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Toward Conservation of Midcontinental Shorebird Migrations

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Abstract: *Shorebirds represent a highly diverse group of species, many of which experience tremendous energy demands associated with long-distance migratory flights. Transcontinental migrants are dependent upon dynamic freshwater wetlands for stopover resources essential for replenishment of lipid reserves and completion of migration. Patterns of shorebird migration across midcontinental wetlands were detected from migration reports to* American Birds *and information provided by U.S. Fish and Wildlife Service national wildlife refuges. Patterns in species composition and abundance varied geographically, emphasizing the uniqueness of different regions to migrating shorebirds. Smaller species and neotropical migrants moved primarily across the Great Plains, whereas larger species and North American migrants predominated in assemblages in the intermountain west. Shorebirds were broadly dispersed in wetland habitats with dynamic water regimes. Whereas populations of shorebirds in coastal systems appear to concentrate at sites of seasonally predictable and abundant food resources, we propose that transcontinental shorebirds disperse and use wetlands opportunistically. This migration system exemplifies the need for large-scale, coordinated regional management efforts that recognize the dynamic nature of ecosystem processes.*

Hacia la conservación de las migraciones de aves costeras del continente medio

Resumen: *Las aves costeras representan un grupo de especies muy diverso, muchos de los cuales experimentan demandas energéticas tremendas asociadas con vuelos migratorios de largo alcance. Los migrantes continentales dependen de la dinámica de los humedales para obtener recursos esenciales para el reabastecimiento de las reservas de lípidos y para llevar a cabo la migración. Patrones de migración de aves que atraviesan humedales del continente medio fueron detectados a partir de reportes de migración de* "American Birds" *y de información provista por los refugios Nacionales para vida silvestre del Servicio Nacional de Pesca y Vida Silvestre de los Estados Unidos (*"U.S. Fish and Wildlife Service"*). Los patrones de composición de especies y abundancia variaron geográficamente, enfatizando la singularidad de las diferentes regiones para las aves migratorias. Las especies pequeñas y los migrantes neotropicales se trasladaron principalmente a través de las Grandes Planicies, mientras que especies más grandes y migrantes de Norte América predominaron en grupos en el oeste intermontañoso. Las aves costeras estuvieron ampliamente dispersadas en hábitats de humedales con regímenes de agua dinámicos. Dado que en los sistemas costeros las poblaciones de aves costeras parecen concentrarse en sitios con recursos alimenticios abundantes y estacionalmente predecibles, nosotros proponemos que las aves costeras transcontinentales se dispersan y usan los humedales en forma oportunística. Este sistema de migración ejemplifica la necesidad de esfuerzos regionales coordinados y a gran escala que reconozcan la naturaleza dinámica de los procesos ecosistémicos.*

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Introduction

Several species of shorebirds (*Charadriiformes: Charadriidae, Scolopacidae, Phalaropodidae*) migrate long distances between arctic and subarctic breeding grounds to Central and South American nonbreeding areas. The tremendous energy demands associated with flights of several thousand kilometers require that birds be able to repeat the cycle of accumulating then using substantial lipid reserves (Morrison 1984; Myers et al. 1987). Because long-distance migrants cannot make the journey without periodically replenishing fat reserves, stopover sites become critical to the survival of many of these species (Myers 1983; Morrison 1984; Myers et al. 1987).

Three major flyways or main migration corridors link breeding and wintering sites across the Western Hemisphere (Morrison 1984; Morrison & Myers 1989:90). Current views on the migration of shorebirds are derived primarily from studies of the coastal Atlantic and Pacific flyways. In coastal areas, several species of shorebirds stop at relatively few sites where food is abundant and predictable (Morrison 1984:139; Morrison & Myers 1989:85). There are probably no alternative coastal sites that could provide enough food for these large aggregations of shorebirds at precisely the right times to ensure successful migration (Senner & Howe 1984).

In contrast to coastal areas, the dynamic patterns of rainfall and hydrology in the Great Plains result in extreme spatial and temporal variability in both occurrence and condition of wetlands. Large permanent wetlands may provide the most predictable resources for interior migrants, but even they are less predictable than coastal intertidal areas.

Shorebirds as a group are extremely diverse in body size and shape as well as in habitat-use patterns and foraging behavior. Migrants in the Western Hemisphere span ranges of 130–650 mm in body length, 13–219 mm in bill length, and 17–92 mm in tarsal length (Hayman et al. 1986). Patterns of microhabitat use are determined in part by species morphology (Baker 1979, Colwell & Oring 1988). Collectively, shorebirds use a broad range of habitats, including grassy uplands, wet meadows, unvegetated mud substrates, shallow water, and deeper open water (Colwell & Oring 1988). While feeding, shorebirds glean invertebrates from the surface of mud, water, or emergent vegetation, probe deeply into moist soil, or even catch flying insects.

This paper addresses regional patterns of stopover use and distribution of the diverse group of migrant shorebirds that use continental wetlands. We examined reports to *American Birds* and responses to our own questionnaires to national wildlife refuges designed to identify spatial patterns and regional differences in shorebird use of these wetlands. Specifically, we sought

to clarify the relative use of wetlands in the central plains and intermountain areas by neotropical-migrating shorebirds enroute between arctic breeding grounds and Central and South American wintering grounds. This paper represents part of ongoing research on shorebird migration systems. Findings will be used to develop plans for protection and management of stopover areas in the interior U.S.

Methods

We compiled totals of all shorebirds reported to *American Birds* from 11 states during 10 years of southward and northward migrations from late summer and fall of 1979 through the spring of 1990. For ambiguous entries ("were noted at," "dropped in," "in diminished numbers," "handful," "few," "several," "numerous"), we assigned conservative values ranging from 2 to 20. Because shorebirds (with the exception of phalaropes) are primarily limited to water depths proportional to leg length and body size, we classified shorebirds by size after Morrison and Ross (1989). Small birds are primarily small sandpipers and plovers in the genera *Calidris* and *Charadrius* with total body lengths of ≤ 190 mm (Appendix). Medium-sized shorebirds range in body length from 195 to 350 mm, and large birds exceed 350 mm.

We also classified shorebirds by migration distance (short, intermediate, and long) based on range maps in Hayman et al. (1986) and maps in the National Geographic Society Atlas (1981). We calculated an index I ($\times 1000$ km) as a weighted average of D_s, D_m, and D_e, where D_s = the shortest distance between breeding and wintering areas (if areas overlap, $D_s = 0$), D_m = distance between estimated midpoints of breeding and wintering ranges, and D_e = distance between extremes of breeding and wintering areas (Fig. 1; Appendix). I is highly correlated ($r = 0.97$) with D_m, the distance between midpoints of breeding and wintering areas.

We mailed questionnaires to 100 U.S. Fish and Wildlife Service national wildlife refuges in 18 states in the Great Plains and intermountain regions, requesting information on shorebird use of refuges and adjacent lands during northward (April–May 1990) and southward (August–September 1990) migrations. Respondents were asked to categorize peak shorebird abundance as 1–100, 100–500, 500–1000, 1000–2000, 2000–5000, 5000–10,000, and >10,000 birds and to estimate percentages of small, medium-sized, and large birds (phalaropes included among medium-sized birds for ease of identification). Additional information requested from refuges included the total surface area of water (*AREA*), the number of discrete water units (*UNIT*) on the refuges during migration, and rank estimates of the amount of available shorebird habitat. We
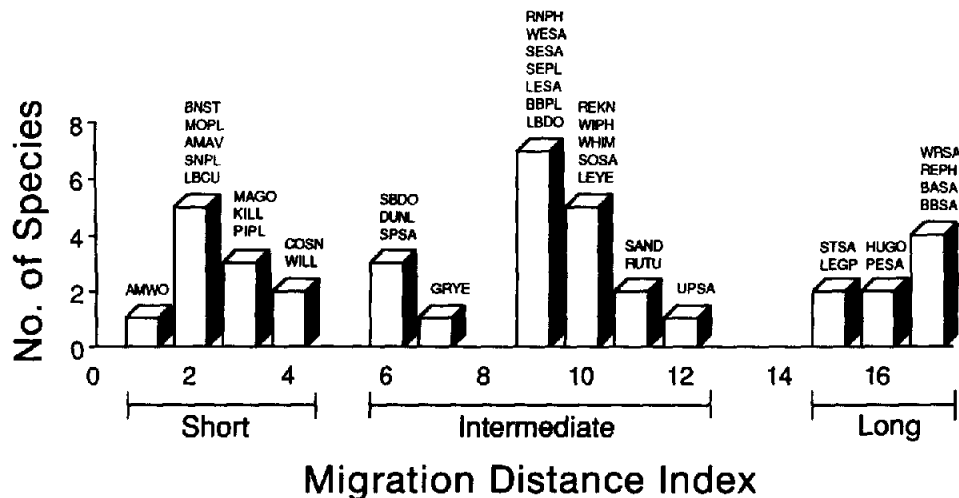
Figure 1. *Classification of shorebirds by migration distance (short, intermediate, and long) based on a migration distance index, the weighted average of* D_s, D_m, *and* D_c, *where* D_s = *the shortest distance between breeding and wintering areas,* D_m = *the distance between estimated midpoints, and* D_c = *the distance between extremes of breeding and wintering areas. All measurements were based on maps in Hayman et al. (1986) and the National Geographic Society Atlas (1981). See Appendix for species identification.*

asked for area estimates in English units because refuge personnel use English units more commonly than metric units. We then converted areas to the following metric categories: 1 = <4 ha, 2 = 4–20 ha, 3 = 20–80 ha, 4 = >80 ha. Habitat types were expressed as A = wet mud and water <2.5 cm and B = shallow water 2.5–20 cm deep. Rank estimates of A and B were totalled to provide an overall estimate of shorebird habitat (HAB). We also included information from one state-owned refuge, Cheyenne Bottoms Wildlife Management Area, Kansas.

Calculations of maximum reported shorebird numbers were based on midpoints of the first six categories above (50, 300, 750, 1500, 3500, and 7500). A shorebird abundance of >10,000 was assigned as 10,000 (i.e., no midpoint), resulting in a conservative estimate. To examine seasonal differences in refuge use, we evaluated information from 80 refuges that submitted both spring and fall responses. Precision of the data do not merit quantitative assessments of dispersion. AREA and UNIT were log transformed for statistical procedures below.

We recognize the potential biases in data that are not based on systematic surveys. Such sources of data, however, can reveal continent-wide patterns of avian geographical ecology (Bock & Root 1981) that may otherwise go undetected. We assumed that the responses to refuge questionnaires held no regional biases in estimated numbers or classification of birds by body size. We also assumed that, over a ten-year period, there were collectively no regional biases in the relative frequencies of species reported to *American Birds*.

Results

Geographic Patterns in Shorebird Distribution During Migration

Use of wetlands by shorebirds was stratified across six regions in the Great Plains and intermountain areas. Below we contrast bird use of the intermountain states represented in this study (Nevada, Utah, Idaho, western Montana) with bird use of the central plains (eastern Alberta, Saskatchewan, Manitoba, eastern Montana, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma).

In spring, the intermountain area hosts primarily short-distance migrants and species whose breeding range lies south of 65°N (Fig. 2; Table 1). In contrast, long-distance migrants and species that breed exclusively north of 60°N stop primarily in the central plains for replenishing reserves (Fig. 2; Table 1). During fall migration, species that winter in the U.S. are more heavily represented in the intermountain region than in the plains, whereas species that travel south of the equator are more heavily represented in the plains (Table 1).

Grouping shorebirds by body size also revealed a striking pattern. During spring migration, small shorebirds comprised a larger proportion of populations in the central plains than in the intermountain areas, according to reports to *American Birds* (Fig. 3; G = 1618.28, df = 1, p < 0.001). This pattern was substantiated by our own data (unpublished), which reveal even greater percentages (50–70%) of small birds in
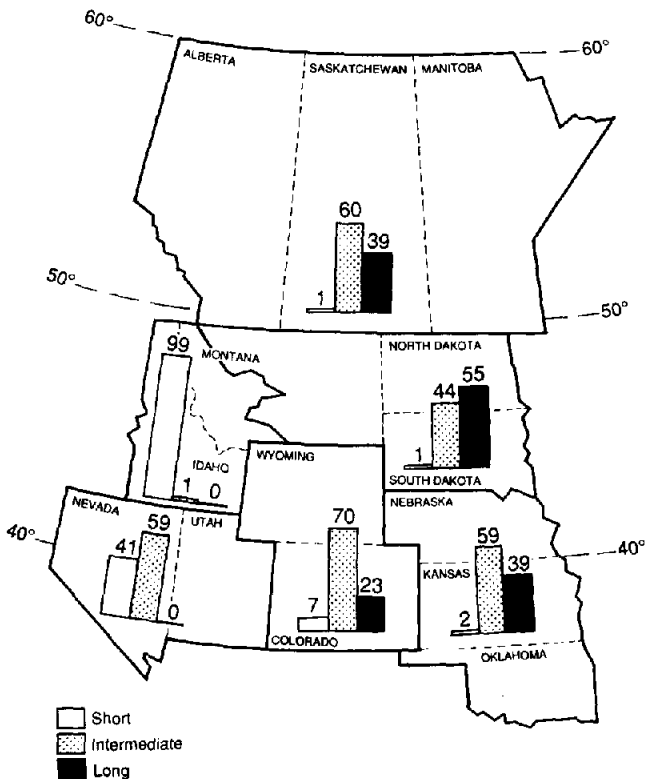
Figure 2. Geographic distribution of shorebirds by migration distance during spring migration. Bar graphs and numbers depict percentage of short-, intermediate-, and long-distance migrants within six regions designated by solid lines. Data from American Birds spring migration reports 1980–1990. *See Appendix for classification of shorebird species by migration distance.*

the central plains. Large shorebirds were more heavily represented in the intermountain regions than in the central plains (Fig. 3; $G = 204.99, df = 1, p < 0.001$). Medium-sized shorebirds were a large proportion ($\geq 50\%$) of aggregations throughout the 11 states and 3 provinces, except in western Montana and Idaho. Phalaropes were not reported in Idaho and western Montana, whereas they were 9–21% of the medium-sized shorebirds from North Dakota south of Oklahoma and 33–56% of the medium-sized shorebirds in the remaining states and provinces.

The greatest number of species was reported in the central Canadian plains in spring, and the smallest number of species in the northern intermountain area (Table 1). Abundance of species differed substantially by region (Table 1). For example, White-Rumped Sandpipers were reported only in the three eastern regions during spring, whereas Long-Billed Dowitchers were among the most abundant species only in the three southern regions.

Dynamics of Water Levels and Shorebird Habitat on Refuges

During both spring and fall migration, total water area (*AREA*) on refuges correlated highly with estimated potential shorebird habitat (*HAB;* $r = 0.521, df = 73, p < 0.001$ for spring; $r = 0.576, df = 74, p < 0.001$ for fall; 1-tailed). In spring, the number of water units (*UNIT*) also correlated with estimates of shorebird habitat ($r = 0.230, df = 73, p < 0.05$). In both seasons, northern refuges reported more potential shorebird habitat per refuge than did southern refuges (Table 2).

Many refuges (69% of 94) reported profound changes in water levels; 41% reported water present only in some years. Seventeen respondents at northern refuges, primarily in North Dakota, South Dakota, and Nebraska, perceived an increase in shorebird habitat in spring and fall of 1990 and accredited it to drought conditions. Most refuges (74% of 95) have some capability to manage water levels.

Distribution and Habitat Relationships of Shorebirds on Refuges

Shorebirds were broadly dispersed throughout the entire region during spring and during late summer and fall; 13 refuges reported more than 10,000 birds (Fig. 4). Most responses were based on best estimates of refuge personnel, although some (21% of 90 responses in spring, 17% of 85 responses in late summer and fall) were based on ongoing surveys. Because most of the refuges were in the plains, we did not make comparisons between shorebird use of plains and intermountain areas.

In spring and fall, shorebird numbers were greater on refuges with abundant habitat (wet mud and shallow water <2.5 cm) than on refuges with sparse habitat (Table 3). The abundance of shorebirds increased with latitude in both seasons ($r = 0.293, df = 89, p < 0.01$ in spring; $r = 0.330, df = 83, p < 0.05$ in fall).

Variability in the Abundance of Shorebirds within and between Seasons

From April to May during the spring migration, respondents in northern refuges generally perceived increases and respondents in southern refuges reported decreases in the abundance of shorebirds ($X^2 = 14.36, df = 4, p = 0.006$). These patterns were not reported for migration during late summer and fall migration ($X^2 = 3.86, df = 4, p = 0.43$).

Small shorebirds, but not medium or large shorebirds, were more numerous ($p < 0.10$) in the fall than in the spring in northern refuges (latitude $\geq 43°N$; Table 4). This trend was reversed on the southern refuges (latitude $<43°N$), where small shorebirds were significantly more numerous in the spring than in the fall (Table 4).

Table 1.   Composition of shorebirds reported in *American Birds* at stopover sites in six geographic regions during spring migration, 1980–1990, and late summer/fall migration, 1979–1989.

| | Spring migration | | | | | |
| | Intermountain | | | Great plains | | |
Region[1]	ID/wMT	NV/UT	WY/CO	eAL/MA	ND/SD	NE/OK
No. of species	21	29	23	39	32	31
Breeding Range[2]						
≤65° N (%)	98.6	61.8	36.5	1.5	6.7	17.0
≥60° N (%)	0.7	25.7	35.9	50.6	39.6	78.5
Most Abundant	AMAV***	AMAV***	WIPH**	RNPH**	WRSA*	LBDO**
Species	MAGO	LBDO**	RNPH**	BASA*	SESA*	WRSA**
		WIPH*	REPH*	WRSA*	LEGP*	WIPH*
		BNST*	LBDO*	SAND*	DUNL*	STSA
		LESA	STSA	STSA	STSA*	
No. of Species	24	29	30	30	27	27
Winter Range[3]						
in U.S. (%)	86.8	87.0	71.6	57.4	59.3	16.6
<0° (%)	12.4	13.0	28.4	32.4	40.7	39.8
Most Abundant	AMAV***	RNPH***	LBDO**	RNPH**	LBDO**	LBDO**
Species	KILL*	LBDO*	KILL**	HUGO*	PESA**	PESA*
	BASA	WIPH*	BASA*	LBDO*	LEYE*	UPSA*
		AMAV	WIPH*	AMAV*	LEGP*	SNPL*
			LEYE	WRSA*	RNPH*	LEGP
				SESA*		

Refer to Appendix for definitions of alpha codes.
Percentages are based on total numbers of birds reported in region.
* >10%, ** >20%, *** >50% of total number of birds reported in region.
[1] *ID/wMT: Idaho and western Montana; NV/UT: Nevada and Utah; WY/CO: Wyoming and Colorado; eAL/MA: eastern Alberta, Saskatchewan, and Manitoba; ND/SD: eastern Montana, North Dakota, and South Dakota; NE/OK: Nebraska, Kansas, and Oklahoma.*
[2] *Breeding range lies exclusively south of 65°N or north of 60°N.*
[3] *Winter range is partially in U.S. or exclusively south of the equator.*

Twenty-four respondents offered comments on year-to-year variability in the abundance of shorebirds related to water conditions. Of these, 10 respondents in North and South Dakota reported a greater abundance of shorebirds than expected in 1990 and attributed it to drought. Three southern refuges reported that flooding and high water drastically reduced habitat in spring, and two southern refuges reported that flooding of fields increased habitat.

Consistency among Data Sets

We compared broadscale trends derived from *American Birds* migration reports (*ABMR*) and from refuge questionnaires (*RQ*), and, when possible, checked these trends against patterns in our own recent (1990–1991) shorebird survey data from Kansas, Oklahoma, and South Dakota (*NERC*; unpublished data). The data sets were in general agreement for the following trends.

In spring, large shorebirds were only a minor portion of shorebird communities in the central plains (≤5% *ABMR* and *NERC*; 8–16%, *RQ*), but were the major proportion of birds in wetlands in the intermountain area (*ABMR* and *RQ*). Short-distance migrants were rare in the central plains in spring (≤3% of sightings), but more plentiful (10–20% of sightings) in fall (*ABMR* and *NERC*). Long-distance migrants formed a large compo-

nent of shorebird communities in the central plains in spring (35–55%; *ABMR* and *NERC*; see also Eldridge & Johnson 1988). There were many species in the central plains in spring (31–34 species) and slightly fewer in fall (27–30; *ABMR* and *NERC*). *ABMR* and *NERC* data sets were in agreement on the relative importance of spring-migrant White-Rumped Sandpipers and Semipalmated Sandpipers in the Dakotas, spring-migrant White-Rumped Sandpipers and Long-Billed Dowitchers in Nebraska, Kansas, and Oklahoma (NE/OK), and fall-migrant long-billed Dowitchers in NE/OK.

Data sets did not agree consistently. *ABMR* and *RQ* estimates of small shorebirds were fairly consistent for the central plains in spring (27–43% of sightings). However, data of *NERC* and of Eldridge and Johnson (1988) suggest that the percentage of small shorebirds was considerably higher (50–70% of assemblages). The relative importance of Wilson's Phalaropes, Lesser Golden Plovers, and Least Sandpipers differed somewhat between the *ABMR* and the *NERC* data sets.

Discussion

Complexity of the Interior Migration System

Efforts to maintain regional shorebird diversity must address the complexity of this migration system. Shore-
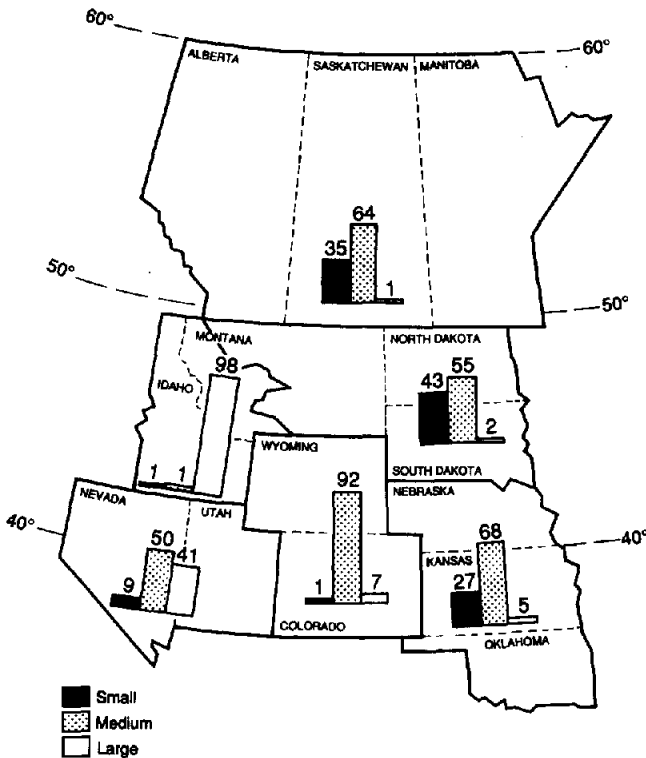
Figure 3. Geographic distribution of shorebirds by body size during spring migration. Bar graphs and numbers depict percentage of small, medium-sized, and large shorebirds within six regions designated by solid lines. Data from American Birds *spring migration reports 1980–1990. See Appendix for classification of shorebird species by body size.*

birds are broadly dispersed throughout the U.S. and Canadian interior during spring and fall migration. Species composition and abundance patterns, however, vary substantially between seasons and geographic areas; this variation clearly illustrates the uniqueness of different regions to migrating shorebirds.

Stopover sites in the Great Plains provide essential resources for long-distance and intermediate-distance neotropical migrants, such as White-Rumped Sandpiper, Baird's Sandpiper, Pectoral Sandpiper, Stilt Sandpiper, Dunlin, Hudsonian Godwit, and Semipalmated Sand-

piper. Birds travelling long distances are under severe physiological and ecological constraints, and resources at stopover sites are critical to their survival.

Wetlands in the central plains are of particular importance to small-bodied shorebirds that experience more constraints than larger birds. Smaller birds have higher basal metabolic rates than larger birds (Calder 1984) and are able to accumulate less body fat. Furthermore, short legs and a short bill confine small shorebirds to a narrower range of water depths than larger birds. An additional constraint that primarily affects spring rather than fall migrants is the exact timing of resource availability. In spring, resources must be available during a fairly narrow window of time in order for birds to refuel and reach their breeding grounds in time to complete the nesting cycle. This constraint is less pronounced during the more leisurely fall migration.

The intermountain area differs markedly from the Great Plains because its wetlands host many larger-bodied, short-distance migrants that breed in the U.S., such as the American Avocet, Black-Necked Stilt, and Marbled Godwit, and fall migrants that winter in the U.S., such as the Least Sandpiper and Long-Billed Dowitcher. Long-distance migrants were comparatively rare in the intermountain region.

Habitat Protection in Dynamic Ecosystems

The highly dynamic nature of freshwater wetlands, described by Fredrickson and Reid (1990) and others, and substantiated by refuge reports, undoubtedly had a strong influence on the evolution of shorebird migration routes and strategies. We propose that, because wetlands are dynamic and unpredictable during migration, shorebird movements across the plains are characterized by dispersion and opportunism rather than by concentration and predictability, as in coastal systems.

The occurrence of mudflats and shallow water habitats is highly variable yet is critical to refueling efforts of small shorebirds. These ephemeral and dynamic habitats are perhaps some of the most endangered habitats in the continental U.S. because of the rapid loss of wetlands due to conversion of lands to agriculture (Tiner 1984; Dahl 1990) and extensive alteration of hydrologic processes (Fredrickson & Reid 1990). Ephemeral and shallow wetlands will receive even less protection in the near future under the new wetlands designation policy (U.S. Environmental Protection Agency 1991).

Protection of habitat for species that use disjunct patches of habitat opportunistically or irregularly during migration is a difficult challenge that has received little attention (Takekawa & Beissinger 1989). The dynamic nature of such systems requires a new management perspective that does not depend on the maintenance of a few sites in a static condition (Szaro 1990). Wetlands known to support large numbers of migrant shorebirds,

Table 2. Latitudinal trends in estimates of shorebird habitat on U.S. Fish and Wildlife Service national wildlife refuges, 1990 (numbers are refuges in each category).

	Estimated habitat (ha)					
	Spring			*Fall*		
Latitude	*<20*	*20–120*	*>120*	*<20*	*20–120*	*>120*
Lat ≥ 43°	7	15	25	5	14	26
Lat < 43°	7	17	19	6	22	10
Correlation of		$r = 0.156$			$r = 0.332$	
Habitat and		$df = 89$			$df = 83$	
Lattitude (1%)		$p > 0.10$			$p < 0.002$	

Shorebird numbers

○ 0 - 100
◑ 100 - 1,000
◕ 1,000 - 2,000
◕ 2,000 - 5,000
● 5,000 - 10,000
◉ > 10,000

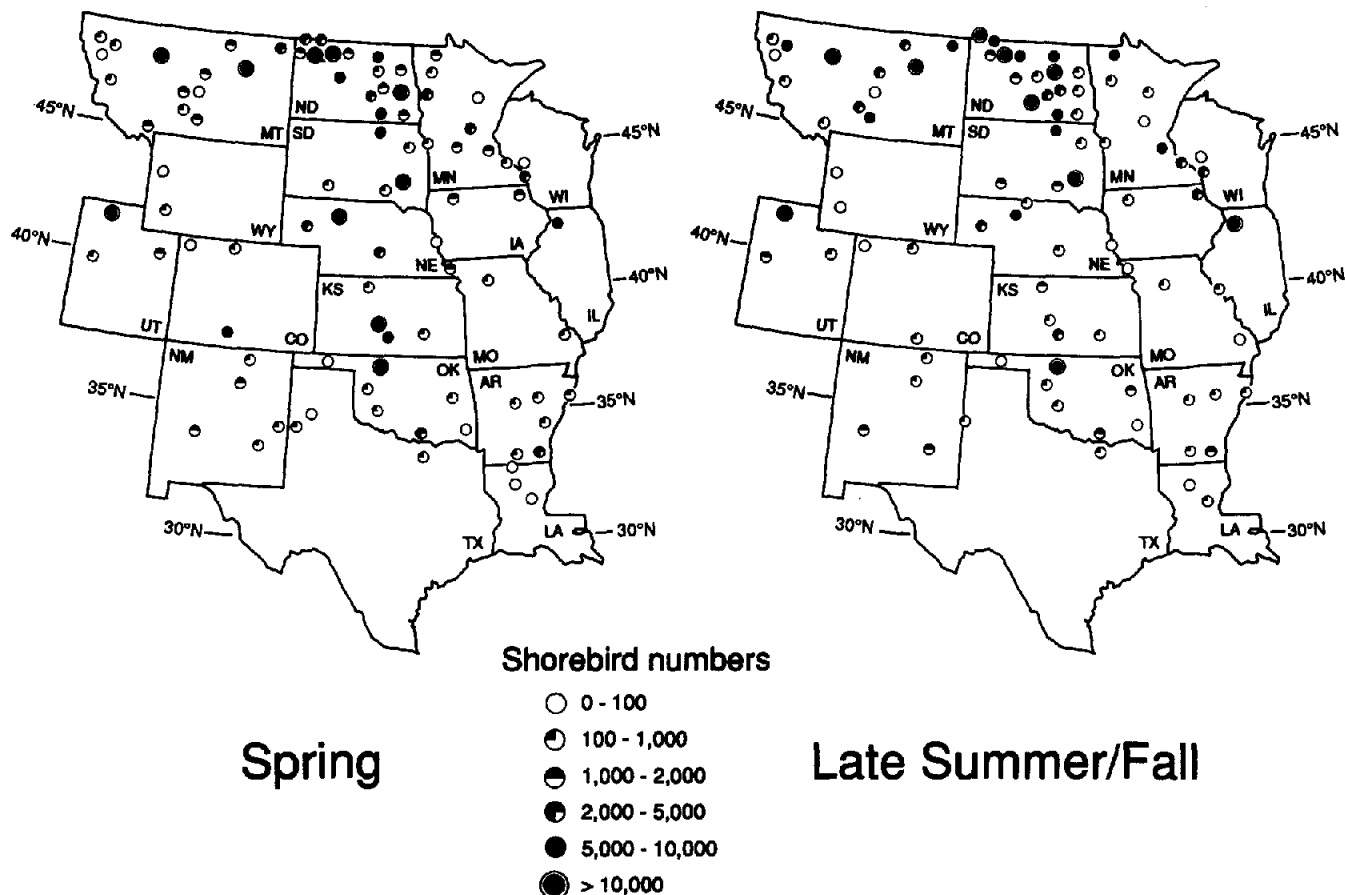Spring   Late Summer/Fall

Figure 4. Distribution of shorebirds at U.S. Fish and Wildlife Service national wildlife refuges (NWR) in the Great Plains and intermountain areas during spring and late summer/fall migration. Estimates are from responses by NWRs to questionnaires. Estimates from the state-owned Cheyenne Bottoms Wildlife Management Area in central Kansas are also included.

such as the Cheyenne Bottoms Wildlife Management Area in central Kansas, do not always have habitat suitable for small shorebirds during migration (Castro et al. 1990; personal observation). At these times, alternative sites become increasingly important. Also, some species require a network of sites or "stepping stones" to complete migration (Smit & Piersma 1989), and many options must be maintained to provide those links.

Large-scale regional management perspectives are crucial to the protection of breeding, migration, and wintering habitats for shorebirds in arctic, temperate, and tropical regions (Myers et al. 1987). Here we describe an opportunistic migration system that is very different from the coastal paradigm upon which current

Table 3. Mean ± SE (N) maximum numbers of shorebirds reported at U.S. Fish and Wildlife Service national wildlife refuges relative to estimates of shorebird habitat.

Estimated habitat (ha)	Number of shorebirds	
	Spring	Fall
<20	240 ± 100 (14)	470 ± 190 (12)
20–120	1570 ± 420 (32)	980 ± 250 (35)
>120	4820 ± 590 (43)	5700 ± 610 (36)
Tests of Significance[1]	H = 40.6 df = 2, 88 p < 0.0001	H = 40.3 df = 2, 80 p < 0.0001

Data are rounded to the nearest 10.
[1] *Kruskal-Wallis test.*

Table 4. Latitudinal trends in spring and fall shorebird distribution on 44 northern (≥43°N) and 36 southern (<43°N) U.S. Fish and Wildlife Service national wildlife refuges.

Body Size	Latitude	N	Number of shorebirds		P
			Spring Mean + SE	Fall Mean + SE	
All	≥43°	44	2960 ± 500	4140 ± 570	0.044*
	<43°	36	2560 ± 580	1740 ± 480	0.047*
Small	≥43°	43	1300 ± 250	1870 ± 320	0.098**
	<43°	35	1010 ± 310	550 ± 180	0.024*
Medium	≥43°	43	1200 ± 200	1580 ± 240	0.108
	<43°	35	1300 ± 370	870 ± 260	0.202
Large	≥43°	43	530 ± 120	540 ± 130	0.884
	<43°	35	320 ± 120	360 ± 240	0.754

*Data are rounded to nearest 10. * p < 0.05.*

thinking is founded. To expand protection of shorebird habitat within continental regions, the complexity and the dynamic nature of transcontinental migration must be addressed.

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Appendix

Classification of shorebirds by migration distance. Categories of short-, intermediate-, and long-distance migrants are based on an index I, a weighted average of D_s, D_m, and D_e where D_s represents the shortest distance ($\times 1000$ km) between breeding and wintering ranges, D_m the distance between the approximate midpoints of the ranges, and D_e the distance between the extreme edges of the ranges. Alpha codes follow Klimkiewicz and Robbins (1978). Body sizes are expressed as small, medium, and large (see methods). Extent of range is given as N latitude unless otherwise specified. All distance estimates are based on range maps in Hayman et al. (1986) and maps in the National Geographic Society Atlas (1981).

Short-distance Migrants

Alpha Code	Body Size	Common Name	Scientific Name	I	D_m ($\times 1000$ km)	Extent of Range (°Lat) South Breed	North Winter
AMWO	M	American Woodcock	*Scolopax minor*	0.9	.5	27	40
LBCU	L	Long-Billed Curlew	*Numenius americanus*	1.7	1.7	35	40
SNPL	S	Snowy Plover	*Charadrius alexandrinus*	2.1	2.0	30	45
AMAV	L	American Avocet	*Recurvirostra americana*	2.1	2.8	30	37
MOPL	M	Mountain Plover	*Charadrius montanus*	2.4	2.3	37	40
BNST	L	Black-Necked Stilt	*Himantopus himantopus*	2.5	.5	40S	37
PIPL	S	Piping Plover	*Charadrius melodus*	3.0	2.5	42	32
KILL	M	Killdeer	*Charadrius vociferus*	3.4	2.1	20	45
MAGO	L	Marbled Godwit	*Limosa fedoa*	3.5	3.2	40	40
WILL	L	Willet	*Catoptrophorus semipalmatus*	3.6	4.2	40	40
COSN	M	Common Snipe	*Gallinago gallinago*	3.9	3.7	38	50
SPSA	M	Spotted Sandpiper	*Actitis macularia*	6.3	7.8	35	48
DUNL	M	Dunlin	*Calidris alpina*	6.3	5.8	55	50
SBDO	M	Short-Billed Dowitcher	*Limnodromus griseus*	6.4	5.9	52	45
GRYE	M	Greater Yellowlegs	*Tringa melanoleuca*	6.7	8.0	50	45
LBDO	M	Long-Billed Dowitcher	*Limnodromus scolopaceus*	8.9	9.0	62	50
BBPL	M	Black-Bellied Plover	*Pluvialis squatarola*	8.9	9.0	62	50
LESA	S	Least Sandpiper	*Calidris minutilla*	9.1	9.8	52	42
SEPL	S	Semipalmated Plover	*Charadrius semipalmatus*	9.4	10.5	52	38
SESA	S	Semipalmated Sandpiper	*Calidris pusilla*	9.5	8.7	52	21
WESA	S	Western Sandpiper	*Calidris mauri*	9.5	9.6	63	42
RNPH	M	Red-Necked Phalarope	*Phalaropus lobatus*	9.5	9.5	55	35
LEYE	M	Lesser Yellowlegs	*Tringa flavipes*	9.7	11.2	50	34
SOSA	M	Solitary Sandpiper	*Tringa solitaria*	9.8	11.6	50	26
WHIM	L	Whimbrel	*Numenius phaeopus*	10.0	10.6	58	40
WIPH	M	Wilson's Phalarope	*Phalaropus tricolor*	10.1	9.6	30	55
REKN	M	Red Knot	*Calidris canutus*	10.1	10.9	65	35
RUTU	M	Ruddy Turnstone	*Arenaria interpres*	11.0	10.7	62	40
SAND	M	Sanderling	*Calidris alba*	11.4	11.2	65	50
UPSA	M	Upland Sandpiper	*Bartramia longicauda*	12.4	10.7	36	20S
LEGP	M	Lesser Golden Plover	*Pluvialis dominica*	14.8	12.7	54	10S
STSA	M	Stilt Sandpiper	*Micropalama himantopus*	15.0	14.0	60	12S
PESA	M	Pectoral Sandpiper	*Calidris melanotos*	16.5	16.3	5S	12S
HUGO	L	Hudsonian Godwit	*Limosa haemastica*	16.5	15.4	70	53
BASA	S	Baird's Sandpiper	*Calidris bairdii*	16.7	13.7	60	0
BBSA	M	Buff-Breasted Sandpiper	*Tryngites subruficollis*	16.8	14.4	67	20S
REPH	M	Red Phalarope	*Phalaropus fulicarius*	17.1	13.4	62	15S
WRSA	S	White-Rumped Sandpiper	*Calidris fuscicollis*	17.2	14.7	62	28S