FOOD HABITS OF FALL MIGRANT SHOREBIRDS
ON THE TEXAS HIGH PLAINS

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Abundance and availability of food appear the major natural factors limiting population size of most birds (Lack 1954). However, the impact of dynamics in food resources on bird populations cannot be ascertained fully until the food habits of each species are studied throughout the annual cycle. Such information does not exist for shorebirds although this group of birds has been investigated intensively.

Previous works have demonstrated that at least some shorebird species spend a substantial portion of their annual cycle on migration (Holmes and Pitelka 1968, Baker and Baker 1973). However, most food habits studies have concentrated on breeding areas (Holmes 1966, Holmes and Pitelka 1968, Baker 1977), winter quarters, and/or marine environments (Reeder 1951, Bengston and Svensson 1968, Baker and Baker 1973, Goss-Custard and Jones 1976, Pitelka 1979, Duffy et al. 1981). Baker and Baker (1973) noted that evaluation of competition for resources among populations of breeding birds can be misleading. Published food habits studies of migrant shorebirds using freshwater habitats are sparse. Brooks (1967) reported data from 9 species using a small midwestern pond, but sample sizes were less than 5 for most species. Rundle (1982) recently presented data on shorebirds using freshwater impoundments in Missouri, but he collected only 4 species.

These data are particularly important because outside the breeding period food shortages may be an important density-dependent cause of mortality in birds (Lack 1954). Baker and Baker (1973) speculated that winter was the period of lowest resource availability and thus the most probable time that density-dependent mortality acted to limit populations of shorebirds (but see Duffy et al. 1981). Goss-Custard (1969) showed that a fall decline in the numbers of Redshank (*Tringa totanus*) was followed by fairly stable numbers during winter, therefore migration could have been the critical period for population regulation. Schneider and Harrington (1981) concluded that availability of food resources was an important factor shaping migratory patterns of shorebirds. Regardless, competition seems more intense on nonbreeding areas. This study was designed to determine diets and dietary differences among shorebirds using inland freshwater habitats (playa lakes) on the Texas High Plains as a means of assessing the hypothesis that competition among shorebirds occurs on migration areas.

STUDY AREA

The Texas High Plains contains 20,000–30,000 playa lakes that can provide migrating shorebirds nearly 138,000 ha of freshwater habitat (Huddleston and Ward 1969). Playa lakes are ephemeral, closed basins

TABLE 1. The mean (±SE) number and volume of chironomid larvae collected from shorebird feeding zones within the study playa on the Texas High Plains, September 1980.

	Number (per m²)	Volume (ml/m²)
Zone 2 (n = 24)	6730 ± 996[a]	5.33 ± 0.83[b]
Zone 3 (n = 24)	5622 ± 907[a]	5.84 ± 0.10[b]
Total (n = 48)	6175 ± 671	5.59 ± 0.64

[a,b] Means within a column denoted by the same letter are not significantly different ($P > 0.05$).

that fill during the rainy seasons of May–June and September–October. Playa lake hydrology is described by Hauser (1966), Reeves (1974), and others. Vegetation and geology of playas are discussed by Rowell (1971) and Reeves (1966), respectively.

A 10.5 ha playa lake immediately northeast of Hart, Castro County, Texas, was chosen as a study site representative of playa lakes receiving intensive use by foraging shorebirds. This playa contained a periphery of moist soil vegetation dominated by smartweed (*Polygonum* spp.), millet (*Echinochloa crusgalli*), and dock (*Rumex* spp.), with pigweed (*Amaranthus* spp.) on drier, disturbed sites. Emergent and submergent vegetation were absent. Mudflats and decaying vegetation were classified into 3 zones: (1) upland-moist shoreline with no standing water, (2) moist shoreline and interspersed water up to 4 cm depth, and (3) 4–16 cm water-depth.

METHODS

Migrant shorebirds were collected from 7–21 September, 1980, choosing only individuals foraging for at least 10 min. Their digestive tracts were injected with 10% formalin to retard post-mortem digestion; each bird was then frozen until analysis. The esophagus, together with proventriculus and buccal cavity (Rundle 1982), was excised in the laboratory and the volume of identifiable food items determined using a syringe measuring device (Myers and Peterka 1974). Gizzards were not analyzed because they can substantially bias food habits studies (Swanson and Bartonek 1970, Rundle 1982). These data were expressed using the aggregate (average) percentage and percentage frequency methods defined by Swanson et al. (1974).

Percentage data are not normally distributed (Zar 1974), therefore differences among species in the aggregate percentage of each food item were compared using the Kruskal-Wallis test and appropriate mean separation procedures (Conover 1980). Dietary overlap among species was determined using an index developed by Schoener (1968). Sample sizes were not adequate for interpretable analysis of frequency data using Chi-square methods.

The percentage of time each species spent foraging among the 3

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TABLE 2. Diets of shorebirds collected from the study playa on the Texas High Plains. Data are expressed as aggregate percentage and % frequency of occurrence (number in parentheses) of food item groups.[a]

Items	Least Sandpiper n = 8		Western Sandpiper n = 11		Baird's Sandpiper n = 9		Long-billed Dowitcher n = 14		Stilt Sandpiper n = 8		Lesser Yellowlegs n = 10		American Avocet n = 8		Wilson's Phalarope n = 12		Killdeer n = 7	
Chironomidae	44[b]	(75)	67[a]	(100)	0[c]	(0)	77[a]	(100)	48[b]	(75)	0[c]	(0)	70[a]	(100)	0[c]	(0)	0[c]	(0)
Adult Coleoptera	13[ab]	(38)	13[a]	(73)	19[ab]	(67)	1[b]	(36)	15[ab]	(75)	14[a]	(80)	10[ab]	(25)	9[ab]	(33)	16[ab]	(71)
Larval Coleoptera	10[a]	(38)	0[b]	(0)	0[b]	(0)	0[b]	(0)	0[b]	(33)	0[b]	(0)	0[b]	(0)	0[b]	(0)	10[a]	(29)
Adult Diptera	11[b]	(13)	2[b]	(9)	0[c]	(0)	0[c]	(0)	0[c]	(0)	10[b]	(20)	0[c]	(13)	71[a]	(83)	0[b]	(14)
Other larval Diptera	0[c]	(0)	0[c]	(0)	26[b]	(44)	0[c]	(0)	0[c]	(0)	0[c]	(0)	0[c]	(0)	6[c]	(8)	58[a]	(71)
Corixidae	4[bc]	(13)	0[c]	(0)	0[c]	(0)	0[c]	(0)	0[c]	(0)	52[a]	(80)	0[c]	(13)	9[b]	(33)	0[c]	(0)
Larval Lepidoptera	0[c]	(0)	0[c]	(0)	54[a]	(67)	0[c]	(0)	0[c]	(0)	15[b]	(30)	0[c]	(0)	0[c]	(0)	11[bc]	(29)
Seeds	19[bc]	(38)	18[ab]	(64)	0[c]	(0)	18[a]	(79)	37[a]	(100)	1[c]	(10)	19[a]	(100)	2[c]	(17)	0[c]	(17)
Miscellaneous	0[b]	(0)	0[b]	(0)	2[ab]	(11)	5[ab]	(21)	0[b]	(0)	9[a]	(50)	2[ab]	(25)	3[ab]	(8)	5[ab]	(29)

[a,b,c] Aggregate percentages across each row that are denoted by the same letter are not significantly different ($P \leq 0.05$ except for Chironomidae where $P \leq 0.10$).

[d] Seeds were *Polygonum* spp, *Scirpus* sp., and 3 unidentified species.

TABLE 3.   Indices of dietary overlap among shorebird species collected from the study playa on the Texas High Plains. Data are expressed using aggregate percentage.[a]

	Least Sand-piper n = 8	West-ern Sand-piper n = 11	Baird's Sand-piper n = 9	Long-billed Dow-itch-er n = 14	Stilt Sand-piper n = 8	Lesser Yel-low-legs n = 10	Ameri-can Avocet n = 8	Wil-son's Phala-rope n = 12	Kill-deer n = 7
Least Sandpiper	100	71	12	51	72	32	55	24	24
Western Sandpiper		100	13	84	73	16	85	12	14
Baird's Sandpiper			100	1	14	28	10	14	54
Long-billed Dowitcher				100	59	2	81	2	2
Stilt Sandpiper					100	14	60	11	16
Lesser Yellowlegs						100	11	28	31
American Avocet							100	11	12
Wilson's Phalarope								100	16
Killdeer									100

[a] Index of Overlap, $D = 1 - \frac{1}{2} \Sigma |X_{i,l} - Y_{i,l}|$ where D = index of overlap and $X_{i,l}$ and $Y_{i,l}$ are the aggregate percentage of the ith food item for species X and Y (Schoener 1968).

mudflat zones was recorded by randomly choosing 12 h for observation between sunrise and sunset of the 7–21 September period. All shore-birds using the mudflat were counted at 1-min intervals in the zone they were located. The number of each species counted in each zone was divided by the total counted for that species to determine percent use per zone.

Benthic invertebrates were sampled randomly on 10 September from zones 2 and 3 using a 15.2 cm² Ekman grab (24 samples/zone). Each sample was washed through a U.S. No. 30 soil sieve and preserved with 10% formalin. Taxa were identified, counted, and measured volumet-rically (Myers and Peterka 1974). Differences between zones in the mean number and volume of invertebrates were compared using a *t*-test.

RESULTS

Chironomid (midge) larvae were the only invertebrates found in the benthic samples, excepting 1–2 oligochaetes in 6 of the 48 samples. The number and volume of chironomids did not differ ($P > .05$) between zones (Table 1).

Chironomid larvae were the major dietary component (44–77%) of the Least Sandpiper (*Calidris minutilla*), Western Sandpiper (*Calidris mauri*), Stilt Sandpiper (*Calidris himantopus*), Long-billed Dowitcher (*Limnodromus scolopaceus*), and American Avocet (*Recurvirostra americana*), but were not used by the Baird's Sandpiper (*Calidris bairdii*), Lesser Yellowlegs (*Tringa flavipes*), Wilson's Phalarope (*Phalaropus tricolor*), or Killdeer (*Charadrius vociferus*) (Table 2). The aggregate percentage of chironomids taken by shorebirds formed 3 different ($P < .10$) groups

TABLE 4.   Mean size of intact prey items removed from the esophagus of shorebirds collected on the Texas High Plains.

Species	Number of birds sampled	Number of items measured	Mean (±SE) item size (mm)
Least Sandpiper	2	140	4.81 ± 0.46
Western Sandpiper	4	101	5.89 ± 0.15
Baird's Sandpiper	5	145	8.67 ± 0.64
Wilson's Phalarope	2	46	7.15 ± 0.20
Lesser Yellowlegs	3	26	16.30 ± 2.03
Killdeer	5	341	8.15 ± 0.18
Stilt Sandpiper	3	80	7.18 ± 0.19
Long-billed Dowitcher	9	345	8.08 ± 0.15
American Avocet	4	199	8.62 ± 0.43

of the Western Sandpiper, Long-billed Dowitcher, and American Avocet, compared to the Least Sandpiper and Stilt Sandpiper, compared to the remaining 4 species (Table 2).

Of the species not feeding on chironomids, Wilson's Phalaropes fed on more ($P < .05$) adult Diptera than did the other shorebird species. Killdeer fed on more ($P < .05$) larval Diptera than the Baird's Sandpiper (58% versus 26%), while Lesser Yellowlegs fed on the most corixids ($P < .05$).

Seeds were an important dietary item of 5 species, comprising 18–37% volume and occurring in 38–100% of the individuals (Table 2). Seeds were not eaten by the Baird's Sandpiper, and rarely used by the Wilson's Phalarope, Lesser Yellowlegs, or Killdeer. Seeds occurred at a 100% frequency in only the Stilt Sandpiper and American Avocet.

The Killdeer and Baird's Sandpiper had a 54% dietary overlap, but a 31% or less overlap with other species (Table 3). Species foraging largely on chironomids had a 51–85% overlap, while species not foraging on chironomids, exclusive of the Killdeer compared to the Baird's Sandpiper, had only a 14–31% overlap with other species. The greatest dietary overlap (85%) occurred between the American Avocet and Western Sandpiper, while the least overlap (1%) was between the Baird's Sandpiper and Long-billed Dowitcher. The larger shorebirds tended to select larger prey items (Table 4). Exceptions were the Baird's Sandpiper and to some extent the Wilson's Phalarope.

Only Killdeer foraged in zone 1 (Table 5). The Baird's Sandpiper, which foraged largely on terrestrial items, probably spent time in zone 1, but was possibly overlooked because of its small size and inconspicuous behavior. Of the larger shorebirds, only the Lesser Yellowlegs and American Avocet foraged exclusively in zone 3. Western and Least sandpipers foraged in zone 2, while the Long-billed Dowitcher, Stilt Sandpiper, and Wilson's Phalarope foraged in zones 2 and 3.

TABLE 5.   Percentage of time spent by shorebirds foraging on the 3 mudflat zones of the study playa on the Texas High Plains.[a]

Species	Number of birds observed[b]	Time spent in each zone—%		
		Zone 1	Zone 2	Zone 3
Killdeer	70	67.4	32.6	0
Baird's Sandpiper	20	0	100.0	0
Lesser Yellowlegs	30	0	0	100.0
Western Sandpiper	100	0	100.0	0
Least Sandpiper	200	0	100.0	0
Long-billed Dowitcher	250	0	12.2	87.8
Stilt Sandpiper	110	0	21.4	78.6
Wilson's Phalarope	250	0	26.2	73.8
American Avocet	200	0	0	100.0

[a] Percentages are based on 12 h observation of the mudflat zones (see text).
[b] Values <100 are ±5 and ±10 if >100.

DISCUSSION

Lack (1945) concluded that closely related species of birds would differ in one or more of their diet, habitat, or region requirements. Recher (1966) noted that morphologically similar species of shorebirds tended to frequent different habitats, migrated along different routes, or migrated at different times. Species collected during this study appeared to avoid competition by differing diets, foraging in different microhabitats, or using different foraging behaviors.

The Baird's Sandpiper segregated from other *Calidris* by not feeding on chironomids and from other species by probably spending more time in zone 1 where more terrestrial items prevailed. The larger prey size selected by the Baird's Sandpiper may not be an important factor reducing competition because relationships between bill size and prey size are generally not correlated among coexisting guild members (Wiens and Rottenberry 1980) although these variables were correlated for several shorebird species breeding on arctic tundra (Holmes and Pitelka 1968). The Killdeer was the nearest competitor to the Baird's Sandpiper, but foraged more on larval Diptera and less on larval Lepidoptera. Rundle (1982) noted somewhat similar food habits for 15 Killdeer collected in Missouri from July–November.

However, Rundle (1982) reported that plant foods were not important items in shorebird diets. Holmes and Pitelka (1968) also did not report seeds as food items of shorebirds breeding on arctic tundra, although Baker (1977) recorded some use of seeds by breeding shorebirds. Brooks (1967) recorded some seed use by migrant shorebirds, but they comprised 5% or less of the diet in all but 2 species. Perhaps the birds collected in this study used more seeds because (a) lipid reserves would be more depleted as migration progressed south and (b) seeds, because

of their high carbohydrate content, would replenish reserves faster than
invertebrates.

The larger species foraging on chironomids (Long-billed Dowitcher,
Stilt Sandpiper, American Avocet) had a high dietary overlap (51–85%)
with the Least Sandpiper and Western Sandpiper, but may avoid com-
petition because the latter 2 species foraged exclusively in zone 2 while
the larger species spent no more than 21% foraging time in this zone.
However, because the Least and Western sandpipers exhibited high
dietary overlap, were morphologically similar, occurred together at this
migration stop, and used the same mudflat zone, there may be evidence
for competition. Recher and Recher (1969) noted that aggression during
migration was common among foraging conspecifics and recorded 31
interactions of the Western Sandpiper attacking the Least Sandpiper.
They discussed habitat segregation between the Least and Semipalmated
(*Calidris pusillus*) sandpipers on the east coast, with the former preferring
freshwater marshes and the latter tidal mudflats. Ashmole (1970) re-
ported that the Least Sandpiper was rarely seen on the same winter
areas as the Western or Semipalmated sandpiper, but rather occurred
in fresh or brackish marshes and not tidal mudflats. Such segregation
obviously is not possible on playa lakes. Thus, although natural selection
pays a high premium for development of strategies that reduce com-
petitive severity (Mayr 1963), competition between these species ap-
peared to be quite visible at this migration site. No Semipalmated Sand-
pipers were collected during this study, but they did migrate through
the area several weeks before.

The remaining species appeared to segregate from each other. The
Wilson's Phalarope differed from all other species by foraging on adult
dipterans at the water surface. Wetmore (1925) reported that flies com-
prised 43% of the food in 106 stomachs of Wilson's Phalaropes. The
Lesser Yellowlegs did not have a high dietary overlap with other species
(>32%), foraging heavily on corixid adults as also shown by Bent (1927)
and Brooks (1967). However, Brooks (1967) noted that chironomids
occurred in 100% of the Lesser Yellowlegs collected in September,
whereas their occurrence was 0% in this study. The American Avocet,
Long-billed Dowitcher, and Stilt Sandpiper had a high dietary overlap
and largely foraged in the same zone, but may not compete for food
items because of different feeding methods as shown for Stilt Sandpipers
and Dowitchers (Burton 1972). Also, while the American Avocets spent
100% of their time in zone 3, the other 2 species also spent 12–21%
time in zone 2.

Overall, based on indices of dietary overlap and occurrence in feeding
zones, there is probably not much competition occurring at this migra-
tory site. For example, only 11 of 36 possible comparisons of dietary
overlap among species were greater than 50%, but most of the species
involved exhibited differential habitat use. These results may be true
on migration areas in general and within ephemeral habitat regimes in
particular (playa lakes) because food resources may be abundant at only

a few "pocket" areas where shorebirds will tend to concentrate and feed. Thus, food may be limited on a broad scale because "pockets" of abundant shorebird prey may be at a premium. However, once it is located, it then becomes advantageous for shorebirds to minimize competition and exploit this food supply efficiently.

The irregular occurrence of food resources, rigors associated with migration, and reduced daylight foraging time compared to arctic breeding areas may act synergistically whereby the migration period exerts the greatest effect on population regulation of shorebirds and is a strong selective pressure for character divergence. Baker and Baker (1973) also suggested that the migratory period may significantly influence the evolution of foraging behavior in shorebirds. Holmes and Pitelka (1968) hypothesized that various bill configurations evolved primarily in relation to foods exploited on nonbreeding areas.

More studies of shorebird ecology on nonbreeding areas are necessary to elucidate arguments presented here. They should account for food habits, food availability, foraging behavior, and interaction and comparison of foraging sites used and not used by aggregations of shorebirds.

SUMMARY

The feeding ecology of 9 migrant shorebird species using inland freshwater habitats (playa lakes) on the Texas High Plains was studied from 7–21 September, 1980. Shorebirds were collected from a representative playa lake where species-specific dietary and foraging site comparisons were determined. Migrant shorebirds seemed attracted to specific foraging sites where food was abundant. The occurrence of these sites within the overall playa lake regime was probably limited, but shorebirds appeared to use food resources efficiently. Based on diets, coefficients of dietary overlap, behavior, and foraging sites selected by each species, shorebirds did not appear to be competing. An hypothesis is presented that shorebirds experience some population regulation during the migratory portion of their annual cycle.

ACKNOWLEDGMENTS

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