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HABITAT USE BY BREEDING AND MIGRATING SHOREBIRDS IN SOUTHCENTRAL SASKATCHEWAN

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ABSTRACT.—Habitat use by breeding and migrating shorebirds was studied at three sites in southcentral Saskatchewan from May through August 1984, a year of extreme drought conditions. Habitat use among species was examined using ordination and classification analyses. At each site, analyses identified four major species groups in different zones of a terrestrial–aquatic habitat gradient. Patterns of habitat use differed between breeders and migrants at the one site with large numbers of nesting individuals; the average seasonal shift in habitat use was greater for breeders than for migrants. Overall, habitat use differed among taxonomic groups at two of three sites, but this pattern was reduced to only one site when seasonal patterns were examined. There was no significant difference among taxa in seasonal changes of habitat use. Interspecific differences in habitat use are discussed with regard to morphology, annual cycles, and migration chronology. *Received 7 Jan. 1988, accepted 6 June 1988.*

Habitat use by assemblages of migrating (Recher 1966, Recher and Recher 1969, Burger et al. 1977, Burger 1984), breeding (Holmes and Pitelka 1968, Baker 1979, Connors et al. 1979a), and wintering shorebirds (Baker and Baker 1973, Baker 1979, Myers and Myers 1979) has received considerable attention, particularly in marine habitats (Pitelka 1979, Evans et al. 1984, Davidson and Pienkowski 1987). However, habitat use has been studied less often in mixed groups of breeding and migrating species, and relatively few studies have examined shorebird habitat use at inland, freshwater sites in North America. As a result, an understanding of habitat requirements of many shorebird species that use wetlands of the continental interior of North America, either as breeding sites or migratory staging areas, is negligible. Such a dearth of knowledge may compromise management endeavors that seek to maintain viable populations.

Although management schemes for prairie wetlands are founded on a mixed-species, multi-use approach, waterfowl have been the focus of most such efforts (Peek 1986). Since shorebirds as a group are more terrestrial than waterfowl, waterfowl management practices that maximize availability of deep-water areas in close proximity to nesting habitat may benefit some shorebird species. However, patterns of habitat use of most

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migrant shorebirds may run counter to common waterfowl management efforts that seek to restrict some terrestrial habitats.

We studied shorebirds in southcentral Saskatchewan, Canada during 1984, a year of extreme drought conditions when approximately 90% of local wetlands were dry. As a result, shorebirds were concentrated at a limited number of wetlands, and locally breeding species may have experienced restricted breeding opportunities (Colwell 1986). This paper presents data on habitat use by breeding and migrating shorebirds at three prairie wetlands and makes suggestions for shorebird management practices in the prairies.

METHODS

Study areas.—Shorebirds were censused in northern prairie habitat at Last Mountain Lake National Wildlife Area (51°10′N, 110°2′W) in southcentral Saskatchewan, Canada. For comparative purposes, three wetland sites (Colwell 1987) were chosen that differed in substrate, vegetation, and open-water features. Additionally, census data from 1982 and 1983 (Colwell, unpubl. data) indicated that, together, these sites included habitat that enabled a complete survey of both migrating and breeding shorebirds in the area (Colwell 1987).

Shorebirds were censused from 30 April to 30 August 1984 at Lanigan Creek, a 100-ha site with a permanent wetland and surrounding pasture that was grazed by 45–50 cattle from late May to autumn. The study area was divided by a steep-banked, deep-water creek that was dammed on its northern half by a man-made structure. Dense bulrush (*Scirpus paludosus*) stands bordered open-water areas. During spring, wet meadow dominated the study area, and mudflats constituted a small amount of available habitat. However, as summer progressed, mudflats became increasingly available to shorebirds. Salt-tolerant grasses (*Distichlis stricta, Puccinellia nuttalliana*) and forbs (*Plantago eriopoda, Salicornia rubra, Glaux maritima*) bordered the creek and wet meadow. During spring, flooded grasses (*Hordeum jubatum, Koeleria gracilis, Poa* spp.) and sedges (*Carex* spp.) rimmed deep-water areas. In upland habitat, over-grazed grasses (*Poa* spp.) and forbs (*Anemone canadensis, Achillea millefolium*) separated patches of buckbrush (*Symphoricarpos occidentalis*) and rose (*Rosa acicularis*). Shorebirds also were observed from 8 May to 28 August 1984, 1.5 km south of Lanigan Creek at Basin A, a 10-ha shallow-water site typified by expansive mudflats under varying moisture conditions. Bulrush and foxtail barley dominated the vegetation. Drought conditions combined with gently sloping terrain to expose extensive mudflats during July and August. Shorebirds also were censused from 3 May to 20 August 1984 at Perry's Beach, a 1.5-km stretch of sandy and rocky beach on the shore of Last Mountain Lake. Beach width varied from approximately 5 to 30 m; areas of the beach used by shorebirds were unvegetated. Lake water levels changed little at Perry's Beach during the study.

Sampling methods.—At Lanigan Creek and Basin A, one to three observers censused shorebirds from 3-m towers using 20–25× spotting scopes and 7× binoculars. At Perry's Beach, one observer walked the beach and recorded data at vantage points that maximized observations of shorebirds. A stratified random sampling scheme was used to schedule Lanigan Creek censuses (N = 222); during each successive week, observations were made during random sampling periods that included all daylight hours (05:00–21:00 h). Most Basin A censuses (N = 53) were paired with a Lanigan Creek survey. Perry's Beach was sampled less frequently (N = 23), particularly in the spring.

Observers scan-sampled (Altmann 1974) a site and recorded each bird's habitat and

TABLE 1

HABITATS USED BY SHOREBIRDS

UG[a]	Upland grasses (*Agropyron, Koeleria, Stipa, Distichlis, Poa*), forbs (*Anemone, Antennaria, Galium, Plantago, Glaux*), and shrubs (*Symphoricarpos, Rosa*)
HR	Wetland margins of foxtail barley (*Hordeum jubatum*)
GS	Unflooded grasses and sedges (*Triglochin maritima, Carex*)
WM	Wet meadows of flooded grasses, sedges (*Carex*), and forbs
MV	Compressed mats of aquatic vegetation resulting from standing water of early spring runoff
BR	Dense stands of thickstem bulrush (*Scirpus paludosus*)
SR	Unvegetated lakeshore substrate of rocks and sand
AD	Dried mud substrate occasionally sparsely vegetated (*Salicornia*)
AW	Unvegetated, wet mud substrate, dampened by proximity to standing water
AF	Unvegetated, mud substrate covered by a thin film of water
WL	Mud or sand substrate with water level less than the birds' upper tarso-metatarsal joint
WG	Mud or sand substrate with water level equal to or greater than the birds' upper tarso-metatarsal joint
OW	Unvegetated aquatic habitat with bird floating on surface
RK	Large rock elevated above substrate or vegetation

[a] Habitat acronyms are given for reference to figures.

behavior (Table 1). Wading shorebirds were assigned to habitats following Baker's (1979) scale relating water level to an individual's upper tarso-metatarsal joint. Distance to wetland edge was estimated on a logarithmic scale (1 = 0–10 cm, 2 = 11–100 cm, 3 = 1–10 m, 4 = 10–100 m, and 5 = greater than 100 m) and involved a bird's position relative to the aquatic–vegetative or aquatic–terrestrial interface.

Statistical methods.—For each site, data were summarized as the percent of total observations for a species in each habitat × distance category. Five distance categories and 9–14 habitats described 45–70 possible habitat classes. The number of habitat classes tallied was much less owing to unrepresented combinations of some habitat and distance measures (e.g., UG less than 10 cm from the wetland edge, AF greater than 100 m from the edge). Site differences resulted from the types of available habitat. Distances were not used for birds occupying some habitats (Table 1; GS, WM, and HR) because of difficulty in determining where edges occurred. Species were excluded from ordination (see below) if they were observed less than 10 times, and habitats were eliminated if they were used by one species exclusively. We did this to minimize distortion of analyses owing to rare occurrences.

The matrix consisting of species percent total observations in each habitat class was analyzed using detrended correspondence analysis (DCA, Hill 1979a). DCA, an improved ordination technique (Gauch 1982), has as its fundamental criterion the rescaling of second and higher axes resulting in no systematic relation to lower axes. This feature caused expansion and contraction of small segments along the species ordination, with the result that species turnover occurred at a uniform rate along ordination axes. Consequently, equal ordination distances among species corresponded to equal differences in sample composition (Gauch 1982).

Using shorebirds (species) and habitat classes (samples), DCA organized shorebirds based on similarities in habitat use. Shorebirds with similar patterns of habitat use were assigned similar axis scores. When species differed widely in the types of habitat they occupied, differences in axis scores were correspondingly greater. Thus, a species' axis score represents a composite of habitat use based on all habitats frequented by that species in relation to habitat use by all other species.

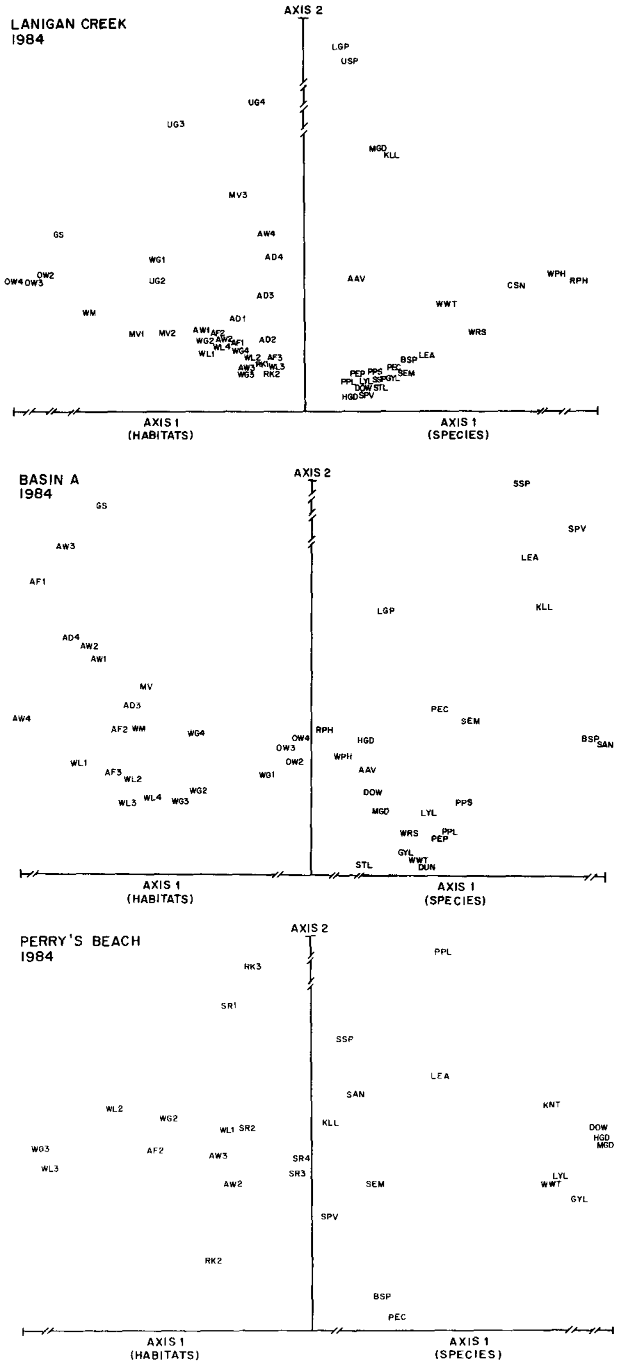
Indicator species analysis (ISA, Hill et al. 1975, Hill 1979b), a polythetic, divisive classification method, was used to categorize shorebird species based on similarities in habitat use. ISA used the same species × habitat matrix as DCA (percent total observations of a species in each habitat). Based on the ordination method of reciprocal averaging, ISA first ordinated the data and then used those habitats that characterized the extremes of ordination axes to polarize the species (Gauch 1982). Species were divided into two clusters by breaking the ordination axis at its middle, and the process continued with each subset of species until a minimum number of members was included (Gauch 1982). Gauch (1982) presents a thorough discussion of DCA and ISA.

Seasonal habitat use was examined by a combined ordination of spring and summer observations, based on the chronology of migration and breeding at Last Mountain Lake. A mid-June decline in the number of migrants followed by a July increase represented the hiatus between north and south migratory periods (Colwell et al., 1988a). Observations of shorebirds before and after 1 July were placed into spring and summer totals, respectively. Observations of breeding individuals, based on behavioral data, were placed into spring totals, regardless of date. Otherwise seasonal status of individuals of locally breeding species was judged by the same date criterion as migrants. Seasonal analyses were restricted to fewer species (see above) owing to diminution of sample sizes caused by the restricted sampling periods.

Patterns of habitat use were examined using nonparametric statistical tests (Siegel 1956, Sokal and Rohlf 1981) of DCA axis scores, and $P < 0.05$ was used for determining statistical significance. Species were divided into breeders and migrants based on the presence of locally breeding individuals in the area. Analyses of taxonomic correlates of habitat use were made at the level of the tribe or subfamily (AOU 1983).

RESULTS

Patterns of habitat use.—Shorebirds varied in their patterns of habitat use at each site. At Lanigan Creek, DCA portrayed a terrestrial–aquatic habitat gradient (Fig. 1); and ISA distinguished several groups (Table 2). Wilson's Phalaropes (*Phalaropus tricolor*) and Red-necked Phalaropes (*P. lobatus*) were conspicuous in their use of open-water areas. Wilson's Phalarope, which bred in large numbers at Lanigan Creek (Colwell and Oring, 1988), was less aquatic and frequented a greater range of habitats than Red-necked Phalarope. Lesser Golden Plover (*Pluvialis dominica*), Killdeer (*Charadrius vociferus*), American Avocet (*Recurvirostra americana*), Spotted Sandpiper (*Actitis macularia*), and Upland Sandpiper (*Bartramia longicauda*) occurred in terrestrial habitats. Marbled Godwits (*Limosa fedoa*) also used upland areas, but were grouped with most calidridine sandpipers (Sanderling, *Calidris alba*; Red Knot, *C. canutus*; Semipalmated Sandpiper, *C. pusilla*; Least Sandpiper, *C. minutilla*; Baird's Sandpiper, *C. bairdii*; Stilt Sandpiper, *C. himantopus*; Pectoral Sandpiper, *C.*


LANIGAN CREEK
1984
AXIS 2
LGP
USP
UG4
UG3
MGD
KLL
MV3
GS
AW4
WG1
AD4
OW4 OW3 OW2
UG2
AD3
AAV
CSN
WPH
RPH
WWT
WM
AD1
MV1
MV2
AW1
AF2
WG2
AW2
AF1
AD2
WRS
WL1
WL4
WG4
WL2
AF3
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RK1
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WG3
RK2
BSP
LEA
PEP
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SEM
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LYL
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GYL
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HGD
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AXIS 1
(HABITATS)
AXIS 1
(SPECIES)
BASIN A
1984
AXIS 2
SSP
GS
SPV
AW3
LEA
AF1
LGP
KLL
AD4
AW2
AW1
MV
AD3
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AW4
SEM
AF2
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WG4
RPH
OW4
HGD
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OW3
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OW2
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WL2
WG1
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DOW
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WG3
MGD
LYL
PPS
WRS
PPL
PEP
GYL
WWT
DUN
STL
AXIS 1
(HABITATS)
AXIS 1
(SPECIES)
PERRY'S BEACH
1984
AXIS 2
PPL
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SR1
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LEA
SAN
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WG2
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AW3
SR4
WL3
SR3
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GYL
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AXIS 1
(HABITATS)
AXIS 1
(SPECIES)

melanotus), tringine sandpipers (Willet, *Catoptrophorus semipalmatus*; Lesser Yellowlegs, *Tringa flavipes*; Greater Yellowlegs, *T. melanoleuca*), Hudsonian Godwit (*L. haemastica*), and Common Snipe (*Gallinago gallinago*), based on use of wet meadow and mudflats in close proximity to the wetland edge.

At Basin A, DCA portrayed a habitat continuum spanning open-water and mudflat habitats (Fig. 1). Four discrete groups were identified by the classification (Table 2). Phalaropes and American Avocet used open-water areas nearly exclusively. Dowitchers (*Limnodromus* spp.), Marbled Godwit, and Stilt Sandpiper waded in deep-water areas, greater than 10 m from shore. Shallow-water areas within 10 m of the wetland edge were frequented by tringine sandpipers and a group of calidridine sandpipers, including Dunlin (*Calidris alpina*). Mudflats were used by Semipalmated Plover (*Charadrius semipalmatus*), Killdeer, and several calidridine sandpipers.

At Perry's Beach, DCA depicted species across habitats from rocky shore to deep-water (Fig. 1); ISA identified four species assemblages (Table 2). Baird's Sandpiper was grouped with Spotted Sandpiper, Solitary Sandpiper (*T. solitaria*), and small plovers that frequented rocky shore zones greater than 10 m from the wetland edge. Closer to the lakeshore, but still using rocky shore habitat, were Black-bellied Plover (*P. squatarola*), Lesser Golden-Plover, Wilson's Phalarope, and several calidridine sandpipers. Lesser Yellowlegs and Willet also used the immediate lakeshore habitat, but were slightly more aquatic. American Avocet, godwits, dowitchers, Red Knot, tringines, and Stilt Sandpiper occupied aquatic habitats.

As a group, local breeders did not use different habitats than migrants, based on axis 1 scores (Mann-Whitney *U*-test: Lanigan Creek, $P = 0.58$;

←

FIG. 1. Habitat use by shorebird assemblages at Lanigan Creek, Basin A, and Perry's Beach, portrayed by species axis scores of detrended correspondence analysis. Species' habitat use (right side of each figure) can be viewed as the mirror image of habitats (left side of figure). Habitats are a combination of habitat acronyms (Table 1) and distance estimates (see text). Species acronyms: LGP, Lesser Golden-Plover; SPV, Semipalmated Plover; PPV, Piping Plover; KLL, Killdeer; AAV, American Avocet; GYL, Greater Yellowlegs; LYL, Lesser Yellowlegs; WWT, Willet; SSP, Spotted Sandpiper; USP, Upland Sandpiper; HGD, Hudsonian Godwit; MGD, Marbled Godwit; KNT, Red Knot; SAN, Sanderling; SEM, Semipalmated Sandpiper; LEA, Least Sandpiper; WRS, White-rumped Sandpiper; BSP, Baird's Sandpiper; PEC, Pectoral Sandpiper; DUN, Dunlin; STL, Stilt Sandpiper; PEP, unidentified small calidridine sandpiper, either SEM, LEA, WRS, or BSP; PPL, unidentified calidridine sandpiper, either WRS or BSP; PPS, unidentified calidridine sandpiper, either SEM or LEA; DOW, dowitcher spp.; CSN, Common Snipe; WPH, Wilson's Phalarope; RPH, Red-necked Phalarope.

TABLE 2

CLASSIFICATION OF SHOREBIRDS AT THREE WETLANDS, BASED ON INDICATOR SPECIES ANALYSIS OF % OBSERVATIONS IN VARIOUS HABITATS

Species	Lanigan Creek	Basin A	Perry's Beach
Lesser Golden-Plover	III	III	II
Black-bellied Plover		III	II
Semipalmated Plover	IV	IV	IV
Killdeer	III	IV	IV
Amerian Avocet	III	I	I
Greater Yellowlegs	II	III	I
Lesser Yellowlegs	II	IV	III
Willet	II	IV	III
Solitary Sandpiper		III	IV
Spotted Sandpiper	III	IV	IV
Upland Sandpiper	III		
Hudsonian Godwit	IV	III	I
Marbled Godwit	II	II	I
Red Knot	IV		I
Sanderling	IV	IV	II
Semipalmated Sandpiper	IV	IV	II
Least Sandpiper	IV	IV	II
Baird's Sandpiper	IV	IV	IV
White-rumped Sandpiper	III	III	
Pectoral Sandpiper	IV	IV	II
Stilt Sandpiper	IV	II	I
Dunlin		III	
Common Snipe	IV		
Dowitcher spp.	IV	II	I
Wilson's Phalarope	I	I	II
Red-necked Phalarope	I	I	I

Within each site, species sharing Roman numerals occupied similar habitats (see text and Fig. 1).

Basin A, $P = 0.19$; Perry's Beach, $P = 0.54$). However, axis 2 scores of breeders were significantly greater than migrants at Lanigan Creek ($P = 0.005$), but not at Basin A ($P = 0.75$) or Perry's Beach ($P = 0.47$), reflecting a greater use of terrestrial habitats.

Patterns of habitat use differed among taxonomic groups, based on axis 1 (Kruskal-Wallis test: Lanigan Creek, df = 7, $P = 0.12$; Basin A, df = 6, $P = 0.05$; Perry's Beach, df = 4, $P = 0.03$), but not axis 2 (Lanigan Creek, $P = 0.44$; Basin A, $P = 0.41$; Perry's Beach, $P = 0.98$).

Seasonal patterns.—Seasonal habitat use and the magnitude of shift in habitat use differed among species (Table 3). Overall, breeders used significantly different habitats than migrants during spring and summer at Lanigan Creek; there was no difference in habitat use between these two

TABLE 3

SEASONAL PATTERNS OF HABITAT USE AMONG SHOREBIRDS, EXPRESSED AS PROBABILITY LEVEL ASSOCIATED WITH NONPARAMETRIC ANALYSES[a]

	Group averages				Magnitude of seasonal habitat use shift	
	Spring		Summer			
Study site and comparison	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Lanigan Creek						
Breeders/migrants[b]	0.19	0.03	0.05	0.03	0.05	0.49
Taxonomic group[c]	0.07	0.06	0.10	0.27	0.11	0.11
Basin A						
Breeders/migrants	0.46	0.30	0.83	0.67	0.39	0.46
Taxonomic group	0.15	0.06	0.05	0.08	0.38	0.27
Perry's Beach						
Breeders/migrants	0.44	0.12	0.23	0.11	0.12	0.12
Taxonomic group	0.41	0.26	0.02	0.14	0.26	0.26

[a] Axis scores of breeders and migrants were compared using Mann-Whitney *U*-test, scores of taxa were analyzed with Kruskal-Wallis test, and seasonal shifts were analyzed using Wilcoxon matched-pairs signed-rank test.

[b] Species were classified according to the presence of breeding individuals at Last Mountain Lake National Wildlife Area (Colwell 1987).

[c] Analyses were conducted at the level of tribe or next highest level of classification if no tribe was available (AOU 1983).

groups at Basin A or Perry's Beach. The seasonal shift in habitat use was greater for breeders than migrants at Lanigan Creek, but not Basin A or Perry's Beach. At Lanigan Creek, however, both assemblages showed a significant shift between spring and summer on axis 2 (Wilcoxon matched-pairs signed-rank test: breeders, $N = 7$, $P < 0.05$; migrants, $N = 9$, $P < 0.01$). At Basin A, habitat use changed significantly for migrants (axis 2: $N = 9$, $P < 0.05$), but not breeders ($N = 5$, $P > 0.05$).

Taxonomic groups differed in seasonal habitat use at Lanigan Creek and Basin A, but not Perry's Beach (Table 3). However, there were no differences among taxa in the magnitude of shift in habitat use from spring to summer.

DISCUSSION

Habitat use patterns.—Migrating and breeding shorebirds differed in their use of habitats at Last Mountain Lake. Interspecific differences in habitat use reflect coadapted morphological and behavioral traits that may be influenced by proximate factors affecting habitat availability. Baker (1979) examined habitat use in assemblages of breeding and wintering shorebirds and noted relationships between a species' morphology and feeding microhabitat: culmen and tarsus length were positively correlated with vegetation height and water depth, respectively. While we did not quantify microhabitats used by shorebirds at Last Mountain Lake, qualitative relationships between morphology and habitat use were suggested by differences in habitat use among taxa. Aquatic habitats were frequented by taxa with long culmens and tarsi (e.g., godwits, dowitchers, and avocet), or species with specialized aquatic adaptations (e.g., lobe-toed phalaropes). Wetland edges and terrestrial habitats were used by smaller species such as plovers and calidridine sandpipers.

Interspecific variation in habitat use also reflects fundamental behavioral differences associated with feeding and reproduction, which may operate on a daily or seasonal basis. In marine environs, daily tidal rhythms affect shorebird habitat use by inundating preferred habitat (Burger et al. 1977, Connors et al. 1979b). Although shorebirds at inland sites may not be confronted by regular diurnal changes in habitat, habitat use may be altered over short periods by climatic conditions. Wind-related "tides," drought, and cold temperatures may restrict habitat availability.

Habitat use also varies over longer intervals associated with periods of a species' annual cycle. Of several factors influencing seasonal habitat use by Arctic shorebirds at Barrow, Alaska, Connors et al. (1979a) stressed the importance of whether use occurred during periods of breeding, post-breeding, or migration. During the Arctic breeding season, most shorebirds used tundra, with a subsequent shift to coastal littoral habitat during post-breeding and migratory periods (Connors et al. 1979a).

Differences in habitat use between breeders and migrants at Lanigan Creek stemmed from the greater use of terrestrial habitats by breeding individuals that were defending territories, courting, nest building, incubating, or brooding. In contrast, nearly exclusive use of wetland habitats by most migrants was related to a predominance of foraging activities. At Lanigan Creek, breeders showed a larger seasonal shift toward aquatic habitats than did migrants, which reflected a shift from reproductive behavior to foraging activities. A similar pattern did not hold for assemblages at Basin A and Perry's Beach, and the magnitude of seasonal change in habitat use was not different between breeders and migrants. Although local breeders were present at these sites, few individuals nested there owing to unsuitable habitat.

Differences among species in migration chronology may account for differences in habitat use. Recher (1966) noted that the distribution of migratory shorebird species differed temporally and spatially, perhaps reflecting the effects of interspecific interactions. Regardless of underlying mechanisms, interspecific differences in habitat use may result from the timing of migratory movements in relation to habitat availability (Connors et al. 1979a). Peak migration periods for shorebirds at Last Mountain

Lake vary among species (Colwell et al., 1988a), especially during summer. As a result, species that exhibit disjunct migration peaks may experience differences in habitat availability at the times of their presence.

Our data represent a coarse view of habitat use by an assemblage of shorebirds during a year of extreme drought. Nevertheless, seasonal shifts in habitat use were discernible. However, we suspect that seasonal patterns may be evident on a much finer temporal scale owing to interspecific differences in migration chronology. Moreover, within species, habitat use may vary with age (a variable we did not record) and sex of individuals. On a larger geographic scale, van der Have et al. (1984) showed that differences in habitat use by adult and juvenile Dunlin in the Dutch Wadden Sea were related to density of individuals; they suggested that age-related dominance behavior may cause habitat segregation. Juveniles occurred in secondary habitat where densities were lower. Numbers of shorebirds at Lanigan Creek, Basin A, and Perry's Beach changed dramatically during the study (Colwell et al., 1988a). If intraspecific habitat segregation occurs at prairie wetlands, one might predict the pattern to be most prevalent during drought episodes, when high densities of birds are coupled with resource limitation. In nondrought years, greater habitat availability and lower bird densities likely result in less dramatic habitat shifts within and among species.

Although drought conditions may offer an atypical view of habitat use by shorebirds in the northern prairies, it is at times of resource limitation that natural selection may operate most strongly (Wiens 1977). Much attention has been paid to the seasonal changes in resource abundance that affect numbers of wintering and migrating shorebirds in marine environs (Evans and Dugan 1984), where habitats and their food resources are influenced strongly by daily tidal cycles. Few studies have examined the relationship between prey availability and shorebird numbers at inland sites. We suspect that there may be marked differences between marine and interior subpopulations of nearctic shorebird species with regard to fidelity to staging and breeding sites and tenure of stay at these areas; these differences are probably habitat- and resource-related. Specifically, unpredictable and seasonally diminishing resources at ephemeral prairie wetlands likely are correlated with low annual fidelity of species to migratory staging areas and breeding sites (Colwell et al., in press) and to short stays. By contrast, species using permanent wetlands or predictable habitats, such as lakeshore sites, probably exhibit greater site-faithfulness.

Management implications.—At Last Mountain Lake, shorebird habitat use occurred across a broad habitat gradient, spanning terrestrial and aquatic zones; some species were restricted in their use of habitats, whereas other species used a variety of habitats (Colwell 1987, Colwell et al., 1988b). The importance of maintaining habitat diversity for shorebird populations is particularly striking in the northern prairie, where a large shorebird assemblage can be strongly affected by extreme climatic conditions (Colwell 1986). Topographically simple wetlands with uniform habitat, such as Basin A, may be inundated during wet years, resulting in a predominance of deep-water habitats of limited value for calidridine sandpipers and small plovers. Moreover, simple shallow wetlands may be left entirely dry during drought, affording little use by breeding (Colwell 1986) or migrating species. By contrast, complex wetlands, such as Lanigan Creek, that offer a mix of habitats and topography, ensure the availability of a variety of habitats under extreme conditions.

Areas managed for waterfowl could benefit other avian taxa by employing manipulations other than the common practice of inundating large areas. Additional habitats could be created by relatively minor habitat alterations prior to impoundment construction. For instance, construction of sparsely vegetated nesting islands with gently sloping beaches surrounded by deep-water zones would benefit colonial-breeding Avocets and migrant shorebirds, as well as providing waterfowl with loafing areas.

Like many waterfowl species (Peek 1986), breeding shorebirds appear most strongly influenced by the proximity of nesting areas to wetlands. Extensive upland and wet meadow habitat at Lanigan Creek supported nesting individuals of most (8 of 9) local breeders (Colwell 1986), whereas unsuitable nesting habitat at Basin A and Perry's Beach restricted nesting opportunities of most breeders (Colwell, unpubl. data). By maintaining flooded meadows adjacent to deep-water basins, especially during brood-rearing periods, a benefit would accrue to both upland nesting shorebirds and waterfowl. In the absence of such a wetland complex, adults may be forced to move broods long distances to rearing areas (Colwell and Oring 1988).

The shorebird assemblage in the northern prairie constitutes a large proportion of nearctic-breeding shorebirds (Colwell 1987). With loss of wetland acreage to human development (Peek 1986), some populations of prairie-breeding shorebirds are threatened (Haig and Oring 1985). Populations of Arctic-breeding shorebirds that use prairie wetlands as migratory staging sites also may be at risk. Remaining habitats, essential to the maintenance of populations of many avian taxa, must be managed according to more than the needs of waterfowl alone.

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LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49: 227–265.

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. American Ornithologists' Union, Washington, D.C.

BAKER, M. C. 1979. Morphological correlates of habitat selection in a community of shorebirds (Charadriiformes). Oikos 33:121–126.

——— AND A. E. M. BAKER. 1973. Niche relationships among six species of shorebirds on their wintering and breeding ranges. Ecol. Monogr. 43:192–212.

BURGER, J. 1984. Abiotic factors affecting migrant shorebirds. Pp. 1–72 *in* Shorebirds. Migration and foraging behavior. Vol. 6 (J. Burger and B. L. Olla, eds.). Plenum Press, New York, New York.

———, M. A. HOWE, D. C. HAHN, AND J. CHASE. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. Auk 94:743–758.

COLWELL, M. A. 1986. Intraspecific brood parasitism in three prairie-breeding shorebirds. Wilson Bull. 98:473–475.

———. 1987. Seasonal shorebird abundance at Last Mountain Lake Wildlife Management Unit. Blue Jay 45:261–266.

———, S. D. FELLOWS, AND L. W. ORING. 1988a. Chronology of shorebird migration at Last Mountain Lake National Wildlife Area, Saskatchewan, Canada. Wader Study Group Bull. 52:18–22.

——— AND L. W. ORING. 1988b. Breeding biology of Wilson's Phalarope in southcentral Saskatchewan. Wilson Bull. 100:567–582.

———, J. D. REYNOLDS, C. L. GRATTO, D. SCHAMEL, AND D. M. TRACY. Phalarope philopatry. Proceedings XIXth Intl. Ornithol. Congress. Ottawa, Ontario. In press.

CONNORS, P. G., J. P. MYERS, AND F. A. PITELKA. 1979a. Seasonal habitat use by arctic Alaskan shorebirds. Pp. 101–111 *in* Shorebirds in marine environments. Studies in avian biology, No. 2 (F. A. Pitelka, ed.). Cooper Ornith. Soc., Allen Press, Lawrence, Kansas.

———, ———, C. S. W. CONNORS, AND F. A. PITELKA. 1979b. Intertidal movements by Sanderlings in relation to foraging profitability and the tidal cycle. Auk 98:49–64.

DAVIDSON, N. C. AND M. W. PIENKOWSKI. 1987. The conservation of international flyway populations of waders. Wader Study Group Bull. 49.

EVANS, P. R. AND P. J. DUGAN. 1984. Coastal birds: numbers in relation to food resources. *In* Coastal waders and wildfowl in winter (P. R. Evans, J. D. Goss-Custard, and W. G. Hale, eds.). Cambridge Univ. Press, Cambridge, England.

———, J. D. GOSS-CUSTARD, AND W. G. HALE. 1984. Coastal waders and wildfowl in winter. Cambridge Univ. Press, Cambridge, England.

GAUCH, H. G. 1982. Multivariate analysis in community ecology. Cambridge Univ. Press, Cambridge, England.

HAIG, S. M. AND L. W. ORING. 1985. Distribution and status of the piping plover throughout the annual cycle. J. Field Ornithol. 56:334–345.

HILL, M. O. 1979a. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Section of ecology and systematics, Cornell Univ. Press, Ithaca, New York.

———. 1979b. TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of individuals and attributes. Section of ecology and systematics, Cornell Univ. Press, Ithaca, New York.

———, R. G. H. Bunce, and M. W. Shaw. 1975. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. J. Ecology 63:597–613.

Holmes, R. T. and F. A. Pitelka. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. Syst. Zool. 17:305–318.

Myers, J. P. and L. P. Myers. 1979. Shorebirds of coastal Buenos Aires Province, Argentina. Ibis 121:186–200.

Peek, J. M. 1986. A review of wildlife management. Prentice-Hall, Englewood Cliffs, New Jersey.

Pitelka, F. A. 1979. Shorebirds in marine environments. Studies in avian biology, No. 2. Cooper Ornithol. Soc., Allen Press, Lawrence, Kansas.

Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.

——— and J. A. Recher. 1969. Some aspects of the ecology of migrant shorebirds. II. Aggression. Wilson Bull. 81:140–154.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. 2nd ed. Freeman, San Francisco, California.

van der Have, T. M., E. Nieboer, and G. C. Boere. 1984. Age-related distribution of Dunlin in the Dutch Wadden Sea. Pp. 160–176 *in* Coastal waders and wildfowl in winter (P. R. Evans, J. D. Goss-Custard, and W. G. Hale, eds.). Cambridge Univ. Press, Cambridge, England.

Wiens, J. A. 1977. On competition in variable environments. Amer. Sci. 65:590–597.

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