Foraging Ecology of Migrant Shorebirds in Saline Lakes of the Southern Great Plains

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Abstract.—Tens of thousands of shorebirds use saline lakes as migratory stopovers in the Southern Great Plains, USA. To assess their foraging strategies and understand how they replenish energy reserves during spring and summer/fall migrations, we examined diets, prey taxa selection, and prey size selection of American Avocets (*Recurvirostra americana*), Least Sandpipers (*Calidris minutilla*), Wilson's Phalaropes (*Phalaropus tricolor*), and Lesser Yellowlegs (*Tringa flavipes*). Migrant shorebirds foraged opportunistically by taking most prey taxa according to their availability. Least Sandpipers preferred small prey (2-5 mm), whereas American Avocet, Wilson's Phalaropes, and Lesser Yellowlegs generally preferred intermediate and large prey (6-20 mm). By consuming prey taxa according to their availability and prey sizes that require minimum energy to capture and ingest, shorebirds increase their ability to replenish energy reserves while migrating through interior North America. Drought and drying of freshwater springs will reduce availability of prey in saline lakes for migrating shorebirds. To preserve the saline lakes as important habitats where shorebirds replenish nutrient reserves while migrating through the Great Plains, it is important to conserve groundwater so that freshwater springs continue to discharge into the lakes. *Received 30 January 2008, accepted 2 September 2008.*

Key words.—American Avocet, invertebrates, Least Sandpiper, Lesser Yellowlegs, migration stopovers, Ogallala aquifer, saline lakes, shorebirds, Southern Great Plains, Wilson's Phalarope.

To complete their migrations through interior North America, shorebirds rest and accumulate lipid reserves by foraging on aquatic invertebrates in freshwater playas and saline lakes of the Southern Great Plains (SGP) (Davis and Smith 1998; Andrei *et al.* 2007). The saline lakes of the SGP are discharge wetlands that provide important stopover sites for tens of thousands of migrating shorebirds (Andrei *et al.* 2006). Historically, numerous springs fed by the Ogallala aquifer discharged into the saline lakes, providing reliable water (Brüne 1981). By the 1970s, spring flows were reduced, many lakes were perpetually dry, and vegetation and wildlife have been negatively affected by lack of water (Brüne 1981). Presently, spring flows continue to decrease due to declining aquifer levels (Triplet 1998; Sophocleous 2000), resulting in shortened hydroperiods and increased salinization of the lakes (Andrei *et al.* 2008).

The more numerous freshwater playas of the SGP also serve as migration stopovers for shorebirds (Davis and Smith 1998). Playas are recharge wetlands, depending on precipitation as their only source of water and serving as recharge points for the Ogallala aquifer, which feeds springs in the saline lakes (Osterkamp and Wood 1987; Nativ 1992; Smith 2003). While using the dynamic and unpredictable freshwater playas in the Great Plains as stopover sites during their migrations through interior North America, shorebirds increase their chances of accumulating energy reserves by foraging opportunistically for invertebrates (Davis and Smith 1998; Smith 2003), but information

about foraging strategies of shorebirds using saline lakes in the SGP is lacking. In playas, shorebirds foraged opportunistically, by consuming invertebrate prey taxa proportionate to their availability (Davis and Smith 2001). An opportunistic foraging strategy would enable shorebirds using saline lakes to switch to alternative prey taxa when increased salinity alters invertebrate communities (Herbst 1992, 1999, 2006). Dietary flexibility allows shorebirds to exploit a large variety of invertebrates (Skagen and Oman 1996). Migrant shorebirds may also increase energy intake by foraging selectively on prey of certain sizes because small-bodied shorebirds are more efficient foragers when taking small prey, whereas large-bodied birds likely gain more energy per unit time when taking larger prey (Lifjeld 1984). However, the average invertebrate weighs less, and total biomass is less, in saline lakes than in the surrounding freshwater playas (Davis and Smith 1998; Andrei *et al.* 2008). Thus, prey size selectivity may not be energetically feasible for large bodied shorebirds because of the increased time and energy needed for locating the potentially scarce large prey. Herein, the term "opportunistic" refers to shorebirds consuming prey taxa in proportion to availability. The term "prey size selectivity" refers to shorebirds consuming prey of certain sizes in greater or lesser proportion than available.

As populations of shorebirds decline throughout the Western Hemisphere (Brown *et al.* 2001; Fellows *et al.* 2001; International Wader Study Group 2003), information about foraging strategies of shorebirds migrating through the SGP will help conservationists understand how reduced availability of prey caused by declining water tables and salinization will affect migrant shorebirds. In this paper, we assess foraging strategies employed by migrant shorebirds using saline lakes of the SGP as stopovers. Our objectives were to examine overall diets, prey type selection, and prey size selection by American Avocets (*Recurvirostra americana*), Least Sandpipers (*Calidris minutilla*), Wilson's Phalarope (*Phalaropus tricolor*), and Lesser Yellowlegs (*Tringa flavipes*) during spring and summer/fall migration. We se-

lected these four species because they represent the wide range of body sizes and guilds of shorebirds migrating through the SGP (Skagen and Oman 1996; Andrei *et al.* 2006).

METHODS

Study Site

The study was conducted in saline lakes in Andrews, Bailey, Castro, Dawson, Gaines, Lamb, Lynn, Parmer, and Terry counties in northwest Texas (Fig. 1). Formed by wind erosion and dissolution of salts (Reeves and Reeves 1996) and ranging in size from approximately 4 ha (Frost Lake, 32°49'34.77" N and 102°00'42.77" W) to greater than 6000 ha (Cedar Lake, 32°49'06.64" N and 102°16'21.89" W), the approximately 45 saline lakes are sparsely vegetated (≤1%) (Andrei *et al.* 2008). When present, vegetation of the shallow (0-100 cm) saline lakes consisted of species such as saltgrass (*Distichlis spicata*), pickleweed (*Salicornia* spp.), bulrush (*Scirpus* spp.), and saltcedar (*Tamarix* spp.) (Andrei *et al.* 2006). Hydroperiods of saline lakes depend on precipitation and springs fed by the Ogallala aquifer (Brüne 1981). Preceding and during data collection, precipitation recorded in Lubbock, Texas, was below the 48-cm annual average (2001: 32.9 cm; 2002: 47.6 cm; 2003: 20.9 cm) (NOAA 2004).
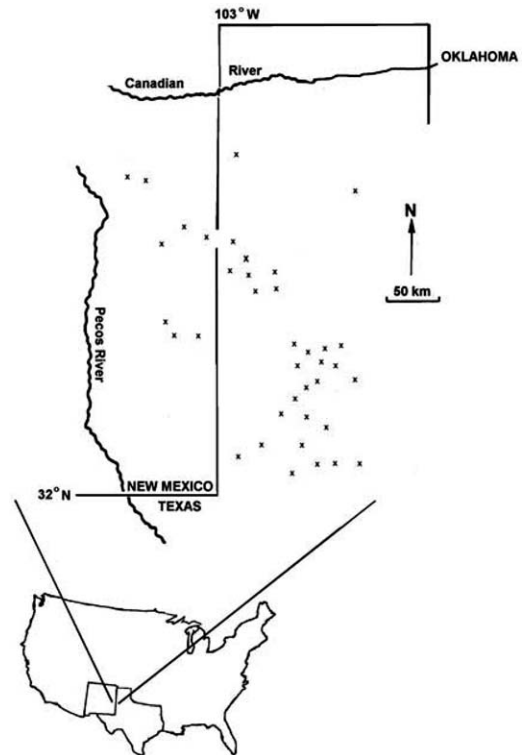

Figure 1. Saline lakes in the Southern Great Plains of Texas and New Mexico, after Reeves, Jr. and Reeves (1996).

Field and Laboratory Methods

The study was conducted in all saline lakes for which access was permitted by landowners. One hundred American Avocets from eleven lakes, 100 Least Sandpipers from eleven lakes, 100 Wilson's Phalaropes from nine lakes, and 25 Lesser Yellowlegs from four lakes were collected by shooting during spring (10 Mar-15 Jun 2002 and 2 Mar-7 Jun 2003) and summer/fall (7 Jul- 9 Nov 2002 and 7 Jul-8 Nov 2003) migrations. Overall, shorebirds were collected from twelve lakes, according to United States Fish and Wildlife Service (MB 053072), Texas Parks and Wildlife Department, and Texas Tech University permits (ACUC 011157-09). Prior to collection, shorebirds were observed feeding for at least 15 minutes to ensure that esophagi contained food items (Davis and Smith 1998). Shorebird esophagi were removed immediately after collection and preserved in 80% ethanol. Shorebirds were collected because prey (i.e., invertebrate larvae) could not be reliably identified from feces. Further, it would have been impossible to determine prey selection of random individual birds at the exact time and location of their foraging using mist nets and emetics. To determine invertebrate availability in benthos and the water column, five 5 x 10-cm benthic core samples (Swanson 1983) and five water column samples (up to 2000 ml in volume) (Swanson 1978) were collected immediately after collection of shorebirds. For sampling invertebrate availability at the same locations where shorebirds foraged, benthic core and water column samples were collected at equally spaced intervals on transects between the points where birds were first observed and the points where they were collected after 15 minutes of foraging, but not less than 5 m in length (i.e., if birds were stationary when foraging). Benthic core samples were taken from surface of substrate to a depth of 10 cm, whereas water column samples generally included the entire water column. In the few lakes deeper than 1 m, water column samples were taken from surface to a depth of 50 cm. Further, water column samples were taken from areas with water depths >3 cm because water depths ≤3 cm were too shallow for the water column sampler to effectively collect invertebrates. Where water depth was 3 cm or less we collected invertebrates, located in the water column and the substrate, with the benthic core sampler. Benthic core and water column samples were washed through a 0.5-mm sieve and invertebrates were removed and preserved in 80% ethanol. Invertebrates from esophageal, benthic core and water column samples were counted, identified to family (Peterson 1979a; Peterson 1979b; McAlpine et al. 1981; Pennak 1989; Merritt and Cummins 1996), classified to life stages, measured to the nearest mm in length, categorized in 1-mm increments between 1 and 19 mm and ≥20 mm, oven dried at 65 C to constant mass and weighed to nearest 0.001 g. Seeds from esophageal samples were identified by comparison to herbarium specimens at Texas Tech University.

Statistical Analyses

Diet compositions and availability samples for each shorebird species during each season of each year were summarized as average aggregate percent dry mass (i.e., proportion of each prey taxa in each sample averaged for all individuals; Prevett et al. 1979). For each species of shorebird and migration season, aggregate percent dry mass of each prey taxa in the paired esophageal and availability samples were used to determine selection for the most frequently encountered invertebrate taxa, such as: Artemiidae (brine shrimp), Ceratopogonidae (biting midges), Chironomidae (non-biting midges), Corixidae (water boatmen), Ephydridae (brine flies), Stratiomyiidae (soldier flies) and Tipulidae (crane flies). Combined, these seven invertebrate families represented >90% of the invertebrates in shorebird diets and availability samples (Andrei et al. 2008). Wilcoxon signed rank sum tests (Thomas and Taylor 2006) were used to examine prey type selection because data were not independent (i.e., aggregate percent consumption or availability of one prey depended on percent use or availability of other prey) and paired (i.e., esophageal and availability samples were collected at identical times and locations). The S statistic and its associated probability (Lehmann 1975; Conover 1980) were used to test hypotheses that the medians of the differences between percent use and percent availability were zero. Other selection analyses methods would have resulted in high Type I error rates or would have been inappropriate (Bingham and Brennan 2004; Alldredge and Griswold 2006; Thomas and Taylor 2006). We considered signed rank sum tests significant at $P \leq 0.10$.

Selection for each prey size category (i.e., in 1-mm increments between 1 and 19 mm and ≥20 mm) present in esophagi and samples collected from foraging areas was examined with χ^2 tests and Bonferonni Z-statistics (Neu et al. 1974). The Neu et al. (1974) method was used because it is robust to Type I error (Bingham and Brennan 2004). Because many prey size categories were absent or were not used by shorebirds, other selection analyses would have generated high error rates (Bingham and Brennan 2004; Alldredge and Griswold 2006; Thomas and Taylor 2006).

Prey size selection was examined for each shorebird species within each season of each year. Expected use of a prey size was based on percent availability in the benthic core and water column samples within all lakes during each migration season. Observed use of a prey size was based on the proportion of the prey size present in the esophageal samples collected from all individuals of a shorebird species during each migration season. Population level inferences were made by pooling data by species during each season of each year.

RESULTS

Diptera were the most consumed prey for American Avocets, Least Sandpipers, Wilson's Phalarope and Lesser Yellowlegs. Ceratopogonidae and Chironomidae were dominant (>25%) in the diet of American Avocets (Table 1); whereas, Ephydridae and Tipulidae dominated the diet of Least Sandpipers (Table 2). Ephydridae, Artemiidae, Corixidae, Ceratopogonidae, Tipulidae and Tabanidae were present in the diet of Wilson's Phalarope, but Chironomidae (17%-51%) were dominant (Table 3).

Table 1. Aggregate percent dry mass of prey in diets of 100 American Avocets and availability samples collected from eleven saline lakes in the Southern Great Plains of Texas during spring and summer/fall migrations of 2002 and 2003 and Wilcoxon signed rank sum tests[1] for prey selection. Prey with negative S values (P ≤ 0.10) (Lehmann 1975) were consumed in greater proportion than their availability at foraging locations, and vice versa.

2002	Spring				Summer/Fall			
	Avail.	Diet	S	P	Avail.	Diet	S	P
Artemiidae	0.00	0.00	—	—	0.00	0.00	—	—
Ceratopogonidae	7.94	44.23	27.0	0.175	6.34	6.62	-12.0	0.320
Chironomidae	4.40	19.17	-14.0	0.240	50.48	57.40	-10.0	0.469
Corixidae	0.70	0.00	0.5	1.000	1.94	6.14	-21.5	0.007
Ephydridae	5.16	11.00	1.5	0.843	8.87	24.98	1.5	0.843
Stratiomyidae	0.05	0.00	-0.5	1.000	0.00	0.00	—	—
Tipulidae	4.50	14.61	-2.5	0.927	0.00	0.45	-0.5	1.000
Tabanidae	0.00	0.00			0.00	0.00		
Seeds	—	0.05			—	0.05		
Miscellaneous[2]	0.00	0.00			0.00	0.00		
Artemiidae	2.69	0.00	14.0	0.016	4.55	4.00	0.5	1.000
Ceratopogonidae	29.10	28.06	26.0	0.019	14.44	23.55	7.0	0.382
Chironomidae	12.52	14.73	-2.0	0.500	25.40	27.56	-7.5	0.625
Corixidae	0.25	0.67	-0.5	1.00	0.12	0.03	3.0	0.250
Ephydridae	11.34	29.06	-22.5	0.003	19.51	12.67	1.0	0.875
Stratiomyidae	0.00	0.00	—	—	0.00	0.00	—	—
Tipulidae	11.97	19.82	-10.0	0.110	10.67	13.30	-5.5	0.313
Tabanidae	0.00	0.00			0.00	0.01		
Seeds	—	0.13			—	0.02		
Miscellaneous	0.00	0.03			0.00	0.06		

[1]We tested whether medians of the differences between percent use and percent availability were 0.
[2]Unidentified animal matter.

Lesser Yellowlegs diets consisted of Chironomidae, Ephydridae, and Corixidae (Table 4). In small proportion, seeds (*Scirpus* spp.) were consumed by American Avocets, Wilson's Phalarope and Lesser Yellowlegs.

There were notable seasonal and among-species differences of selection for prey type. For example, Tipulidae were 14.6% and 19.8% of the diets of American Avocets (Table 1) during spring 2002 and 2003, but only 0.45% and 13.3% during fall migrations. Chironomidae were found in greater proportion in summer/fall diets (57.4% and 27.5%) than in spring diets (19.1% and 14.7%). Similarly, Least Sandpipers (Table 2) did not consume Stratiomyiidae during spring, but did so during summer/fall (7.9% and 15.5% of diets). Chironomidae were present in significant proportions in the diets of American Avocets, Lesser Yellowlegs and Wilson's Phalarope, but not in the diets of Least Sandpipers, where dominant prey were Ephydridae and Tipulidae.

Prey Taxa Selection

With few exceptions, the four shorebird species did not exhibit dietary preferences and consumed prey according to availability. In spring 2002 American Avocets consumed prey according to availability. During summer/fall 2002, avocets consumed Corixidae in greater proportion than they were available. In spring 2003, avocets avoided Artemiidae and Ceratopogonidae, but preferred Ephydridae. During summer/fall 2003, avocets consumed all prey types according to availability (Table 1).

Least Sandpipers consumed all prey according to availability during spring migration. They avoided Ceratopogonidae and consumed Tipulidae in greater proportion than available during summer/fall migration (Table 2).

Wilson's Phalaropes consumed all prey according to availability during spring 2002. During summer/fall 2002, phalaropes consumed Ceratopogonidae and Tipulidae in

Table 2. Aggregate percent dry mass of prey in diets of 100 Least Sandpipers and availability samples collected from eleven saline lakes in the Southern Great Plains of Texas during spring and summer/fall migrations of 2002 and 2003 and Wilcoxon signed rank sum tests[1] for prey selection. Prey with negative S values ($P \le 0.10$) (Lehmann 1975) were consumed in greater proportion than their availability at foraging locations, and vice versa.

2002	Spring				Summer/Fall			
	Avail.	Diet	S	P	Avail.	Diet	S	P
Artemiidae	0.00	0.00	—	—	0.00	0.00	—	—
Ceratopogonidae	6.97	13.00	9.0	0.464	35.35	24.33	0.5	1.000
Chironomidae	0.00	0.00	—	—	3.20	4.18	-0.5	1.000
Corixidae	0.00	0.00	—	—	0.29	1.60	-0.5	1.000
Ephydridae	25.29	57.36	-7.5	0.669	3.09	12.53	-9.0	0.518
Stratiomyidae	0.00	0.00	—	—	6.29	7.97	-0.5	1.000
Tipulidae	18.32	29.64	1.5	0.921	34.65	46.84	-38.5	0.010
Carabidae	0.00	0.00			0.00	0.10		
Miscellaneous[2]	0.00	0.00			0.00	0.00		
Artemiidae	0.03	0.00	0.5	1.000	0.24	0.86	0.5	1.000
Ceratopogonidae	22.71	36.04	3.5	0.769	29.37	24.13	13	0.002
Chironomidae	0.00	0.00	—	—	0.00	1.69	-0.5	1.000
Corixidae	0.00	0.00	—	—	0.00	0.00	—	—
Ephydridae	8.11	13.33	10.5	0.250	9.06	8.81	5.5	0.625
Stratiomyidae	0.00	0.00	—	—	14.03	15.55	-3.0	0.375
Tipulidae	16.22	30.51	-3.5	0.734	35.07	42.86	-28	0.026
Carabidae	0.00	0.00			0.00	0.00		
Miscellaneous	0.00	1.11			0.00	0.07		

[1]We tested whether medians of the differences between percent use and percent availability were 0.
[2]Unidentified animal matter.

lesser proportion and Ephydridae in greater proportion, than they were available. In spring 2003, phalaropes avoided Ephydridae and consumed Artemiidae in greater proportion than they were available. In summer/fall 2003, phalaropes consumed Artemiidae in greater proportion than they were available (Table 3). Lesser Yellowlegs consumed all invertebrate prey families according to availability (Table 4).

Prey Size Selection

Proportions of consumed prey sizes and available prey sizes differed for all shorebird species during both migration periods of both years (all P's for χ^2 tests <0.001). During spring 2002, American Avocets consumed prey 1-3 mm and 9-17 mm long less than expected and preferred 4-6-mm prey (Fig. 2). During summer/fall 2002, avocets preferred 10-17-mm prey, and avoided smaller prey. During spring 2003, prey 8-14 mm in length were consumed more than expected, whereas, smaller prey items were used less than ex-

pected. During summer/fall 2003, 9-20-mm prey was preferred and smaller prey items were avoided (Fig. 2).

Least Sandpipers generally consumed small prey (1-5 mm) more than expected based on availability samples, and avoided prey longer than 5 mm (Fig. 3). Lesser Yellowlegs generally selected 7-19-mm prey and avoided smaller prey, but during summer/fall 2002 they also consumed seeds and selected small prey (Fig. 4). Wilson's Phalaropes selected 8-15-mm prey and generally avoided smaller prey. During summer/fall 2003, phalaropes consumed 1-mm prey (brine shrimp eggs) in greater proportion than expected based on the availability samples (Fig. 5).

DISCUSSION

Invertebrate prey of shorebirds using saline lakes of the SGP during spring and summer/fall migration consisted primarily of Diptera (midges, biting midges, and crane flies) larvae, but other prey, such as brine

Table 3. Aggregate percent dry mass of prey in diets of 100 Wilson's Phalarope and availability samples collected from nine saline lakes in the Southern Great Plains of Texas during spring and summer/fall migrations of 2002 and 2003 and Wilcoxon signed rank sum tests[1] for prey selection. Prey with negative S values ($P \le 0.10$) (Lehmann 1975) were consumed in greater proportion than their availability at foraging locations, and vice versa.

2002	Spring				Summer/Fall			
	Avail.	Diet	S	P	Avail.	Diet	S	P
Artemiidae	0.00	0.00	—	—	0.00	0.00	—	—
Ceratopogonidae	10.41	31.33	-5.0	0.733	8.95	0.15	33.0	0.001
Chironomidae	48.60	50.99	17.5	0.468	31.77	35.54	-6.0	0.460
Corixidae	5.10	4.00	0.5	1.000	12.66	12.71	-4.5	0.652
Ephydridae	4.71	4.56	1.0	0.945	23.99	39.96	-29.0	0.021
Stratiomyidae	0.00	0.00	—	—	0.00	0.00	—	—
Tipulidae	4.20	7.97	-0.5	1.00	1.57	0.00	7.5	0.06
Tabanidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seeds	—	0.00			—	0.56		
Miscellaneous[2]	0.00	0.00			0.00	0.00		
Artemiidae	8.26	17.82	-13.0	0.07	6.23	21.34	-10.5	0.031
Ceratopogonidae	3.47	7.72	6.0	0.375	13.57	18.63	2.0	0.812
Chironomidae	34.00	39.80	11.50	0.501	17.35	17.14	0.00	1.000
Corixidae	11.43	15.59	-10.0	0.195	0.55	1.08	-0.5	1.000
Ephydridae	12.14	7.81	13	0.078	28.12	21.65	11.5	0.275
Stratiomyidae	0.00	0.00	—	—	0.00	0.00	—	—
Tipulidae	0.01	0.00	0.5	1.000	7.27	10.73	1.5	0.500
Tabanidae	0.00	0.00			0.00	0.00		
Seeds	—	0.31			—	0.18		
Miscellaneous	0.00	0.03			0.00	0.15		

[1]We tested whether medians of the differences between percent use and percent availability were 0.
[2]Unidentified animal matter.

shrimp, water boatmen, and small beetles also were consumed. These diets differ from those reported for shorebirds using the playas of the SGP (Davis and Smith 1998), probably because of the different hydrologies and salinities of the two wetland types. Unlike shorebirds foraging in playas, birds using the saline lakes did not consume segmented worms (Hirudinea), or roundworms (Oligochaeta), because they were not present (Andrei *et al.* 2008). As in other saline lakes in the western USA (Colwell and Jehl 1994), brine shrimp and brine flies were important prey for Least Sandpipers and Wilson's Phalarope. Seasonal differences in diets were possibly due to different availabilities of invertebrate prey, caused by drought and variable hydrologies and salinities in the saline lakes (Andrei *et al.* 2008). Unlike the other three species, Least Sandpipers consumed small proportions of Chironomidae likely because they could not forage in deeper water or at greater depth, where these prey are usually found (Andrei, unpubl. data).

In general, the four species of shorebirds consumed invertebrate foods according to availability and did not exhibit preferences among prey types, suggesting an opportunistic foraging strategy. This supports the hypothesis of opportunistic feeding by migrant shorebirds in the interior of North America (Skagen and Knopf 1994; Davis and Smith 2001). Opportunistic feeding may be advantageous to migrant shorebirds because of dynamic and unpredictable wetlands in the SGP (Smith 2003). Because spring flows have diminished due to lowering of the water table, precipitation has become the sole source of water for an increasing number of lakes. Precipitation and availability of wetlands influence the ability of shorebirds to replenish fat stores while migrating through the Great Plains. In dry years, sandpipers migrating through the Great Plains have 7-9% lower fat reserves than in wet years (Davis *et al.* 2005). Opportunistic foraging may be especially important strategy during dry years. By taking whatever prey are available, mi-

Table 4. Aggregate percent dry mass of prey in diets of 25 Lesser Yellowlegs and availability samples collected from four saline lakes in the Southern Great Plains of Texas during spring and summer/fall migrations of 2002 and 2003 and Wilcoxon signed rank sum tests[1] for prey selection. Prey with negative S values ($P \leq 0.10$) (Lehmann 1975) were consumed in greater proportion than their availability at foraging locations, and vice versa.

	Spring				Summer/Fall			
2002	Avail.	Diet	S	P	Avail.	Diet	S	P
Ceratopogonidae	14.48	25.00	5	0.250	0.20	0.00	0.5	1.00
Chironomidae	37.29	50.00	-5.5	0.187	74.79	87.66	-3	0.250
Corixidae	0.00	0.00	—	—	3.93	10.00	0.5	1.00
Ephydridae	19.77	25.00	0.5	1	1.000			
Tipulidae	0.00	0.00	—		0.00	0.00	—	—
Seeds	—	0.00			—	0.16		
2003[2]								
Ceratopogonidae	—	—	—	—	0.22	2.05	-1.5	0.500
Chironomidae	—	—	—	—	67.44	68.54	4	0.250
Corixidae	—	—	—	—	0.75	16.50	-1.5	0.500
Tipulidae	—	—	—	—	1.55	0.00	1.5	0.500
Ephydridae	—	—	—	—	7.05	11.67	-0.5	1.000
Seeds	—	—	—	—	—	0.05		

[1]We tested whether medians of the differences between percent use and percent availability were 0.
[2]Lesser yellowlegs were not collected during spring 2003.

grant shorebirds are likely to deposit sufficient fat reserves to enable them to survive and continue their migrations.

Our tests suggest that shorebirds selected a few prey taxa in proportions greater or lesser than the proportional availability of these prey. For example, Least Sandpipers consumed biting midges proportionately less and crane flies more than were available. Wilson's Phalaropes consumed brine shrimp more and biting midges less than their proportional availability. It is possible that some of the prey could not be reached or captured by some shorebirds. Because we sampled all invertebrates equally for all shorebird species, and we considered prey as being available if they were present, we likely defined availability differently than do shorebirds themselves. From a shorebird perspective, only a fraction of prey is harvestable, and prey harvestable by one shorebird species may not be harvestable by another (Piersma *et al.* 1993; Zwarts and Wanink 1993; Kober and Bairlein 2006). While we collected all benthic core samples to a depth of 10 cm, Least Sandpipers are not able to forage at such depth, nor could American Avocets when the substrate was dense and could not be penetrated by the sweeping motions of

their bills. Some invertebrates, while present, may have been too large, small, deep, or mobile to be accessible to some shorebirds. While our study offers sufficient evidence of opportunistic foraging, it is possible that the few discrepancies between proportions of used and available prey were due to our interpretation of prey availability.

The four representative species of shorebirds selected prey of specific sizes. Least Sandpipers selected small prey, whereas American Avocets, Wilson's Phalaropes and Lesser Yellowlegs selected intermediate and large prey. Profitability of arthropod prey is a trade-off between time and energy necessary for extracting and ingesting and the resulting energy gain (Zwarts and Blomert 1992). The four species in our study likely foraged in habitat patches within saline lakes that had high prey densities (Andrei *et al.* 2008), offering high energy intakes per unit of time (van Gils *et al.* 2003), rather than selecting each individual prey item. When foraging gains decreased, shorebirds likely moved elsewhere (Goss-Custard 1977; van Gils *et al.* 2003). By foraging on whatever prey is available and in patches where prey requires minimum energy expenditure for searching, handling and ingestion, migrant shorebirds
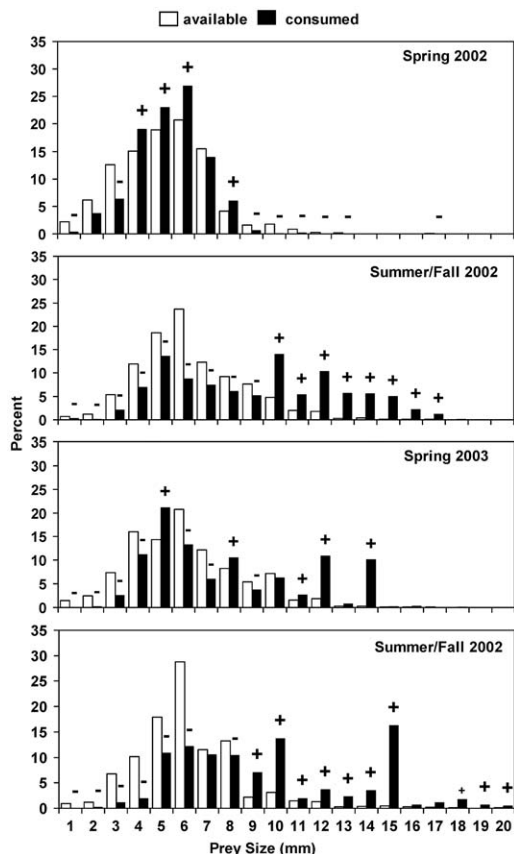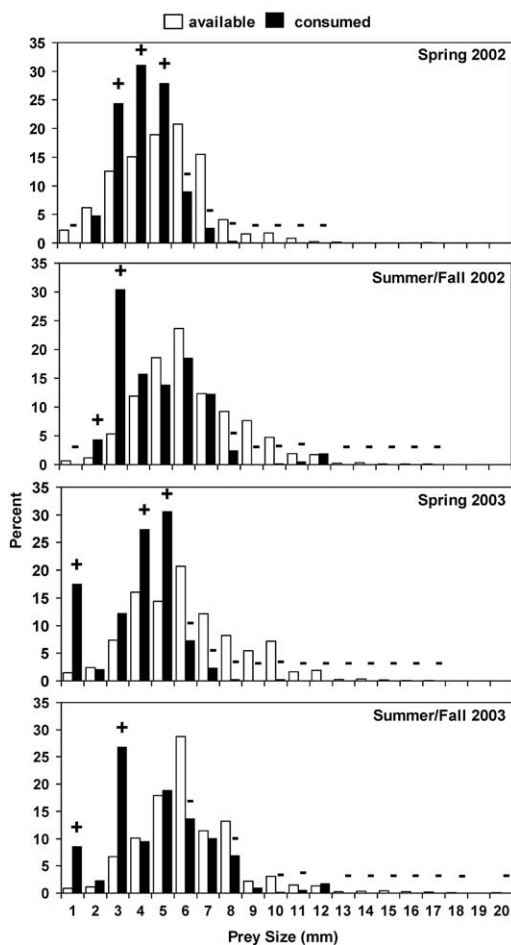
Figure 2. Prey size selection by American Avocets in saline lakes of the Southern Great Plains, USA, during spring 2002 (N = 25), summer/fall 2002 (N = 25), spring 2003 (N = 25), and summer/fall 2003 (N = 25) migrations. Preference (+) or avoidance (-) of prey size categories was determined (*P* < 0.05) with Bonferonni Z-statistics (Neu *et al.* 1974).

Figure 3. Prey size selection by Least Sandpipers in saline lakes of the Southern Great Plains, USA, during spring 2002 (N = 25), summer/fall 2002 (N = 25), spring 2003 (N = 25), and summer/fall 2003 (N = 25) migrations. Preference (+) or avoidance (-) of prey size categories was determined (*P* < 0.05) with Bonferonni Z-statistics (Neu *et al.* 1974).

using saline lakes in the SGP increase their chances of replenishing energy reserves and completing their migrations in good physical condition. Correlations between shorebird densities and prey densities have been reported (Colwell and Landrum 1992). Other studies (Davis and Smith 2001; Kober and Bairlein 2006; Zwarts and Blomert 1992) also suggest that shorebirds do not select prey based on their nutritional and energy content, but forage on prey that is most abundant. Commonly available and abundant prey require the least energy expenditure to find and offer shorebirds the highest probability of replenishing fat stores.

At least two thirds of the prey of all four shorebird species consisted of invertebrates found at low to moderate salinity (<40 g/L) (Andrei *et al.* 2008). Because arthropod biomass decreases exponentially when salinity increases above 40 g/L (Andrei *et al.* 2008), salinization due to decreased spring flow into saline lakes will have a negative effect on shorebirds and their ability to replenish energy reserves. While opportunistic foraging may enable shorebirds to switch to different prey when invertebrate communities are altered by increased salinity, shorebirds may
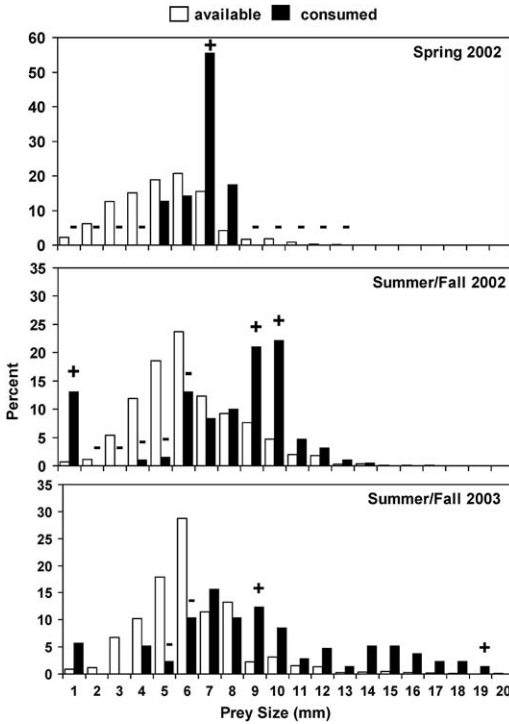
Figure 4. Prey size selection by Lesser Yellowlegs in saline lakes of the Southern Great Plains, USA, during spring 2002 (N = 8), summer/fall 2002 (N = 9), and summer/fall 2003 (N = 8) migrations. Preference (+) or avoidance (-) of prey size categories was determined ($P < 0.05$) with Bonferonni Z-statistics (Neu *et al.* 1974).
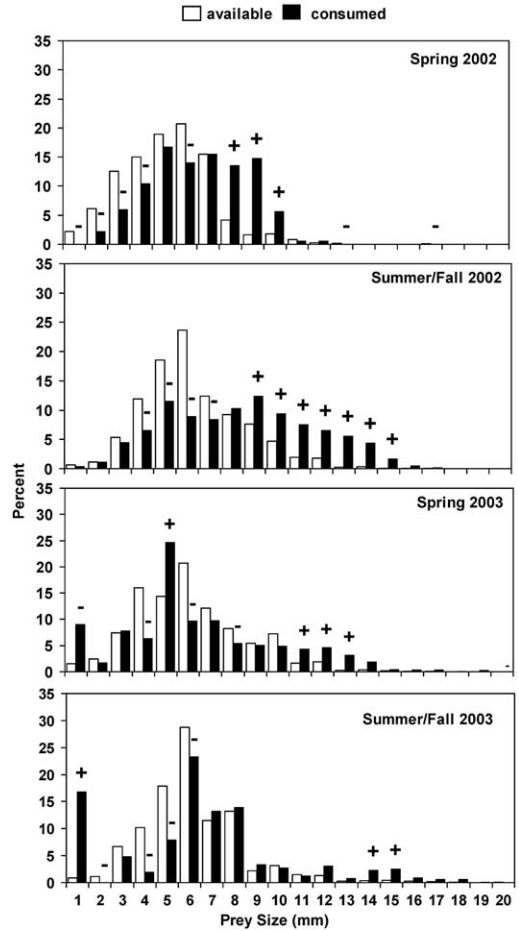

Figure 5. Prey size selection by Wilson's Phalaropes in saline lakes of the Southern Great Plains, USA, during spring 2002 (N = 25), summer/fall 2002 (N = 25), spring 2003 (N = 25), and summer/fall 2003 (N = 25) migrations. Preference (+) or avoidance (-) of prey size categories was determined ($P < 0.05$) with Bonferonni Z-statistics (Neu *et al.* 1974).

not be able to find enough prey to replenish lipid stores. This may have hemispheric ramifications. If unable to replenish energy stores while migrating through the Great Plains, shorebird populations may be negatively affected. In saline lakes, the existence of seed-producing vegetation also is associated with active freshwater springs (Andrei *et al.* 2008). If drying of springs due to decreasing levels of the Ogallala aquifer continues, the ensuing increase in salinity may eliminate herbaceous vegetation and seeds as a possible source of energy for migrating shorebirds. Alternatively, seeds may have been ingested inadvertently. Because we sampled seed consumption by shorebirds, but not seed availability, we are not able to assess whether seeds were selected or avoided.

Declining water tables, reduced freshwater spring flow and increased salinity could reduce the importance of saline lakes in the

SGP as migration stopovers because the foraging strategies used by shorebirds may become ineffective due to reduced availability of invertebrates. For most saline lakes, water management and moist-soil management are not possible. Managers and conservationists should focus on preserving water and low salinities. Thus, it is important to conserve the Ogallala aquifer and the freshwater springs discharging into saline lakes, especially during dry years. Because the Ogallala aquifer is recharged through playa wetlands (Osterkamp and Wood 1987; Nativ 1992; Smith 2003), the entire complex of

wetlands in the SGP should be protected by reducing groundwater withdrawals (Triplet 1998; Sophocleous 2000) and by preventing sedimentation in playas, which may influence recharge (Luo *et al.* 1997).

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