western Sandpipers, whereas determination of fall niche overlaps was based on 81 American Avocets, 64 Long-billed Dowitchers, 66 Least Sandpipers, and 92 Western Sandpipers.

TABLE 2. Comparison of prey size (millimeter), water depth (centimeter), diet diversity, and feeding-method diversity niche dimensions among American Avocets (AA), Long-billed Dowitchers (LB), Least Sandpipers (LS), and Western Sandpipers (WS) in the Playa Lakes Region of Texas during spring and fall in 1993 and 1994.

		Species[a]							
		AA		LB		LS		WS	
Niche dimension	Season	x̄	SE	x̄	SE	x̄	SE	x̄	SE
Prey size	Spr	7.95A[b]	0.58	10.36B	0.58	5.65C	0.25	4.34C	0.27
	Fall	7.35A	0.36	6.30B	0.40	4.79C	0.27	4.77C	0.23
Water depth	Spr	8.55A	0.52	4.16B	0.26	1.19C	0.08	1.56C	0.12
	Fall	10.70A	0.62	6.36B	0.27	1.06C	0.11	1.30C	0.10
Diet diversity[c]	Spr	1.32A	0.06	1.42A	0.06	1.63B	0.08	1.72B	0.10
	Fall	1.98	0.09	2.11	0.11	1.94	0.08	2.23	0.11
Feeding-method diversity[c]	Spr	1.01A	0.01	1.00A	0.00	1.19B	0.03	1.34C	0.04
	Fall	1.00A	0.00	1.00A	0.00	1.13B	0.03	1.25C	0.03

[a] AA: $n = 73$ for spr, $n = 81$ for fall; LB: $n = 92$ for spr, $n = 64$ for fall; LS: $n = 84$ for spr, $n = 66$ for fall; WS: $n = 68$ for spr, $n = 92$ for fall.

[b] Means with the same letter within rows did not differ ($P > 0.05$).

[c] Diversity indices were determined by reciprocal of Simpson's index (Begon et al. 1990).

consumed the largest prey in fall (Table 2). Least and Western sandpipers consumed the smallest prey during both seasons. During spring, Least Sandpipers exhibited high prey-size overlap with American Avocets and Western Sandpipers (O = 0.82–0.87), whereas during fall, their prey-size overlap with avocets (O = 0.63) declined and their overlap with Western Sandpipers (O = 0.97) increased (Table 3). Prey-size overlaps between Long-billed Dowitchers and Least and Western sandpipers were relatively low (O = 0.40–0.58) during spring and relatively high during fall (O = 0.84–0.85).

Feeding-method diversities differed among the four species in spring (F = 45.56; df = 3 and 313; P < 0.001) and fall (F = 28.39; df = 3 and 299; P < 0.001). During both seasons, Western Sandpipers used more diverse feeding methods than the other three species, whereas American Avocets and Long-billed Dowitchers used the least diverse feeding methods (Table 2). Feeding-method overlaps between American Avocets and the other species and between Long-billed Dowitchers and Least Sandpipers were low during both seasons (O = 0.00–0.10; Table 3). However, Least and Western sandpipers exhibited relatively high feeding-method overlaps during both seasons (O = 0.72–0.89).

Water depth used by the four species differed during spring (F = 129.68; df = 3 and 313; P < 0.001) and fall (F = 179.95; df = 3 and 299; P < 0.001). During both seasons, American Avocets foraged in deeper water than did the other three species (Table 2). Compared to the other three species, Long-billed Dowitchers foraged in moderate water depths and Least and Western sandpipers foraged in the shallowest areas (Table 2). During both seasons, foraging-microhabitat overlap was moderately high between American Avocets and Long-billed Dowitchers (O = 0.68–0.72) and between Least and Western sandpipers (O = 0.76–0.89; Table 3). Foraging-microhabitat overlaps were low between American Avocets and Least and Western sandpipers (O = 0.12–0.28).

Foraging strategies.— All four species did not use prey sizes in proportion to availability during spring (American Avocet: λ = 0.65; F = 7.31; df = 5 and 68; P < 0.0001; Long-billed Dowitcher: λ = 0.86; F = 2.81; df = 5 and 76; P = 0.021; Least Sandpiper: λ = 0.62; F = 10.01; df = 5 and 79; P < 0.0001; Western Sandpiper: λ = 0.39; F = 19.49; df = 5 and 63; P < 0.0001)

and fall (American Avocet: λ = 0.54; F = 12.8; df = 5 and 76; P < 0.0001; Long-billed Dowitcher: λ = 0.81; F = 2.78; df = 5 and 59; P = 0.026; Least Sandpiper: λ = 0.67; F = 6.05; df = 5 and 61; P < 0.0001; Western Sandpiper: λ = 0.69; F = 7.74; df = 5 and 87; P < 0.0001). During spring, prey in size category "A" were most preferred by American Avocets, and Least and Western sandpipers, whereas prey in category "C" were most preferred by Long-billed Dowitchers (Table 4). In the fall, Long-billed Dowitchers, and Least and Western sandpipers most preferred prey in category "A," whereas American Avocets most preferred prey in category "B" (Table 4).

Most (85.7%) of the energy values for shorebird prey ranged from 4.0 to 5.7 kcal/g (Table 5). Crude protein content ranged from 17.7 to 67.4%. Nearly 80% of the prey had fat values < 22%. Only hydrophilids, dytiscids, and notonectids contained fat values >40% (Table 5). During both seasons, abundance of a prey item (aggregate percent dry mass) in the diet of each of species and abundance of a prey item (grams per square meter) in playas were positively correlated (Table 6). However, abundance of a prey item in the diet was not correlated with energy value, protein content, or fat content of a prey item for any of the species during spring and fall (Table 6).

DISCUSSION

Overall foraging niche.—In spring and fall, the largest species (American Avocet), medium species (Long-billed Dowitcher), and smallest species (Least and Western sandpipers) of shorebirds were segregated along a multidimensional niche space. Although no studies have examined shorebird niche segregation on the basis of a multidimensional approach, our results are consistent with studies that examined shorebird niche segregation along single niche dimensions (Holmes and Pitelka 1968, Baker and Baker 1973, Eldridge 1987, Senner et al. 1989).

Schoener (1974) reported that habitat dimensions, food-type dimensions, and temporal dimensions are the most important resource axes that segregate species. In terms of the range of importance of those three axes, Schoener (1974: 33) stated that "habitat dimensions are important more often than food-type dimensions, which are important more often than temporal

TABLE 4. Mean proportions of prey-size selection and availability and prey-size preferences for American Avocets, Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers in playa lakes in the Playa Lakes Region of Texas during spring and fall in 1993 and 1994. Prey sizes are ranked in descending order where "1" is the most preferred prey size. Ranks of preferences with the same capital letter for each species within a season are not significantly ($P > 0.05$) different from each other.

	Spring				Fall			
Species and prey size	n	Use	Available	Rank[a]	n	Use	Available	Rank
American Avocet	73				81			
A (0.1–5.0 mm)		41	30	1A		26	44	6A
B (5.1–10.0 mm)		40	44	5B		65	41	1B
C (10.1–15.0 mm)		6	21	6C		5	8	5C
D (15.1–20.0 mm)		6	3	4B		2	0	2D
E (20.1–25.0 mm)		5	1	3B		0	2	3D
F (≥25.1 mm)		2	1	2B		2	5	4C
Long-billed Dowitcher	92				64			
A (0.1–5.0 mm)		12	21	5A		47	40	1A
B (5.1–10.0 mm)		50	50	3B		47	55	6B
C (10.1–15.0 mm)		24	16	1C		3	2	2C
D (15.1–20.0 mm)		8	5	2B		1	1	3C
E (20.1–25.0 mm)		3	4	4B		0	0	4C
F (≥25.1 mm)		3	4	4B		1	2	5C
Least Sandpiper	84				66			
A (0.1–5.0 mm)		54	17	1A		63	36	1A
B (5.1–10.0 mm)		38	62	6B		35	32	6B
C (10.1–15.0 mm)		7	11	4CD		2	8	5C
D (15.1–20.0 mm)		0	9	5C		0	2	4D
E (20.15–25.0 mm)		0	1	3D		0	0	2D
F (≥ 25.1 mm)		0	0	2D		0	2	3D
Western Sandpiper	68				92			
A (0.1–5.0 mm)		73	34	1A		64	46	1A
B (5.1–10.0 mm)		26	54	6B		32	40	4B
C (10.1–15.0 mm)		1	7	5C		2	11	6B
D (15.1–20.0 mm)		2	5	4C		1	3	5C
E (20.1–25.0 mm)		0	0	2D		1	0	2D
F (≥25.1 mm)		0	0	3D		0	1	3D

[a] Aebischer et al. 1993.

dimensions." We did not include temporal dimensions (e.g. partitioning of time to search and forage for specific foods, amount of time spent on individual playas, timing of migration through the PLR) in the analysis because that type of data would require us being able to determine consumption of specific foods through observation or marking birds, which we were unable to do. However, based on canonical coefficients of the linear combination of dependent factors in the MANOVA (Table 1), habitat dimensions (i.e. water depth) were more important than food-type dimensions (i.e. prey size, diet diversity) for segregating the four species during spring and fall.

Single niche dimensions.—Studies of single-dimensional niche segregation among shorebirds have focused on the relationships between bill length and prey size (Holmes and Pitelka 1968, Baker and Baker 1973, Eldridge 1987), and be-

tween tarsal length and water depth of foraging habitats (Baker 1978, Eldridge 1987). Holmes and Pitelka (1968) reported that shorebird species with long bills consumed larger prey than did shorebird species with small bills, and Eldridge (1987) reported that large shorebird species consumed larger prey and foraged in deeper water than small shorebird species. In our study, American Avocets and Long-billed Dowitchers (the larger species) consumed larger prey and foraged in deeper water than did Least and Western sandpipers (the smaller species). However, Long-billed Dowitchers, which are smaller than avocets (95.9 ± 0.6 g [SE] [$n = 176$] vs. 302.6 ± 3.0 g [$n = 187$] [C. A. Davis unpubl. data]), consumed larger prey than avocets in spring. Although the bills of dowitchers and avocets are relatively close in size (6.7 ± 0.04 cm [SE] for dowitchers [$n = 176$] and 8.9 ± 0.05 cm for avocets

TABLE 5. Gross energy (kilocalories/gram), crude protein (percentage protein), and crude fat (percentage fat) values of shorebird prey collected from the benthos and water column of 20 playa lakes in the Playa Lakes Region of Texas during spring and fall in 1993 and 1994. Determination of energy, protein, and fat were based on composite samples (i.e. more than one individual was included in the sample) and duplicate analyses for prey collected from playa lakes.

Prey taxa	Gross energy	Protein	Fat
Chironomidae (L)[a]	3.9	42.8	10.8[b]
Ephydridae (L)	3.8	17.8	11.8
Tipulidae (L)	5.4[c]	43.8[d]	—
Hydrophilidae (A)	5.6	38.8	42.6
Hydrophilidae (L)	4.4	—	—
Dytiscidae (A)	5.3[c]	47.8	44.6
Notonectidae	5.2	67.2	46.3
Corixidae	5.3	61.0	21.0
Libellulidae (N)	4.9	62.4	17.6
Coenagrionidae (N)	4.8	67.4	—
Baetidae (N)	5.7	54.5[e]	—
Hirudinea	5.3	64.2	19.0
Oligochaeta	5.4[d]	62.0[d]	15.5[f]
Conchostraca	3.2	36.7	10.6
Notostraca	3.6	53.7	10.6
Cladocera	4.8[e]	47.6[e]	—
Anostraca	5.1[c]	49.7[c]	—
Planorbidae	4.2	51.9	10.9
Hydracarina	5.6[d]	65.9[d]	—
Ambystoma tigrinum (L)	4.5	62.9	21.4
Rana catesbeiana (T)	2.1	17.7	6.6

[a] L = larvae, A = adult, N = nymph, and T = tadpole.
[b] From Krapu and Swanson (1974).
[c] From Driver (1981).
[d] From Anderson and Smith (1998).
[e] From Driver et al. (1974).
[f] From Gardner et al. (1985).

[n = 186] [C. A. Davis unpubl. data]), the difference in prey sizes consumed by each species may have been more a function of the size of prey that occur within foraging microhabitats, the foraging method (scything vs. probing) used by each species, or both. Dowitchers use a probing technique to forage primarily in the substrate for invertebrates, whereas avocets use a scything technique to forage primarily in the water column. During spring, the mean size of invertebrates in the water column was smaller than the mean size of invertebrates in the substrate (7.6 ± 1.07 cm [SE] vs. 9.1 ± 0.4 cm [C. A. Davis unpubl. data]).

Although American Avocets and Long-billed Dowitchers consumed larger prey than Least and Western sandpipers, considerable overlap in prey size existed in American Avocet and Least Sandpiper diets (O = 0.87) during spring

and in Long-billed Dowitcher and Least and Western sandpiper diets (O = 0.84–0.85) during fall. Schoener (1984) noted that for certain birds, larger species consume a larger range of food sizes than smaller species because their preferred food (i.e. larger prey) may be relatively more scarce and handling costs may be higher. In playas, large prey (>10 mm) were less available compared to small prey (<10 mm) (Table 4). Thus, avocets and dowitchers may have responded to the scarcity of large prey by consuming a wide range of prey sizes (i.e. large and small prey) resulting in high prey-size overlaps with Least and Western sandpipers. However, the high overlaps in prey size between large and small shorebirds may have been more a consequence of our designation of prey-size categories. Specifically, the size range (e.g. 0.1–5.0 mm, 5.1–10.0 mm) within each of our prey-size categories may have been too large (especially for Least and Western sandpipers) to adequately evaluate prey-size overlaps between small and large shorebirds because small and large shorebirds likely perceive (on the basis of handling costs) small and large prey differently.

Because the tarsal length of American Avocets is longer than Least and Western sandpipers (9.4 ± 0.04 cm [SE] for avocets [n = 189], 1.9 ± 0.01 cm for Least Sandpipers [n = 203], and 2.3 ± 0.01 cm for Western Sandpipers [n = 171]), Avocets potentially can exploit a wider range of water depths, and therefore prey types, than can Least and Western sandpipers. Moreover, avocets frequently swim to exploit deeper water. Hence, the mean foraging-microhabitat overlap between avocets and Least and Western sandpipers was relatively low (O = 0.21). This low overlap emphasizes the role that spacing along a habitat dimension plays in segregating large and small shorebirds such as avocets and Least and Western sandpipers. The importance of spacing is also supported by the high prey-size overlaps between avocets and Least and Western sandpipers (O = 0.70). Species that overlap along one niche dimension should differ from each other along another niche dimension (Schoener 1974, Pöysä 1983, McKenzie and Rolfe 1986, Begon et al. 1990).

Diet overlaps for all species pairs were lower in fall than in spring. Those declines were likely a function of seasonal differences in prey availabilities and diversities. Prey availabilities

TABLE 6. Pearson correlations coefficients (r) between abundance of a prey item in shorebird diets (aggregate percent dry mass) and prey abundance in the environment (grams/meter^2), energy value of prey item (kilocalories/gram), protein content of prey item (percent protein), and fat content of prey item (percent fat) for American Avocets, Long-billed Dowitchers, Least Sandpipers, and Western Sandpipers in the Playa Lakes Region of Texas during spring and fall in 1993 and 1994.

	Species[a]							
Season	American Avocet		Long-billed Dowitcher		Least Sandpiper		Western Sandpiper	
Variable	r	P	r	P	r	P	r	P
Spring								
Prey abundance	0.880	0.004	0.946	0.004	0.998	0.002	0.817	0.047
Energy	−0.503	0.204	−0.332	0.422	−0.351	0.394	−0.272	0.419
Protein	0.107	0.841	0.180	0.700	0.209	0.620	0.169	0.642
Fat	−0.119	0.822	−0.148	0.779	−0.068	0.898	−0.095	0.793
Fall								
Prey abundance	0.594	0.032	0.775	0.008	0.757	0.007	0.651	0.016
Energy	0.195	0.438	−0.185	0.564	0.061	0.835	0.012	0.966
Protein	0.149	0.582	−0.139	0.666	−0.231	0.427	−0.191	0.496
Fat	0.206	0.481	0.116	0.750	0.189	0.579	0.111	0.732

[a] American Avocet: n = 73 for spring, n = 81 for fall; Long-billed Dowitcher: n = 92 for spring, n = 64 for fall; Least Sandpiper: n = 84 for spring, n = 66 for fall; Western Sandpiper: n = 68 for spring, n = 92 for fall.

and diversities were less in spring than fall (Davis and Smith 1998a). For example, chironomids were the most abundant prey in playas during spring, whereas several prey taxa (e.g. hydrophilids, chironomids, leeches, orb snails) were abundant during fall. Moreover, in most cases, only a few prey taxa (1–3 prey) occurred in playas during spring, whereas 10–15 taxa commonly occurred in playas during fall. Because of lower prey availabilities and diversities during spring, American Avocets, Long-billed Dowitchers, and Least and Western sandpipers were restricted to primarily consuming chironomids, oligochaetes, and leeches in spring. In contrast, the four species were able to exploit more prey taxa in fall because of higher prey availabilities and diversities.

Segregation along the feeding-method dimension was exhibited between all species pairs, except between Least and Western sandpipers. Scything was the predominant feeding technique of American Avocets, whereas probing was the predominant feeding technique of Long-billed Dowitchers. Least and Western sandpipers used a pecking and probing technique. Because American Avocets and Long-billed Dowitchers are similar along diet-diversity, prey-size, and water-depth dimensions, the feeding-method diversity dimension may be an important mechanism for segregating American Avocets and Long-billed Dowitchers. Specifically, the bill morphology of the two

species is the mechanism: the curved bill of avocets allows them to more efficiently capture invertebrates from the water column, and the long, straight bill of dowitchers allows them to more efficiently capture invertebrates from the substrate. Differences in the diets of avocets and dowitchers supports this hypothesis: avocet diets had higher occurrences of nektonic invertebrates (e.g. corixids, notonectids, baetids, coenagrionids) than dowitchers, whereas dowitchers had higher occurrences of benthic invertebrates (e.g. chironomids, oligochaetes) than avocets (Davis and Smith 1998a).

In this study, we found niche separation between the large and small shorebirds, but did not find separation between the two small shorebirds. Several researchers have hypothesized that Least and Western sandpipers may be segregated along a temporal dimension (i.e. migration chronologies differ temporally) (Recher 1966, Butler et al. 1987, Butler and Kaiser 1995). In the PLR, the migration chronologies of Least and Western sandpipers exhibited some temporal separation (Davis and Smith 1998a); however, other factors may have played a role in the similarity of niches observed for Least and Western sandpipers. For example, we may have improperly measured and defined niche dimensions relative to the birds' perceptions. Weins (1989) suggested that high overlap among species may be a consequence of researchers improperly measuring or categoriz-

ing niche dimensions rather than an indication of an absence of niche separation. Wiens (1989) also noted that high overlap may occur on several niche dimensions if resources are not limiting. In the PLR, we found that shorebirds depleted invertebrate food resources in spring (Davis and Smith 1998a); however, invertebrate abundances in playas may not reach the point where they become a limited resource to Western and Least sandpipers.

Foraging strategies.—Although American Avocets and Long-billed Dowitchers consumed larger prey than Least and Western sandpipers (Table 2), the prey-size preferences of avocets and dowitchers were similar to Least and Western sandpipers (Table 4). In general, all four species preferred small prey (size category "A"). For Least and Western sandpipers, preference for small prey is likely a function of handling costs because small prey likely have lower handling costs than large prey. Lifjeld (1984) found that Little Stint (*Calidris minuta*) had greater difficulty handling large prey (>10 mm) than small prey that resulted in them spending more time handling large prey than small prey. For avocets and dowitchers, the handling costs of large prey is likely relatively low; however, large prey were relatively scarce compared to small prey (Table 4). Hence, avocets and dowitchers exhibited preferences for the more abundant prey sizes (i.e. small prey).

We were unable to closely examine optimal foraging because we could not determine the amount of time spent handling prey and searching for prey (because that occurs mostly under the water surface), and hence, we could not determine profitability of prey items. However, we did examine the relationship between abundance of a prey item in the diet of each of the species and the nutritional and energetic qualities of the prey item. For all four species, abundance of a prey item in the diet was not correlated with energy value, protein content, or fat content of a prey item; however, abundance of a prey item in the diet was positively correlated with abundance of a prey item in playas. All four species apparently do not select prey items on the basis of the nutritional or energetic quality of a prey item, but rather select prey items on the basis of which prey item is most abundant in a playa. That suggests that during migration, all four species adopt an opportunistic foraging strategy (i.e. select the most abundant prey in the playa). Because shorebirds typically migrate across vast landscapes where wetlands are temporally and spatially dynamic (Fredrickson and Reid 1990, Skagen and Knopf 1993, Farmer and Parent 1997), they likely cannot afford to discriminate between profitable prey and unprofitable prey. Consequently, adopting an opportunistic foraging strategy provides migrant shorebirds with a flexible strategy that allows them to increase their probability of being able to replenish energy and nutrient reserves for continuing their migration to breeding and wintering grounds as well as arriving on the breeding grounds in good condition (Davis and Smith 1998a).

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