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ON DETERMINING THE SIGNIFICANCE OF EPHEMERAL CONTINENTAL WETLANDS TO NORTH AMERICAN MIGRATORY SHOREBIRDS

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Abstract.—Conservation challenges enhance the need for quantitative information on dispersed bird populations in extensive landscapes, for techniques to monitor populations and assess environmental effects, and for conservation strategies at appropriate temporal and spatial scales. By estimating population sizes of shorebirds in the U.S. portion of the prairie pothole landscape in central North America, where most migrating shorebirds exhibit a highly dispersed spatial pattern, we determined that the region may play a vital role in the conservation of shorebirds. During northward and southward migration, 7.3 million shorebirds (95% CI: 4.3–10.3 million) and 3.9 million shorebirds (95% CI: 1.7–6.0 million) stopped to rest and refuel in the study area; inclusion of locally breeding species increases the estimates by 0.1 million and 0.07 million shorebirds, respectively. Seven species of calidridine sandpipers, including Semipalmated Sandpipers (*Calidris pusilla*), White-rumped Sandpipers (*C. fuscicollis*), and Stilt Sandpipers (*C. himantopus*), constituted 50% of northbound migrants in our study area. We present an approach to population estimation and monitoring, based on stratified random selection of townships as sample units, that is well suited to 11 migratory shorebird species. For extensive and dynamic wetland systems, we strongly caution against a monitoring program based solely on repeated counts of known stopover sites with historically high numbers of shorebirds. We recommend refinements in methodology to address sample-size requirements and potential sources of bias so that our approach may form the basis of a rigorous migration monitoring program in this and other prairie wetland regions.
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Key words: calidridine sandpipers, midcontinental North America, migration, monitoring, population estimation, prairie wetlands, shorebird.

Sobre la Determinación de la Importancia de Humedales Continentales Efímeros para las Aves Playeras Migratorias Norteamericanas

Resumen.—Los desafíos de conservación acrecientan la necesidad de contar con información cuantitativa sobre poblaciones de aves dispersas en paisajes extensos para desarrollar técnicas para monitorearlas y evaluar efectos ambientales, y para desarrollar estrategias de conservación a las escalas temporales y espaciales adecuadas. Mediante la estimación de los tamaños poblacionales de aves playeras en la porción perteneciente a los Estados Unidos del paisaje de humedales efímeros de las praderas del centro de Norte América, donde la mayoría de las aves playeras migratorias exhiben un patrón de distribución espacial altamente disperso, determinamos que la región podría jugar un papel vital en la conservación de las aves playeras. Durante la migración hacia el norte, 7.3 millones de aves playeras (IC del 95%: 4.3–10.3 millones) se detuvieron a descansar y a reabastecerse en el área de estudio, mientras que durante la migración hacia el sur, lo hicieron 3.9 millones (IC del 95%: 1.7–6.0 millones). Si se incluyen las especies que se reproducen localmente, los estimados aumentan en 0.1 y 0.007 millones de aves playeras, respectivamente. Siete especies de playeros calidrinos, incluyendo a *Calidris pusilla*, *C. fuscicollis* y *C. himantopus*, constituyeron el 50% de los migrantes que se dirigen hacia el norte en nuestra área de estudio. Presentamos un enfoque para estimar y monitorear las poblaciones que se basa en la selección aleatoria de municipios como unidades de muestreo, y que se ajusta bien al estudio de 11 especies migratorias de aves playeras. Para sistemas de humedales extensos y dinámicos, sugerimos que no es adecuado realizar programas de monitoreo que se basen sólo en conteos repetidos realizados en sitios conocidos de escala migratoria, que siempre han albergado números altos de aves playeras. Recomendamos que las metodologías sean refinadas para evaluar los requerimientos en términos de los tamaños muestrales y las posibles fuentes de sesgo, de manera que nuestro enfoque podría servir como base para un programa riguroso de monitoreo de la migración para esta y otras regiones de humedales de praderas.

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The identification of important habitats in all stages of avian life cycles, including migration, is essential to conservation planning for migratory species. Recent studies suggest that population limitation in birds may occur during migration as well as during breeding and wintering seasons (Sillett and Holmes 2002, Baker et al. 2004, Morrison 2006). Although more is known about migratory habitats and critical staging sites of shorebirds than of many bird groups, there are several aspects of shorebird migration systems that remain unexplored. The Western Hemisphere Shorebird Reserve Network (see Acknowledgments), a voluntary nonregulatory coalition of more than 240 private and public organizations in seven countries, has designated 67 migration sites for protection, totaling ~9 million ha at the international, hemispheric, national, and regional levels. Although the site-based approach used to identify and designate most of the WHSRN sites has been highly successful, especially in coastal areas, it has failed to reveal the significance of ephemeral continental wetlands in prairie landscapes.

The extensive wetland systems in central North America provide stopover resources for large populations of migrating shorebirds during northward and southward migrations (Skagen et al. 1999), yet the sizes of these populations are unknown. In the extreme and variable climate of the central North American prairie region, highly dynamic wetlands shape a landscape with a continually changing spatial configuration of micro- and macrohabitats preferred by shorebirds. Migrating shorebirds seeking stopover resources in prairie wetlands respond to the amount of water and suitable habitat on the landscape and, therefore, disperse broadly and unpredictably each spring and fall migration, making monitoring and conservation efforts highly challenging (Skagen and Knopf 1994a, Skagen 1997, Skagen et al. 1999). As a result, a site-based approach to monitoring shorebirds, although effective in describing chronology and use of selected sites, has been unsuccessful in estimating total populations of transitory birds using the prairie region as a whole.

With forecasts of agricultural intensification to meet growing demands for food and biofuel production and predictions of global warming (Tilman et al. 2001, Johnson et al. 2005, Farrell et al. 2006), the next 50 years will bring profound changes in land use and agricultural practices to the world's agricultural regions, including the prairie region of North America. To adequately address shorebird conservation needs in light of these looming conservation challenges, we must first determine the significance of the prairie regions to shorebird ecology. There is a strong need for quantitative information on migrant population sizes to be used as a baseline in assessing environmental effects and to inspire the development of inventive conservation strategies at appropriate temporal and spatial scales.

Here, we estimated migrant shorebird populations using a dynamic prairie wetland landscape, the U.S. portion of the Prairie Pothole Region, where 3 million wetlands extend over >300,000 km^2. To do so, we used stratified random sampling as an alternative to the standard site-based approach common to shorebird studies. We were especially interested in estimating populations of several long-distance calidridine migrants, such as Stilt Sandpipers and White-rumped Sandpipers (scientific names of species are given in Table 1), that are abundant yet somewhat restricted to a narrow band between 90°W and 100°W longitude during northward migration across the United States (Skagen et al. 1999). As a secondary objective, we also evaluate the use of our population estimation technique as a monitoring tool for highly mobile and dispersed shorebird populations in extensive prairie wetland systems.

Methods

Study area.—The Prairie Pothole Region of central North America is characterized by millions of small depressional wetlands left by receding ice sheets in the late Pleistocene and by a seasonal relatively dry climate punctuated by severe droughts and deluges (Johnson et al. 2005). The region was part of one of the largest grassland–wetland ecosystems on earth until agriculture began transforming the landscape around 1890 (Ringelman 2005). Presently, ~70% of the original grasslands within the region support crop production and >50% of the historical wetlands are gone. Physiographic regions within the study area range from the Drift Prairie, with low relief, fertile soils, and crop agriculture as the dominant land use, to the Missouri and Prairie Coteau regions, with steeper terrain and poorer soils on which grassland is predominant.

Sampling design.—The sampling frame of this study, defined as portions of North Dakota, eastern South Dakota, and western Minnesota that lie within the Prairie Pothole Region, totals 302,250 km^2. We specified townships (an area of 36 square miles [93.3 km^2] in the U.S. public land surveying system) as the sampling unit. We stratified the sampling frame into four landscape types (defined below) on the basis of attributes that influence shorebird abundance as determined by preliminary investigations of northbound migrants in eastern South Dakota. Abundances of several shorebird species, including Semipalmated Sandpipers, White-rumped Sandpipers, and Stilt Sandpipers, were positively associated with total wetland area and cropland area in the landscape surrounding a wetland (Skagen et al. 2005). We determined the total percentage of wetland and cropland area for each township in the sampling frame and calculated the median values (median wetland area = 8%, and median cropland area = 60%). We designated four landscape classes: 1 = low wetland area (<8%) and low cropland area (<60%); 2 = low wetland area (<8%) and high cropland area (>60%); 3 = high wetland area (>8%) and low cropland area (<60%); and 4 = high wetland area (>8%) and high cropland area (>60%). We assigned each township within the sampling frame to one of four landscape classes; 14.4%, 36.5%, 32.7%, and 16.4% fell under landscape classification 1, 2, 3, and 4, respectively, within the 302,250-km^2 study area. We selected a random sample without replacement of townships from each landscape class and allocated a similar number of sample units to each stratum. A preferred method of apportioning effort would be to allocate sample units in relation to strata variation; we did not do this because we had no prior estimates of variance within strata and because we expected within-stratum variance to differ among species.

Within each township, transects (1.6 km long × 200 m wide; one road segment) were specified as the subsampling unit. We surveyed 18–24 systematically selected transects in each township when feasible; when surveying 18 transects was not feasible, we surveyed as many as possible. We prioritized viewing to the north side of east–west roads and modified transect choices for

Table 1. Percentage of townships in which northbound shorebirds were detected and similarity[a] of estimated township populations between spring 2002 and 2003.

Species	Townships spring 2002 (%)	Townships spring 2003 (%)	Sorenson quantitative index C_N	Spearman's rank correlation r_s
***En route*-only species**				
Black-bellied Plover (*Pluvialis squatarola*)	0.0	6.1		
American Golden-Plover (*P. dominica*)	2.5	4.5		
Semipalmated Plover (*Charadrius semipalmatus*)	17.3	9.1	0.016	0.068
Solitary Sandpiper (*Tringa solitaria*)	11.1	4.5	0.000	−0.062
Greater Yellowlegs (*T. melanoleuca*)	17.3	4.5	0.000	−0.092
Lesser Yellowlegs (*T. flavipes*)	51.9	25.8	0.067	0.032
Hudsonian Godwit (*Limosa haemastica*)	8.6	4.5	0.022	0.146
Ruddy Turnstone (*Arenaria interpres*)	0.0	1.2		
Sanderling (*Calidris alba*)	0.0	1.2		
Semipalmated Sandpiper (*C. pusilla*)	24.7	24.2	0.071	0.079
Least Sandpiper (*C. minutilla*)	38.3	30.3	0.066	0.017
White-rumped Sandpiper (*C. fuscicollis*)	37.0	30.3	0.057	0.195
Baird's Sandpiper (*C. bairdii*)	9.9	12.1	0.029	0.160
Pectoral Sandpiper (*C. melanotos*)	28.4	21.2	0.078	0.085
Dunlin (*C. alpina*)	16.0	12.1	0.035	0.160
Stilt Sandpiper (*C. himantopus*)	37.0	18.2	0.012	0.226
Buff-breasted Sandpiper (*Tryngites subruficollis*)	0.0	3.0		
Short-billed (*Limnodromus griseus*) and Long-billed (*L. scolopaceus*) dowitchers	18.5	7.0	0.009	−0.012
Red-necked Phalarope (*Phalaropus lobatus*)	3.7	6.1		
All small calidridines[b]	54.3	50.0		
All *en route*-only shorebirds	71.6	63.6		
Breeding species[c]				
Snowy Plover (*Charadrius alexandrinus*)	1.2	0.0		
Piping Plover (*C. melodus*)	1.2	0.0		
Killdeer (*C. vociferus*)	69.1	87.9	0.247	0.245
American Avocet (*Recurvirostra americana*)	21.0	16.7	0.106	0.619
Willet (*Catoptrophorus semipalmatus*)	33.3	31.8	0.133	0.398
Spotted Sandpiper (*Actitis macularia*)	17.3	21.2	0.037	−0.065
Upland Sandpiper (*Bartramia longicauda*)	9.9	15.2	0.000	−0.130
Marbled Godwit (*Limosa fedoa*)	25.9	13.6	0.048	0.095
Wilson's Snipe (*Gallinago delicata*)	7.4	9.1	0.039	0.353
Wilson's Phalarope (*Phalaropus tricolor*)	40.7	42.4	0.088	0.221
All breeding shorebirds	81.4	92.6		
All shorebirds	86.4	90.9		

[a]Similarity measured by Sorenson quantitative index (C_N) and Spearman's rank correlation (r_s) for 60 townships surveyed in both years. We considered abundances between years to be independent for species with $C_N < 0.10$ and $r_s < 0.255$ ($P = 0.05$, two-tailed). Similarity indices were not calculated for rare and uncommon species (species for which % sites_{2002} + $\%\text{sites}_{2003} < 10$).
[b]Small calidridines, including Semipalmated, Least, Baird's, and White-rumped sandpipers, are often difficult to distinguish visually.
[c]Denotes species that both breed in the prairie potholes and migrate through to more northerly breeding areas.

accessibility and safety reasons. We focused survey efforts on the wetland basins and wet or inundated fields; upland areas were not scrutinized. The same sample of randomly selected townships was used for each year of the study, a decision based on the assumption that most migrating shorebirds select stopover habitats opportunistically each year (Skagen and Knopf 1994a).

Field efforts.—During northward and southward migrations in 2002 and 2003, we surveyed shorebirds and recorded habitat conditions at three site types: randomly selected townships, "known" stopover sites, and incidental sites. We defined "known" sites as wetlands known to host migrating shorebirds historically, such as National Wildlife Refuges, based on counts reported in Skagen et al. (1999). In this group, we also included a site (Mud Lake, Minnesota; 48°48′30″N, 96°35′50″W) where water was drawn down as a management action, immediately creating suitable shorebird habitat. Historical maximum counts at 25 selected known stopover sites totaled >150,000 shorebirds during northward migration. We defined "incidental" sites as any site not designated as part of a township or known site where birds were encountered and recorded *ad libitum* (as observer time allowed). In spring 2002, 81 townships (including ~7,800 wetlands within those townships) were surveyed twice by 4 field technicians, and in spring 2003, 66 townships were surveyed one to three times by 37 volunteers and 3 field technicians. During our southward-migration study period, 72 townships were surveyed once in 2002, and 16 townships were surveyed one to three times by volunteers in 2003. In addition, known sites (25 during northward migration in 2002 and 2003; 24 and 11 during southward migration in 2002 and 2003, respectively) were surveyed as completely as possible from existing roads and vantage points. We provided site maps showing all National Wetlands Inventory wetlands for townships and known sites, comprehensive documents describing field protocol, and data sheets to all volunteers and field assistants.

Surveys were conducted from 24 April to 25 May (32 days) in 2002 and 3–31 May (29 days) in 2003. Survey dates were selected on the basis of existing chronology information on shorebird migration in the region (S. K. Skagen unpubl. data); 90% of northbound migrants were sighted during late April and May. Southward-migration study periods were from 23 July to 5 August 2002 and from 20 July to 13 August 2003; because southward migration is protracted, these dates captured only part of the migration.

Data analyses.—To test our assumption that most *en route* shorebirds select stopover habitats opportunistically each year, we evaluated whether bird abundances were independent between years in 60 townships that were common to both northward migration samples. We evaluated between-year independence for 21 species that occurred, on average, in ≥5% of the township sites. We used Spearman's rank correlation (r_s) and Sorensen's quantitative index of similarity, $C_N = 2_{jN}/(aN + bN)$, where aN is the total number of individuals in spring 2002, bN is the total number of individuals in spring 2003, and jN is the sum of the lower of the two abundances recorded for species found in both years across all sites (Magurran 1988:95). We considered abundances between years to be independent for species with $C_N < 0.10$ and $r_s < 0.255$ ($P = 0.05$, two-tailed).

Population estimates for the entire study area were calculated using only the township counts. For each surveyed township, we estimated the mean numbers of all shorebird species in the township by extrapolating shorebird numbers recorded from the sampled area (road segments) to the entire township area, assuming no biases. We then extrapolated mean numbers from our counts to the respective landscape strata. Formulae for population estimates, standard errors, and degrees of freedom for stratified sampling follow Scheaffer et al. (1986) and Bart et al. (1998) and do not include finite population correction factors. We present population estimates for each season, having combined the northward-migration data to build two-year population estimates only for species whose abundances within sites were independent between years.

We distinguished between two groups of shorebirds based on location of breeding grounds: (1) species that breed north of the prairie potholes and occur in the study area only when migrating between wintering and breeding areas ("*en route*-only" species), and (2) species that breed in the prairie potholes (breeding species), of which some proportion of the population is likely *en route* to more northern breeding grounds. For the second group, we estimated the proportion of each population that is likely *en route* by viewing Breeding Bird Survey distribution maps (Sauer et al. 2005) and assessing the extent of breeding range north of the Prairie Pothole Region. Our estimates of the proportion *en route* were as follows: Killdeer, 0.2; American Avocet, 0.0; Willet, 0.1; Spotted Sandpiper, 0.3; Upland Sandpiper, 0.1; Marbled Godwit, 0.2; Wilson's Snipe, 0.5; and Wilson's Phalarope, 0.1.

For species that are *en route* only, we estimated the total population (i.e., the number of shorebirds stopping in the study area during the study period) as

$$\widehat{N} = \frac{T}{\overline{B}}\overline{y}$$

where T is the length of the survey period in days, $\overline{B}$ is the assumed average residency period in days, and $\overline{y}$ is the estimate of the mean number of birds present in the study area during the study period. For ease of calculation and because more precise information is not yet available, we assumed a seven-day residency period for *en route* migrants for both northward and southward migrations. This estimate was based on average residency periods of a few species in the midcontinental region, notably northbound Semipalmated and White-rumped sandpipers in Kansas (3.8 days and 7.0 days, respectively; Skagen and Knopf 1994b), southbound Least and Pectoral sandpipers in Minnesota (7.2 days and 4.9 days, respectively; N. Thomas pers. comm.), and northbound [and southbound] Least and Pectoral sandpipers in Missouri (9.7 days and 10.5 days [3.6 days and 4.9 days], respectively; Farmer and Durbian 2006). We determined the percentage of *en route* shorebirds that were likely sampled during our study period by using chronology information from a database used to generate chronology histograms in Skagen et al. (1999).

Results

Shorebirds were recorded in 88.4% of townships surveyed during northward migration 2002 and 2003 (86.4% and 90.0%, respectively). During southward migration surveys, shorebirds were recorded in 61.1% of townships in 2002 and in 64.8% of townships across both years. Bird distributions during northward migration were independent between years for all *en route*-only species and breeding species except Killdeer, American Avocet, Willet, and Wilson's Snipe (Table 1). Between-year similarity in distribution (measured by Sorenson's similarity index) was greater for breeders and for widespread species, as indicated by a regression model containing both migration status (coded as 0 for *en route* species and 1 for breeding species; partial $t = 2.243$, df $= 2$ and 18, $P = 0.038$) and frequency of occurrence (percentage of townships with species occurrence; partial $t = 7.117$, df $= 2$ and 18, $P = 0.000$).

Average daily use.—On average, on any day during our northward-migration study period, ~2.3 million (95% confidence interval [CI]: 1.6–3.0 million) shorebirds were present in the prairie pothole landscape (Table 2). Northbound *en route*-only migrants constituted 72% of all shorebirds documented. Small calidridine species, or peeps, constituted 53% of the *en route*-only shorebird population. The average abundances of *en route* migrants in the study area differed between spring 2002 and 2003, with notably more yellowlegs, Hudsonian Godwits, Pectoral Sandpipers, and dowitchers in spring 2002, and more White-rumped, Baird's, and Stilt sandpipers in spring 2003 (Table 2).

During southward migration, 2.4 million (95% CI: 1.2–3.6 million) shorebirds occurred daily in wetland habitats and inundated fields in the study area; 82% were *en route*-only shorebirds (Table 3). Small calidridine sandpipers were less numerous in the fall (16% of all *en route*-only shorebirds) than in the spring,

Table 2. Number of shorebirds (mean ± SE) in the prairie pothole study area during northward migration and coefficient of variation (CV) of population estimates for spring 2002, 2003, and both years combined where appropriate.

	Average number of shorebirds in the study area during the study period					
	Spring 2002 (n = 81)		Spring 2003 (n = 66)		Springs 2002 + 2003 (n = 147)	
Species	(mean ± SE)	CV	(mean ± SE)	CV	(mean ± SE)	CV
***En route*-only species**						
Black-bellied Plover	0		9,758 ± 5,428	0.56	4,337 ± 3,687	0.85
Semipalmated Plover	12,904 ± 5,399	0.42	15,354 ± 7,148	0.47	14,229 ± 4,716	0.33
Greater Yellowlegs	33,312 ± 14,748	0.44	2,677 ± 1,743	0.65	20,832 ± 9,102	0.44
Lesser Yellowlegs	200,980 ± 53,138	0.26	24,435 ± 7,077	0.29	128,101 ± 34,693	0.27
Solitary Sandpiper	5,212 ± 1,800	0.35	1,957 ± 1,309	0.67	3,809 ± 1,330	0.35
Hudsonian Godwit	25,269 ± 12,125	0.48	5,332 ± 3,780	0.71	16,229 ± 6,974	0.43
Semipalmated Sandpiper	168,833 ± 51,881	0.31	177,092 ± 66,886	0.38	170,681 ± 43,645	0.26
Least Sandpiper	165,005 ± 44,653	0.27	122,170 ± 41,781	0.34	145,642 ± 34,152	0.23
White-rumped Sandpiper	222,971 ± 63,369	0.28	605,343 ± 265,590	0.44	388,781 ± 132,773	0.34
Baird's Sandpiper	17,411 ± 8,834	0.51	75,179 ± 48,378	0.64	43,377 ± 32,082	0.74
Pectoral Sandpiper	77,621 ± 24,019	0.31	28,969 ± 12,794	0.44	55,730 ± 14,998	0.27
Dunlin	78,804 ± 35,635	0.45	91,429 ± 58,575	0.64	86,017 ± 36,375	0.42
Stilt Sandpiper	160,552 ± 51,691	0.32	449,592 ± 210,986	0.47	285,440 ± 96,597	0.34
Dowitchers	224,591 ± 124,412	0.55	54,141 ± 36,018	0.67	140,409 ± 63,658	0.45
Red-necked Phalarope	4,446 ± 2,736	0.62	40,468 ± 30,502	0.75	19,171 ± 12,246	0.64
All small calidridines[b]	721,268 ± 169,560	0.24	1,116,407 ± 365,661	0.33	887,189 ± 197,613	0.22
All *en route*-only shorebirds	1,566,201 ± 326,374	0.21	1,844,937 ± 659,213	0.36	1,675,664 ± 346,954	0.21
Breeding species						
Killdeer	109,716 ± 16,925	0.15	208,766 ± 37,777	0.18		
American Avocet	59,148 ± 25,202	0.43	26,777 ± 10,558	0.39		
Willet	56,674 ± 25,101	0.44	33,805 ± 12,404	0.37		
Spotted Sandpiper	9,043 ± 3,958	0.44	20,276 ± 13,160	0.65	14,064 ± 9,223	0.66
Upland Sandpiper	8,129 ± 4,395	0.54	11,211 ± 4,375	0.39	9,464 ± 4,037	0.43
Marbled Godwit	53,363 ± 22,040	0.41	11,429 ± 5,364	0.47	35,767 ± 13,435	0.38
Wilson's Snipe	5,901 ± 2,563	0.43	75,347 ± 69,431	0.92		
Wilson's Phalarope	291,469 ± 90,339	0.31	317,438 ± 92,335	0.29	303,441 ± 65,329	0.22
All breeding shorebirds	597,962 ± 125,861	0.21	705,048 ± 138,667	0.20	651,505 ± 93,634[c]	0.14
All shorebirds	2,159,644 ± 415,747	0.19	2,549,985 ± 695,759	0.27	2,327,169 ± 359,367[d]	0.15

[a] Number of townships surveyed each year is designated by n. American Golden Plover, Ruddy Turnstone, Sanderling, Buff-breasted Sandpiper, Snowy Plover, and Piping Plover are not included, because population estimation using this method was clearly not successful (CV = 1.00).
[b] Semipalmated, Least, Baird's, and White-rumped sandpipers are often difficult to distinguish visually.
[c] Means derived by averaging estimates of 2002 and 2003.
[d] Sum of *en route*-only shorebirds and breeding shorebirds in the combined years of 2002–2003.

primarily because of the absence of White-rumped Sandpipers and Dunlin. Yellowlegs, Pectoral Sandpipers, and dowitchers were more abundant during southward than northward migrations and constituted 17%, 18%, and 23% of the southbound *en route*-only shorebird population, respectively. With the exception of Killdeer and Spotted Sandpipers, breeding species were less abundant during the late-summer–fall than spring study periods.

Precision of estimates.—In 2002, the precision of average daily population estimates (coefficient of variation) was positively correlated with extent of occurrence (for breeding and *en route*-only species combined, Pearson's $r = -0.837$, df = 20, $P < 0.001$ for northward migration; $r = -0.862$, df = 16, $P < 0.001$ for southward migration; Fig. 1). In other words, population estimates for widespread species tended to be more precise than estimates for species with more constrained distributions. Widespread species were also more abundant, as revealed by positive correlations between population estimates and the percentage of townships in which shorebird species were detected ($r = 0.613$, df = 20, $P < 0.005$ for northward migration and $r = 0.601$, df = 16, $P < 0.01$ for southward migration).

To determine whether stratification into four landscape types improved precision of the average daily population estimates over a simple random sample, we calculated the percentage of reduction in standard errors afforded by stratification as $(SE_{srs} - SE_{str}) / SE_{str}$, where SE_{srs} is the standard error under the assumption that townships represent a simple random sample, and SE_{str} is the standard errors obtained from the stratified random samples. (We recognize that a proportional allocation of samples across the four strata would improve the value of this exercise.) Stratification improved population estimates for six species and two groups of *en route*-only migrants; standard errors were reduced by >5% during both of the two spring seasons for Semipalmated Plover (32% average reduction for 2002 and 2003 spring seasons), Hudsonian Godwit (25%), Semipalmated Sandpiper (30%), Least Sandpiper

Table 3. Percentage of townships surveyed ($n = 72$) in which southbound shorebirds were detected (% sites), number of shorebirds (mean ± SE), and coefficient of variation (CV) in late summer and early fall 2002.

	Average number of shorebirds in the study area during the study period		
Species	(% sites)	(mean ± SE)	CV
***En route*-only species**			
Semipalmated Plover	15.3	29,829 ± 13,323	0.45
Greater Yellowlegs	22.2	52,985 ± 15,700	0.30
Lesser Yellowlegs	50.0	283,578 ± 63,956	0.23
Solitary Sandpiper	13.9	12,320 ± 5,578	0.45
Semipalmated Sandpiper	19.4	60,716 ± 26,860	0.44
Least Sandpiper	36.1	96,473 ± 24,022	0.25
Baird's Sandpiper	19.4	59,116 ± 26,977	0.46
Pectoral Sandpiper	40.3	356,712 ± 98,380	0.28
Stilt Sandpiper	16.7	225,412 ± 106,268	0.47
Dowitchers	16.7	444,791 ± 284,791	0.64
All small calidridines[a]	40.3	320,111 ± 90,463	0.28
All *en route*-only shorebirds	55.6	1,946,224 ± 539,160	0.28
Breeding and *en route* species			
Killdeer	58.3	260,322 ± 47,715	0.18
American Avocet	4.2	5,216 ± 3,603	0.69
Willet	5.6	8,088 ± 5,812	0.72
Spotted Sandpiper	19.4	14,503 ± 5,737	0.40
Upland Sandpiper	2.8	2,796 ± 2,416	0.86
Marbled Godwit	2.8	4,683 ± 4,302	0.92
Wilson's Snipe	0	0 ± 0	
Wilson's Phalarope	19.4	141,592 ± 65,893	0.47
All breeding shorebirds	61.1	437,201 ± 98,282	0.22
All shorebirds	61.1	2,383,425 ± 615,004	0.26

[a]Semipalmated, Least, Baird's, and White-rumped sandpipers are often difficult to distinguish visually.

(7%), White-rumped Sandpiper (26%), Stilt Sandpiper (35%), dowitchers (70%), and all small calidridines (29%). The first six species exhibited similar affinities, occurring in greatest densities in stratum 4 (high wetland area and high cropland area, mean ± SE = 844 ± 467 birds per township, $n = 36$), intermediate densities in strata 1 (340 ± 136 birds per township, $n = 37$) and 3 (338 ± 114 birds per township, $n = 38$), and lowest densities in stratum 2 (low wetland area and high cropland area, 129 ± 93 birds per township, $n = 36$). By contrast, dowitchers occurred in greatest densities in stratum 1 (low wetland area and low cropland area, 171 ± 128 birds per township), in intermediate densities in strata 3 (31 ± 14 birds per township) and 4 (51 ± 31 birds per township), and were absent from stratum 2. Consistent increases in standard errors with stratification suggested that a simple random sampling approach (or stratification with differently designated strata) would provide better precision for Baird's Sandpiper; standard errors in 2002 and 2003 increased by 10% and 31% under stratification.

Study periods in relation to migration chronology.—Our northward-migration study period encompassed the major *en route* movements of many, but not all, of the abundant shorebird species. We estimate that 89% of the northbound migrants were sampled in our study, based on species-specific migration chronology data (Skagen et al. 1999; Table 4), including nearly 100% of Least Sandpipers, Dunlin, and Stilt Sandpipers. Existing chronology information suggests, however, that survey coverage extending into early to mid-April would capture a larger portion of northbound Greater and Lesser yellowlegs, Solitary Sandpipers, Hudsonian Godwits, and Baird's Sandpipers, and later surveys would include more Black-bellied Plovers, White-rumped Sandpipers, and Red-necked Phalaropes (Fig. 2).

By contrast, our briefer southward-migration study period encompassed only a fraction of the migration periods of most *en route* species. Survey periods of 8–10 weeks, generally

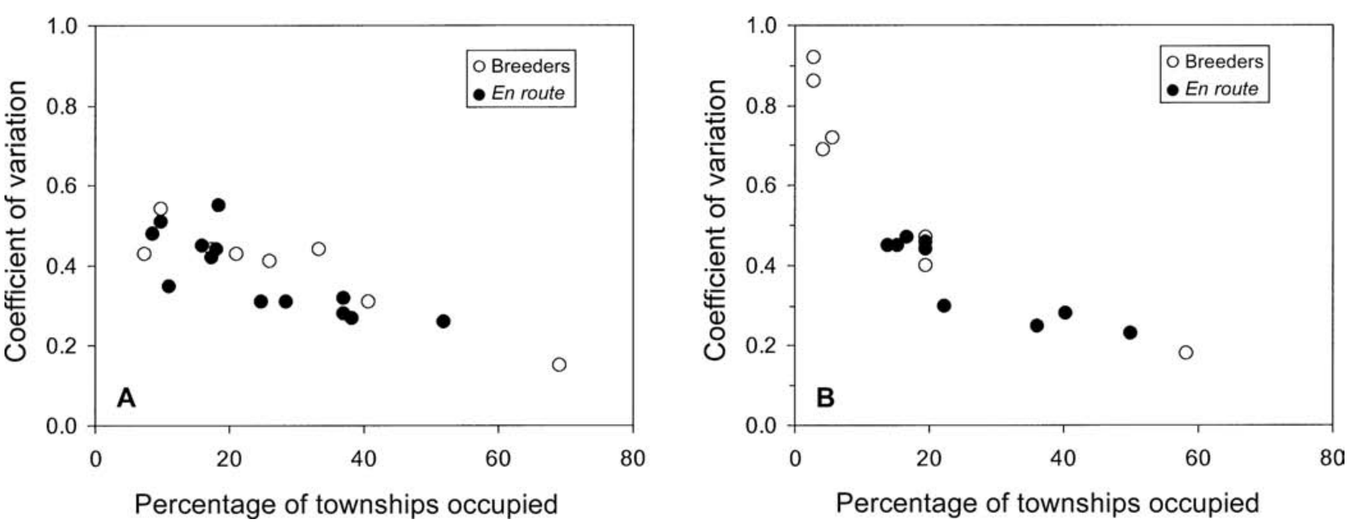

Fig. 1. Precision of population estimates (as expressed by the coefficient of variation) is greater for breeding and migrating shorebirds with broader distributions (species that occupy a larger percentage of surveyed townships) during (A) northward and (B) southward migration across the prairie pothole landscape of the United States, 2002.

Table 4. Estimate (± SE) of the total number of *en route* shorebirds using the prairie pothole study area during northward (average 30.5 days) and southward (14 days) migration study periods, assuming average residency of 7 days for northbound and southbound birds.[a]

	Northward migration 2002–2003		Southward migration 2002	
Species	Sampled (%)	Estimate ± SE	Sampled (%)	Estimate ± SE
Black-bellied Plover	67	18,897 ± 16,064	5	0
Semipalmated Plover	91	61,999 ± 20,546	22	59,658 ± 26,645
Greater Yellowlegs	31	90,766 ± 39,658	16	105,971 ± 31,399
Lesser Yellowlegs	80	558,156 ± 151,163	17	567,156 ± 127,913
Solitary Sandpiper	74	16,596 ± 5,797	23	24,639 ± 11,156
Hudsonian Godwit	73	70,710 ± 30,385	N/A	0
Semipalmated Sandpiper	92	743,683 ± 190,166	26	121,432 ± 53,719
Least Sandpiper	98	634,582 ± 148,806	22	192,947 ± 48,045
White-rumped Sandpiper	83	1,693,976 ± 578,512	N/A	0
Baird's Sandpiper	73	189,000 ± 139,786	19	118,232 ± 53,954
Pectoral Sandpiper	90	242,824 ± 65,349	15	713,424 ± 196,761
Dunlin	99	374,787 ± 158,491	N/A	0
Stilt Sandpiper	100	1,243,703 ± 420,889	29	450,825 ± 212,536
All dowitchers	86	611,784 ± 277,366	10	889,582 ± 569,582
Red-necked Phalarope	86	83,530 ± 53,358	13	0
All small calidridines[b]	86	3,865,609 ± 861,029	24	640,222 ± 180,926
All *en route*-only shorebirds	89	7,301,108 ± 1,511,728	16	3,892,447 ± 1,078,319
En route component of breeding populations[c]		99,347 ± 36,724		71,440 ± 18,430

[a] Estimates of the percentage of the total population sampled (percentage sampled) during the study periods are based on species-specific migration chronology (Skagen et al. 1999).
[b] Semipalmated, Least, Baird's, and White-rumped sandpipers are often difficult to distinguish visually.
[c] The *en route* component of breeding populations calculated as proportion *en route* × average population size for each species.
N/A = not available.

extending to mid-September, would be necessary to cover ≥80% of many southbound shorebird populations (Fig. 2).

Estimates of total migrant population.—When incorporating assumptions of residency periods from township counts, we estimated that 7.3 million *en route*-only shorebirds (95% CI: 4.3–10.3 million) stop to rest and refuel in the study area during northward migration (Table 4). During the shorter southward-migration study period, 3.9 million *en route*-only shorebirds (95% CI: 1.7–6.0 million) stopped in the study area. By adding in the breeding species and their estimated "*en route* proportion," the above estimates would increase by 0.1 million and 0.07 million shorebirds during northward and southward migrations, respectively.

Survey results from known site counts.—When incorporating our assumptions of residency periods, the known stopover sites hosted 26,247 and 29,495 northbound *en route*-only migrants during our study periods in 2002 and 2003, and 13,028 southbound *en route*-only shorebirds in 2002. Breeding birds (adjusted to include the *en route* proportion) totaled 1,506 and 2,042 in springs 2002 and 2003 and 3,333 in fall 2002. Approximately 62% of northbound shorebirds and 27% of southbound shorebirds at the known sites were small calidridines.

Discussion

Several lines of evidence reveal the vital role that wetlands of the central prairies of North America play in the life cycles of migratory shorebirds. Shorebirds following a transcontinental migration route appear to be more vulnerable to population declines than coastal or oceanic migrants (Thomas et al. 2006) and, as is the case with coastal shorebird migrants, the reproductive success of transcontinental migrant shorebirds may be closely linked with foraging conditions at the last few, or the penultimate, spring stopover sites (Krapu et al. 2006, Morrison 2006, Skagen 2006). The population estimates reported here suggest that 7.3 million shorebirds refuel in the U.S. portion of the Prairie Pothole Region during northward migration. Many of these birds, and notably calidridine sandpipers, which constitute more than half of the northbound migrants, may depend highly on these penultimate spring stopover sites to maintain adequate body condition for successful breeding.

Our point estimates of northbound shorebirds (7.3 million, including 3.9 million calidridines) far exceed earlier compilations of maximum counts across the entire interior flyway (2.3 million shorebirds, including 1.4 million calidridines; Morrison et al. 2001). Several million shorebirds sought foraging resources during our study, even though less suitable shorebird habitat was probably available to birds than during wetter years (when calidridine sandpipers primarily use temporary and seasonal wetlands containing water) or after a series of dry years (when calidridines congregate in semipermanent wetlands with exposed muddy shorelines; Skagen et al. 2005). In general, the condition of wetlands in our study area during 2002–2003 reflected a time of transition from a 10-year wet period to a drier period (Johnson et al. 2004); most semipermanent wetlands affected by groundwater levels were still full, yielding little or no shoreline or mudflats, and many temporary and seasonal wetlands normally filled by precipitation and runoff were dry.

There is a growing need for quantitative information on dispersed bird populations during migration, for methods and

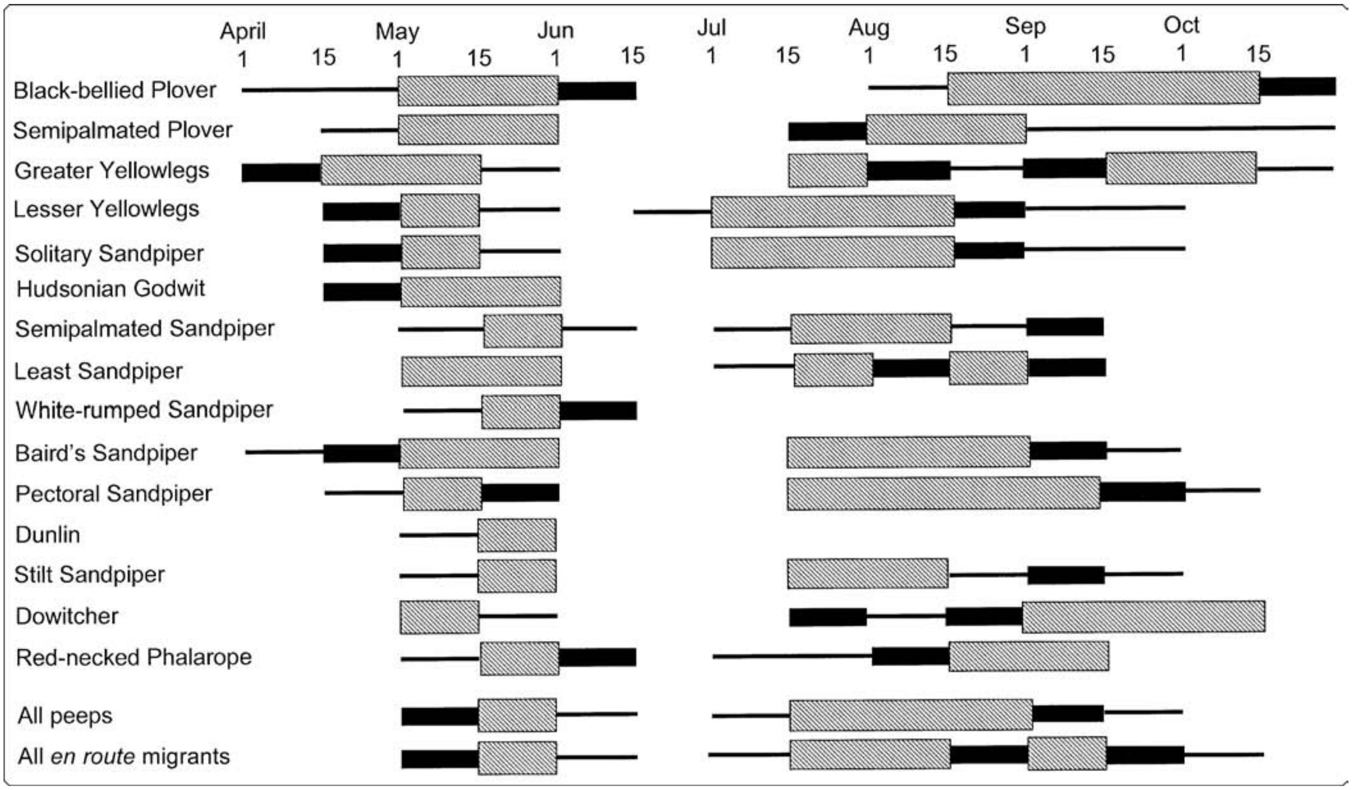

Fig. 2. Expected migration chronology of northbound and southbound shorebirds between 45°N and 50°N latitude (modified from Skagen et al. 1999). Wide hatched bars represent two-week periods that cover 60–75% of the population, wide bars in combination with black bars of intermediate width cover 80–92% of the population, and all bars, including narrow black bars, cover 95–99% of the population.

techniques to monitor populations and to assess environmental effects, and for conservation strategies that can operate at the appropriate temporal and spatial scales. Especially during migration, dispersed bird populations in highly dynamic landscapes often do not gain the attention of scientists and managers as strikingly large avian congregations in well-known important sites do. Our study illustrates a place in time where most migrating birds are highly dispersed. Further, in the extensive wetland landscapes of the Prairie Pothole Region, environmental threats such as erosion and sedimentation can be subtle and far-reaching. This study reveals that many shorebird species, especially calidridines, tend to occur in landscapes of high wetland densities in matrices of tilled croplands (see also Skagen et al. 2005). We commend the Western Hemisphere Shorebird Reserve Network Hemispheric Council for recently creating a new designation—a Landscape of Hemispheric Importance—to supplement their set of conservation tools and to herald a new generation of conservation efforts that can more effectively address shorebird conservation in extensive prairie wetland landscapes.

Our approach to population estimation, based on stratified random selection of townships as sample units, holds promise as a monitoring tool for several migrating wetland-dependent shorebird species, especially those that are common and widespread. The findings of our study and another study of small isolated wetlands in the Drift Prairie of North Dakota are mutually supportive; Niemuth et al. (2006) estimate that 3.6 million (95% CI: 2.0–5.2 million) breeding and *en route*-only shorebirds use the temporary and seasonal wetlands in the Drift Prairie during spring. A target coefficient of variation for the population estimate of 0.31 or lower, based on guidelines of the Program for Regional and International Shorebird Monitoring (PRISM; 80% power to detect a 50% decline occurring during 20 years, using a two-tailed test with the significance level set at 0.15; Bart et al. 2005), was met or nearly met for northbound and southbound Lesser Yellowlegs, Least Sandpipers, and Pectoral Sandpipers, northbound Semipalmated Plovers, Solitary Sandpipers, Semipalmated Sandpipers, White-rumped Sandpipers, and Stilt Sandpipers, and southbound Greater Yellowlegs. This target level of precision could be attained for northbound Hudsonian Godwit, Dunlin, and dowitchers with a larger sample or an alternative design such as a serial alternating panel approach (Roesch and Reams 1999, Manley et al. 2005). However, our method is clearly inappropriate for other species, especially those that are rare or whose distributions are highly aggregated, for example, American Golden-Plovers, Ruddy Turnstones, Sanderlings, Buff-breasted Sandpipers, and Black-bellied Plovers.

In extensive and dynamic wetland systems such as the prairie pothole landscape, we do not recommend a monitoring program based solely on repeated counts of important sites with historically high shorebird numbers. With a few exceptions, such sites in this study did not provide optimal habitat for migrating shorebirds during northward migration in 2002 and 2003, and shorebird counts at these sites were lower than expected on the basis of historical counts. For example, prior spring counts in the drier years of the early 1990s at Dry Lake, South Dakota (44°56′45″N, 97°40′50″W), and Minnewaukan Flats, North Dakota (48°03′50″N, 99°09′20″W), exceeded 50,000 and 80,000 shorebirds, respectively (Skagen 1997), whereas counts of the same areas in 2002 and 2003 were less than 150 and 1,300, respectively. The low counts during our study were a direct result of the exceedingly high water levels at Dry Lake and Minnewaukan Flats (many roads were under water). Because the known stopover sites were not selected randomly from the landscape, there is no statistical basis by which to extrapolate these counts to estimate numbers of shorebirds across the landscape. However, surveying known sites as a separate stratum in conjunction with the randomly selected township-based approach could be especially important when shorebirds tend to congregate (e.g., in drier years when semipermanent wetlands provide substantial suitable habitat). With this dual approach, the area of the known sites would be subtracted from the total area used to extrapolate the township-based estimates, and the resulting census numbers from the known sites would be added to the township-based estimates.

Study design considerations.—The approach we used to estimate populations of migrating shorebirds could apply more broadly to other groups of birds and other regions where suitable habitats are widely dispersed and spatially and temporally unpredictable. We consider the population estimates presented here conservative in light of four potential sources of bias, sources that would need to be addressed before basing a rigorous monitoring program on this approach. First, we suspect a small negative bias because detection probability was <1 in parts of the transect area. Although we surveyed relatively narrow strip transects within 200 m of the road and assumed all birds present were detected, some birds may have been obscured by vegetation or topographical features. We suspect the bias is small because many of our target species avoid dense vegetation and prefer substrates with <25% vegetative cover (Helmers 1992), and most of the wetlands within 200 m in this relatively flat and rolling landscape were fully visible to the surveyor. Similarly, Niemuth et al. (2006) found that <4% of 1,181 temporary and seasonal wetlands in the agricultural Drift Prairie region of North Dakota were not completely visible from the road. In a sample of 759 wetlands, 14.4% (906 of 6,276 ha) of the habitat was wet mud or shallow water covered by vegetation (S. K. Skagen unpubl. data), which suggests that 14.4% of our strip transects was potential shorebird habitat in which the probability of detection was <1. If we adjust our population estimates based on recent estimates of detectability in moderately vegetated Missouri wetlands (Farmer and Durbian 2006), our estimates increase by ~10%.

Second, the population estimates could be positively or negatively biased if shorebirds distribute nonrandomly with respect to roads, either because of varying wetland distribution in relation to roads or because shorebirds avoid or are attracted to roads or roadside habitats. Two studies evaluating the potential for roadside bias in the prairie potholes found no evidence of such bias in waterfowl (Austin et al. 2003) or in areas of temporary and seasonal wetlands along Breeding Bird Survey (BBS) routes in relation to the surrounding landscape (N. D. Niemuth pers. comm.). The area of semipermanent wetlands, however, is significantly underrepresented along roadsides (N. D. Niemuth pers. comm.), which suggests that our methods would underestimate shorebirds associated with this wetland type.

A third potential source of bias in population estimates may derive from assumptions of residency periods at stopover sites. We assumed an average residency period of seven days based on available estimates from the midcontinental region. A handling effect when capturing birds to apply radiotransmitters may increase the length of stay at the point of capture by as many as three days (Warnock and Bishop 1998, Lehnen and Krementz 2005). Because our assumptions of length of stay were based on studies that estimated residency at point of capture only, these estimates may be longer than actual residency periods. If we assumed a shorter average duration of stay, our population estimates would be greater. Finally, our estimates of southbound migrants are negatively biased because the migration window within which we surveyed did not encompass the entire migratory period. Further, to detect potential future shifts in chronology, we advise extending the study periods to encompass the entire migratory season during both spring and fall (Fig. 2).

Central North American prairie wetlands play a vital role in the conservation of migratory shorebirds, hosting >7,300,000 shorebirds, of which half are calidridine sandpipers. Because environmental threats in extensive wetland landscapes are often subtle but far-reaching, there is a pressing need for quantitative information on dispersed bird populations in highly dynamic landscapes. An approach to population estimation and monitoring that is based on stratified random selection of townships as sample units is well suited to at least 11 migratory shorebird species. With the recommended extensions and refinements, this approach may form the basis of rigorous monitoring programs in this and other prairie-wetland regions.

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Literature Cited

Austin, J. E., G. R. Guntenspergen, H. T. Sklebar, and T. K. Buhl. 2003. Differences in distribution of modified basins and ducks relative to roadside transects. Wetlands 23:140–148.

Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. de L. S. do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in Red Knots: Fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proceedings of the Royal Society of London, Series B 271:875–882.

Bart, J., B. Andres, S. Brown, G. Donaldson, B. Harrington, V. Johnston, S. Jones, R. I. G. Morrison, S. Skagen. 2005. The Program for Regional and International Shorebird Monitoring (PRISM). Pages 893–901 *in* Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference, vol. 2 (C. J. Ralph and T. D. Rich, Eds.). U.S. Department of Agriculture, Forest Service, General Technical Report PSW-GTR-191.

Bart, J., M. A. Fligner, and W. I. Notz. 1998. Sampling and Statistical Methods for Behavioral Ecologists. Cambridge University Press, Cambridge, United Kingdom.

Farmer, A., and F. Durbian. 2006. Estimating shorebird numbers at migration stopover sites. Condor 108:778–807.

Farrell, A. E., R. J. Plevin, B. T. Turner, A. D. Jones, M. O'Hare, and D. M. Kammen. 2006. Ethanol can contribute to energy and environmental goals. Science 311:506–508.

Helmers, D. L. 1992. Shorebird Management Manual. Western Hemisphere Shorebird Reserve Network, Manomet, Massachusetts.

Johnson, W. C., S. E. Boettcher, K. A. Poiani, and G. Guntenspergen. 2004. Influence of weather extremes on the water levels of glaciated prairie wetlands. Wetlands 24:385–398.

Johnson, W. C., B. V. Millett, T. Gilmanov, R. A. Voldseth, G. R. Guntenspergen, and D. E. Naugle. 2005. Vulnerability of northern prairie wetlands to climate change. BioScience 55:863–872.

Krapu, G. L., J. L. Eldridge, C. L. Gratto-Trevor, and D. A. Buhl. 2006. Fat dynamics of Arctic-nesting sandpipers during spring in mid-continental North America. Auk 123:323–334.

Lehnen, S. E., and D. G. Krementz. 2005. Turnover rates of fall-migrating Pectoral Sandpipers in the Lower Mississippi alluvial valley. Journal of Wildlife Management 69: 671–680.

Manley, P. N., B. Van Horne, J. K. Roth, W. J. Zielinski, M. M. McKenzie, T. J. Weller, F. W. Weckerly, and C. Vojta. 2005. Multiple species inventory and monitoring technical guide, version 1.0. U.S. Department of Agriculture, Forest Service, Washington, D.C. [Online.] Available at www.fs.fed.us/psw/programs/snrc/featured_topics/msim/documents/msim_preprint.pdf.

Margurran, A. E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey.

Morrison, R. I. G. 2006. Body transformations, condition, and survival in Red Knots *Calidris canutus* travelling to breed at Alert, Ellesmere Island, Canada. Ardea 94:607–618.

Morrison, R. I. G., R. E. Gill, Jr., B. A. Harrington, S. [K.] Skagen, G. W. Page, C. L. Gratto-Trevor, and S. M. Haig. 2001. Estimates of shorebird populations in North America. Canadian Wildlife Service Occasional Paper, no. 104. Ottawa, Ontario.

Niemuth, N. D., M. E. Estey, R. E. Reynolds, C. R. Loesch, and W. A. Meeks. 2006. Use of wetlands by spring-migrant shorebirds in agricultural landscapes of North Dakota's drift prairie. Wetlands 26:30–39.

Ringelman, J. K., Ed. 2005. Prairie Pothole Joint Venture 2005 Implementation Plan, Section I – Plan Foundation. [Online.] Available at www.ppjv.org/pdf/Part1_Foundation.pdf.

Roesch, F. A., and G. A. Reams. 1999. Analytical alternatives for an annual inventory system. Journal of Forestry 97:33–37.

Sauer, J. R., J. E. Hines, and J. Fallon. 2005. The North American Breeding Bird Survey, draft results and analysis 1966–2005, version 6.2.2006. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland. [Online.] Available at www.mbr-pwrc.usgs.gov/bbs/.

Scheaffer, R. L., W. Mendenhall, and L. Ott. 1986. Elementary Survey Sampling, 3rd ed. Duxbury Press, Boston, Massachusetts.

Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Skagen, S. K. 1997. Stopover ecology of transitory populations: The case of migrant shorebirds. Ecological Studies 125:244–269.

Skagen, S. K. 2006. Migration stopovers and the conservation of Arctic-breeding calidridine sandpipers. Auk 123:313–322.

Skagen, S. K., S. Brown, and R. Johnson. 2005. Implications of different shorebird migration strategies for habitat conservation. Pages 680–683 *in* Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference, vol. 2 (C. J. Ralph and T. D. Rich, Eds.). U.S. Department of Agriculture, Forest Service, General Technical Report PSW-GTR-191.

Skagen, S. K., and F. L. Knopf. 1994a. Migrating shorebirds and habitat dynamics at a prairie wetland complex. Wilson Bulletin 106:91–105.

Skagen, S. K., and F. L. Knopf. 1994b. Residency patterns of migrating sandpipers at a midcontinental stopover. Condor 96:949–958.

Skagen, S. K., P. B. Sharpe, R. G. Waltermire, and M. B. Dillon. 1999. Biogeographical profiles of shorebird migration in midcontinental North America. U.S. Geological Survey, Biological Science Report USGS/BRD/BSR—2000–0003. Fort Collins, Colorado. [Online.] Available at www.fort.usgs.gov/Products/Publications/555/toc.html.

Thomas, G. H., R. B. Lanctot, and T. Székely. 2006. Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. Animal Conservation 9:252–258.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science 292:281–284.

Warnock, N., and M. A. Bishop. 1998. Spring stopover ecology of migrant Western Sandpipers. Condor 100:456–467.

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