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HABITAT USE BY BREEDING WILLETS IN THE NORTHERN GREAT PLAINS

MARK R. RYAN AND ROCHELLE B. RENKEN[1]

ABSTRACT.—Willets (*Catoptrophorus semipalmatus*) defended multipurpose territories ($\bar{x}$ = 44 ha) including sizeable upland components. Most breeding pairs (90%) and broods (70%), however, were sighted in or near wetlands where they fed. Willets defended areas with greater densities and diversity of wetlands than generally available across the study area. As wetland availability was reduced by drought, Willet density declined. Willet pairs were most often observed in semipermanent wetlands. But based on use vs availability, Willets preferred ephemeral, temporary, seasonal, and alkali wetlands over semipermanent and permanent wetlands. Wetlands used by Willets had significantly greater proportions of more open cover types than those not used. Within used wetlands, Willets made disproportionately frequent use of lightly vegetated sites. Willets made little use of upland habitats, except for nesting. Little selection for upland land-use types was evident, but Willets avoided tilled land. Upland sites used by Willet pairs were dominated by short (<15 cm), native grass cover. Broods used taller grass cover in uplands than did adults. Willet defense of large, multipurpose territories seems related to limited wetland foraging habitats and possible advantages gained by spacing nests to reduce predation. Continued destruction of wetland and prairie habitats likely will reduce Willet populations in the northern Great Plains. Preservation of wetland complexes and management of wetland and upland habitats with grazing, mowing, and prescribed burning treatments are suggested. *Received 4 Apr. 1986, accepted 23 Sept. 1986.*

Two subspecies of Willets (*Catoptrophorus semipalmatus*) breed in North America. An eastern subspecies (*C. s. semipalmatus*) nests along the Atlantic and Gulf coasts from New Brunswick to Mexico and Venezuela, and the western subspecies (*C. s. inornatus*) breeds locally from Oregon to Manitoba and south to Nebraska and Colorado (AOU 1983).

Intensive studies of Willet life history (Vogt 1938; Tomkins 1932, 1955, 1965; Wilcox 1980), social organization (Howe 1982), and nest-site characteristics (Burger and Shisler 1978) have been limited to the Atlantic seaboard. Sordahl (1979) reported on the behavioral and vocal repertoire of Willets breeding in Utah. Higgins et al. (1979) and Weber et al. (1982) presented limited information on nesting and wetland use in the northern prairie region.

The eastern subspecies typically nests in highly productive salt-marsh habitats. Nest densities in these areas are high (Tomkins 1965, Burger and Shisler 1978, Howe 1982), and territories and home ranges are small (Vogt 1938, Howe 1982). In the northern Great Plains, Willet densities

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[1] School of Forestry, Fisheries, and Wildlife, Univ. Missouri, Columbia, Missouri 65211, and Dept. Animal Ecology, Iowa State Univ., Ames, Iowa 50011. (Present address MRR: School of Forestry, Fisheries, and Wildlife, Univ. Missouri, Columbia, Missouri 65211.)

(Stewart and Kantrud 1972) are much lower than those of the Atlantic coast. Western Willets nest in uplands near brackish or saline wetlands (Bent 1929, Higgins et al. 1979). These prairie habitats likely are less productive and more ephemeral than are salt-marsh communities (cf. Odum 1971:357).

Our objectives were to quantify habitat use and selection by breeding Willets and to compare patterns of habitat use between prairie and salt-marsh populations. Based on the data gathered, we also discuss the possible long-term effects of habitat changes on Willet populations and comment on public land management practices as means for Willet conservation.

STUDY AREA AND METHODS

We gathered data from April through August 1979–1981 on a 1300-km^2 area in Stutsman and Kidder counties in east-central North Dakota. The area is a recently glaciated, irregular plain with numerous shallow wetlands (Bluemle 1977). Approximately 25% of the uplands were comprised of native prairie vegetation, dominated by needlegrasses (*Stipa viridula* and *S. comata*), blue gramma (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*). Most of the native grassland vegetation was grazed, with small percentages cut for hay or left idle. The remainder of our study area consisted of nonnative vegetation, e.g., smooth brome (*Bromus inermis*) and alfalfa (*Medicago sativa*), that was grazed, mowed, or left idle, and annually tilled croplands. Small grains were the most common crop type, but sunflowers, corn, or summer fallow made up a substantial portion of the study area each year (for details see Ryan 1982 and Ryan et al. 1984).

We recognized four basic upland habitat types based on principal land use: (1) pasture—lands currently or recently grazed by livestock, (2) hayfields—lands on which the vegetation was recently mowed, (3) idle grassland—grass-dominated lands showing no evidence of recent grazing or mowing, and (4) tilled—lands on which any recent tillage had occurred. Total availability of upland land-use types was determined once each year by randomly sampling 368 quarter sections along the transect routes.

We measured habitat availability and its use by Willets along 4, approximately 75 km, roadside transects. We drove each transect biweekly throughout the Willet breeding and brood-rearing periods, from late April through July. Transect starting points and times were alternated to compensate for any diurnal patterns of habitat use by Willets. A single transect required from 8 to 14 h to complete.

Along each transect, we mapped and classified all wetland basins within 350 m of the road. Natural wetlands were classified according to Stewart and Kantrud (1971) as ephemeral, temporary, seasonal, semipermanent, and permanent wetlands, which form a continuum of increasing depth and, therefore, probability of retaining water throughout the Willet breeding season. Alkali wetlands vary in size and depth and are highly saline. Many alkali lakes are large and shallow, exhibiting large seasonal fluctuations in the area flooded (Stewart and Kantrud 1971). We recognized manmade stockponds and flooded livestock feedlots as unique wetland habitats. Because Willets confined their use to wetland peripheries, we used shoreline length as a measure of availability of each wetland type. During each transversal of the transects, we remapped wetland boundaries and later recalculated shoreline lengths, resulting in biweekly estimates of the availability of each wetland class.

On transects, we quantified habitat features at the exact site where Willets were observed, as well as habitat available in the immediate vicinity. For comparison, we also measured habitat characteristics at sites where no Willets were observed. During each transect transversal, we randomly sampled 15 unused wetlands and 15 unused upland sites. Wetlands were chosen by assigning numbers to all wetlands and a sample chosen using a random numbers table. Upland sites sampled were centered at points 100 m toward the transect route from numbered wetlands. Upland areas to be sampled also were chosen using a random numbers table.

Each wetland, used or unused, was classified and assigned to salinity categories based on vegetative characteristics (Stewart and Kantrud 1971). We estimated the relative coverage of 5 height-canopy coverage categories (*sensu* Daubenmire 1959) along shorelines of all used and randomly selected unused wetlands. Coverage was quantified in two zones along the shoreline; a 3-m wide shallow water strip and a 5-m wide dry shore area. The cover categories composed a continuum from open habitat to tall, dense cover, and included open water (shallow water zone) or bare soil (shore zone), short-sparse (<15 cm tall and <75% dense) canopy coverage, moderately-short-sparse (<15 cm, >75% dense, or 15–60 cm, <25% dense) canopy coverage, moderately-tall-dense (15–60 cm, >25% dense) canopy coverage, and tall-dense (>60 cm, >25% dense) canopy coverage.

At used and unused upland sites, land-use type was identified and the percentage cover of 3 vegetation height categories estimated for a 200-m radius circle centered at the spot occupied by the Willet and the randomly chosen point. Height categories were <15 cm, 15–60 cm, and >60 cm. We also recorded vegetation height at the point where the Willet was first seen.

Transect data were supplemented with observations of 16 individually color-banded Willets. Long-handled dipnets or spring-loaded hoopnets were used to capture Willets at nests. Territories were mapped by observing responses to taped Willet calls and from long-term observations of individuals. From 25–>100 observations were used to plot territory boundaries. Wetlands within territories were classified and counted. For comparison, 100 randomly selected areas (10 replications of each of the Willet territories) also were mapped and wetlands recorded. These areas were chosen by dividing the 700-m wide transect routes into parcels to match Willet territory sizes, numbered, and selected using a random numbers table. Habitat use by marked birds was quantified by recording cover-type occupancy every 15 sec during focal animal sample periods.

Differential use of habitat types was evaluated in three ways. Used and unused habitat cover types were compared using multivariate analysis of variance (MANOVA). Within used habitats, use and availability were compared with goodness-of-fit procedures (χ^2) and with a rank analysis procedure developed by Johnson (1980). Johnson's "usage-availability" analysis computes the mean difference of use and availability ranks for each habitat component. Larger negative values indicate greater disproportionate use (preference). Preference ranks for each habitat component are then compared by using a Duncan-Waller multiple comparison test. The result is a ranking of habitat components based on preference, with a significance test of the rankings. Arcsine transformations were made of percentage data used in MANOVA analyses.

RESULTS

The Willets that we observed defended large feeding and nesting territories ($\bar{x}$ = 44.3 ± 8.6 ha [SE], N = 10). Although large upland areas were defended, 90% (322/355) of the breeding Willets and 70% (33/45) of the broods seen during transect surveys were in or immediately adjacent to wetlands. Feeding was limited, almost exclusively, to shallow water or adjacent shore areas.

Wetland use and selection.—Total wetland shoreline availability and the relative availability of shoreline along different wetland classes changed annually (Table 1). Pond counts in early May, along our transects, totaled 615 wetlands in 1979, 351 in 1980, and 235 in 1981. The change in wetland conditions was paralleled by a decline in the number of Willet pairs observed during transect samples. During the peak of the nesting seasons, counts averaged 8.8 pairs/transect in 1979, 7.8 in 1980, and 5.8 in 1981 (1979 vs 1981, $P < 0.05$, N = 12, Mann-Whitney U statistic, multiple comparison test).

Although breeding Willets were seen most frequently using semipermanent ponds, comparison of use with availability (Johnson 1980) indicated relatively low preference for this wetland type (Table 1). The proportional use by Willets of ephemeral, temporary, seasonal, and alkali wetlands was consistently greater than the availability of those pond types. And each of those pond types was ranked significantly higher in preference than semipermanent wetlands (Table 1). Permanent lakes were ranked as least preferred each year and received substantial use by Willets only in 1981, when alternative wetland habitats were scarce.

Willets defended areas that had greater wetland densities and diversity than were available across the study area as a whole. Territories had a mean of 7.1 ± 2.3 [SE] (range = 1–22, N = 10) wetlands within their boundaries, whereas randomly located, equal-sized areas averaged only 1.5 ± 0.1 (range = 1–5, N = 100; $P < 0.005$, Mann-Whitney U-test). Territories also had more different types of wetlands than randomly located areas (territories: $\bar{x} = 3.0 \pm 0.3$, range = 1–3; random: $\bar{x} = 1.3 \pm 0.7$, range = 1–3; $P < 0.005$, Mann-Whitney U-test). The frequencies of occurrence of temporary, seasonal, and alkali wetlands were significantly higher in territories than in the randomly chosen areas (Table 2).

Along the Atlantic Coast, Willets are associated closely with saline wetlands, and Tomkins (1965) suggested that Willets in South Carolina and Georgia avoided freshwater sites altogether. We found no evidence that Willet use of wetlands was influenced by salinity. Freshwater ephemeral and highly saline alkali wetlands were equally selected (Table 1). The distributions of salinity categories by wetland class (Stewart and Kantrud 1971) for wetlands used by Willets and those unused did not differ (χ^2 goodness-of-fit tests; temporary, $\chi^2 = 1.3$, df = 1, $P > 0.25$; seasonal, $\chi^2 = 1.4$, df = 2, $P > 0.25$; semipermanent, $\chi^2 = 2.0$, df = 3, $P > 0.5$; permanent, $\chi^2 = 2.3$, df = 3, $P > 0.5$).

Different wetland classes varied in shoreline cover composition. Based on data from randomly selected wetlands over 3 years, ephemeral and

Table 1

Percent Availability of Wetlands and Percent Use by Breeding Willets

Wetland class	1979			1980			1981		
	Use (119)[a]	Availability (1021)[b]	Preference score[c]	Use (120)	Availability (767)	Preference score	Use (83)	Availability (549)	Preference score
Ephemeral	11.8	4.4	−1.3A	3.3	1.2	−1.0A	1.2	0.3	—[d]
Temporary	9.2	6.8	−0.7A	2.5	1.0	−0.9A	1.2	0.3	—
Seasonal	22.7	18.1	−0.6A	12.5	7.5	−0.7A	7.2	3.9	−0.6A
Semipermanent	36.1	42.0	+0.7BC	40.8	49.1	+1.2B	38.6	42.9	+0.4B
Permanent	7.6	17.2	+1.8C	15.0	29.3	+1.5B	34.9	39.8	+0.4B
Alkali	12.6	9.5	−0.1AB	23.3	10.4	−0.2A	12.1	10.8	−0.3A
Feedlot	0.0	1.5	—	2.5	0.7	—	3.6	0.7	—
Stockpond	0.0	0.5	—	0.0	0.8	—	1.2	1.2	—

[a] Number of Willet pairs observed.
[b] Total km of shoreline sampled.
[c] Use vs availability analysis (Johnson 1980). Scores with the same letter are not significantly different ($P > 0.05$).
[d] Insufficient data to include in use vs availability analysis.

TABLE 2

FREQUENCY OF OCCURRENCE OF WETLAND TYPES IN WILLET TERRITORIES AND RANDOMLY SELECTED AREAS OF EQUIVALENT SIZE

Wetland class	Territories (N = 10)	Random[a] (N = 100)	P[b]
Ephemeral	0.1	0.05	>0.05
Temporary	0.6	0.10	<0.005
Seasonal	0.6	0.23	<0.01
Semipermanent	0.8	0.49	>0.05
Permanent	0.5	0.27	>0.05
Alkali	0.3	0.08	<0.05
Feedlot	0.0	0.06	>0.05
Stockpond	0.0	0.02	>0.05

[a] See methods section.
[b] χ^2 contingency test.

alkali wetlands were characterized by low coverage of tall-dense vegetation (6.0 and 5.5%, respectively) and substantial amounts of short-sparse to moderately-tall-dense cover types and open water. Tall-dense vegetation was intermediate in coverage in temporary (23.6%) and seasonal (24.4%) wetlands and dominated the shorelines of semipermanent (53.6%) and permanent (50.6%) wetlands (see Ryan 1982, Ryan et al. 1984).

Wetlands used by Willets differed significantly from unused wetlands in shoreline cover composition (Tables 3 and 4). Changing water levels, related to the drought, resulted in differences in the use and availability of cover types over the 3 years. But in each year, used wetlands had greater proportions of more open cover types than did unused wetlands. Large proportions of tall-dense and moderately-tall-dense cover typified unused wetlands.

Within used wetlands, we frequently saw Willets using all cover conditions except the tall-dense type (Table 3). In the shallow water zone, Willets used short-sparse cover in higher frequencies than its availability each year. The moderately-short-sparse and open water cover types were used disproportionately more in one of the three years. We observed Willets less frequently in the shore zone, and use of cover types there differed from availability to a lesser degree. Moderately-short-sparse, short-sparse, and bare soil cover types received use in excess of availability.

We tested for detection bias in dense cover types (i.e., that fewer Willets than expected were seen in moderately-tall-dense and tall-dense cover) by comparing the transect data with the time Willets spent in different cover types during time budget observations (N = 13.1 h, 19 individuals). Unexpectedly, we saw Willets in the 2 denser cover types more often

TABLE 3

MEAN PERCENT AVAILABILITY OF SHORELINE COVER TYPES AND PERCENT USE BY BREEDING PAIRS OF WILLETS

	Shallow water zone			Shore zone		
		Availability			Availability	
Cover types	Use	Used wetlands	Unused wetlands	Use	Used wetlands	Unused wetlands
1979	(93)[a]	(145)[b]	(189)[b]	(35)	(144)	(189)
Open water or bare soil	9.7	25.6	6.7	11.4	8.8	3.4
Short-sparse	39.8	14.8	5.2	5.7	1.8	1.3
Moderately-short-sparse	17.2	7.9	3.2	34.2	34.0	12.3
Moderately-tall-dense	30.1	40.5	59.9	48.6	48.6	72.9
Tall-dense	3.2	11.3	25.1	0.0	6.9	10.0
	$P < 0.001$[c]		$P = 0.0001$[d]	$P > 0.25$		$P = 0.0001$
1980	(107)	(159)	(270)	(26)	(160)	(270)
Open water or bare soil	37.4	42.5	20.1	42.3	23.0	9.9
Short-sparse	45.8	25.4	13.3	23.1	19.1	7.1
Moderately-short-sparse	3.7	5.9	3.5	19.2	17.9	16.8
Moderately-tall-dense	13.1	15.5	26.0	15.4	27.8	38.4
Tall-dense	0.0	10.7	37.4	0.0	11.9	27.2
	$P < 0.001$		$P = 0.0001$	$P < 0.05$		$P = 0.0001$
1981	(74)	(118)	(272)	(40)	(118)	(272)
Open water or bare soil	64.8	50.9	28.5	55.0	35.3	14.1
Short-sparse	23.0	14.7	6.8	0.0	6.8	2.5
Moderately-short-sparse	4.1	3.2	1.5	17.5	8.4	7.1
Moderately-tall-dense	8.1	11.4	15.8	27.5	17.0	21.9
Tall-dense	0.0	20.0	47.6	0.0	32.9	54.3
	$P < 0.005$		$P = 0.0001$	$P < 0.01$		$P = 0.0001$

[a] Number of Willet pairs observed.
[b] Number of wetlands sampled.
[c] Probability of greater χ^2 value; Goodness-of-fit test, use vs availability within used wetlands.
[d] Probability of greater F-statistic; MANOVA, comparison of availability in used and unused wetlands.

(14% of the time) during transects than during focal animal observations (3%). A hypothesis of fewer Willet sightings in dense cover during transect observations was rejected ($\chi^2 = 137.1$, df = 1, $P < 0.005$, one-tailed goodness-of-fit test).

Sighting Willet broods was difficult, and we obtained few data. Sixty percent of the broods using wetlands were at semipermanent ponds. Seasonal ponds were the most preferred, based on use-availability comparisons (Table 5). The data suggest that ephemeral and temporary ponds were moderately available but were not used. Availability was not predictable, however; ephemeral and temporary ponds held water only briefly after infrequent rains.

TABLE 4

SHORELINE COVER-TYPE PREFERENCES OF WILLET BREEDING PAIRS, 1979–1981 COMBINED

Cover type	Preference score[a]
Shallow water zone	
Short-sparse	−1.5A
Moderately-short-sparse	−0.9B
Moderately-tall-dense	+0.3C
Open water	+0.4C
Tall-dense	+1.8D
Shore zone	
Moderately-short-sparse	−1.0A
Short-sparse	−0.7A
Bare soil	−0.1AB
Moderately-tall-dense	+0.6BC
Tall-dense	+1.1C

[a] Use vs availability analysis (Johnson 1980). Scores with the same letter are not significantly different ($P > 0.05$).

The shoreline cover composition of wetlands at which we sighted Willet broods differed significantly from that of unused wetlands (Table 6). Used wetlands had greater proportions of short-sparse to moderately-tall-dense cover than unused wetlands. Based on our limited sightings, we detected no differential use of cover types within used wetlands.

Upland use and selection.—Despite defending large upland areas, Willets made little use of these habitats except for nesting. The greatest use of uplands for feeding occurred in 1981 when wetland availability was at a minimum. Even with our small sample size, differential use of upland land-use types was evident (Table 7). More than 60% of the breeding pairs and broods were seen in pasture habitats, and idle grasslands also received disproportionately frequent use. Willets, however, seemed to avoid tilled land. Willets selected sites dominated by native vegetation over those comprised of introduced species (tilled areas excluded; $\chi^2 = 16.9$, df = 1, N = 25, $P < 0.005$). Of the 18 nests we located, 15 were in native vegetation. Seven nests were in hayfields, 6 in pastures, and 5 in idle grasslands.

Upland habitats used by Willet breeding pairs differed significantly in cover height composition from randomly sampled unused sites (Table 8). Short vegetation predominated within 200 m of sites where we observed Willet pairs. The distribution of vegetation heights at the exact sites where we saw Willets did not differ from that of the immediately surrounding area (Table 8).

Short, sparse cover characterized Willet nest sites. Based on 1-m^2 sam-

TABLE 5
PERCENT AVAILABILITY OF WETLANDS AND PERCENT USE BY WILLET BROODS, WITH MEAN PREFERENCE SCORES, 1979–1981 COMBINED

Wetland	Use	Availability	Preference score[c]
	(32)[a]	(1174)[b]	
Ephemeral	0.0	2.1	—[d]
Temporary	0.0	3.2	—
Seasonal	18.8	12.9	−1.1A
Semipermanent	59.4	45.3	+0.4AB
Permanent	12.5	24.2	+0.9B
Alkali	9.3	10.3	−0.2AB
Feedlots	0.0	0.7	—
Stockponds	0.0	1.0	—

[a] Number of Willet broods observed.
[b] Total km of shoreline sampled.
[c] Use vs availability analysis (Johnson 1980). Scores with the same letter are not significantly different ($P > 0.05$).
[d] Insufficient data to include in use vs availability analysis.

ples centered at the nest, mean cover percentages were 14.5% bare soil, 77.7% vegetation <15 cm, 7.8% vegetation 15-60 cm, and 0.7% vegetation >60 cm (N = 15).

We observed that Willet broods used significantly taller vegetation in uplands than did breeding pairs ($\chi^2 = 25.9$, df = 2, $P < 0.005$). This difference may, in part, be a function of the greater availability of taller vegetation during the brood-rearing period. We detected no significant difference between cover height in uplands used by Willet broods and the randomly sampled unused sites (Table 8). There was, however, a trend toward a higher percentage of taller cover at used areas. This possible selection of taller cover is further substantiated by the lack of sightings of broods in vegetation less than 15 cm tall. Tomkins (1955) noted the use of tall cover by Willet broods in salt marshes in Georgia.

DISCUSSION

Along the Atlantic Coast, most Willets have been reported defending separate nesting and feeding sites (Tomkins 1965, Howe 1982); although Vogt (1938) recorded multipurpose territories in New Jersey. In all cases, territories of eastern Willets seem to be substantially smaller than those we studied in North Dakota. Territory sizes have not been specified in Atlantic Coast studies but may be inferred to be on the order of several hundred m^2 at maximum. The smallest territory we mapped was 17.1 ha.

Howe (1982) suggested that Willet defense of multipurpose territories along the Atlantic Coast was related primarily to food resources. For

TABLE 6

MEAN PERCENT AVAILABILITY OF SHORELINE COVER TYPES AND PERCENT USE BY WILLET BROODS, 1979–1981 COMBINED

	Shallow water zone			Shore zone		
		Availability			Availability	
Cover types	Use	Used wetlands	Unused wetlands	Use	Used wetlands	Unused wetlands
	(8)[a]	(25)[b]	(330)[b]	(13)	(28)	(329)
Open water or bare soil	0.0	11.4	16.8	0.0	7.7	8.5
Short-sparse	37.5	11.5	2.5	23.1	7.4	1.7
Moderate-short-sparse	0.0	3.7	1.0	0.0	9.0	4.7
Moderate-tall-dense	27.5	39.2	27.4	69.2	49.7	46.1
Tall-dense	25.0	34.1	52.2	7.7	26.3	38.7
	$P > 0.75$[c]		$P = 0.0001$[d]	$P = 0.25$		$P = 0.03$

[a] Number of Willet broods observed.

[b] Number of wetlands sampled.

[c] Probability of greater χ^2 value; Goodness-of-fit test, use vs availability within used wetlands.

[d] Probability of greater F-statistic; MANOVA, comparison of availability in used and unused wetlands.

disjunct territories, he postulated that nest defense probably was an anticuckoldry strategem.

On our study area, Willets persistently defended multipurpose territories throughout the nesting season. We observed relatively few aggressive encounters in upland portions of territories, but we saw song-flights (Sordahl 1979) over the approximate territory boundaries throughout the nesting period. We also elicited aggressive responses to taped *pill-will-willet* calls (Sordahl 1979) played anywhere within the territory boundaries anytime prior to hatching. We did not quantify frequency of territorial song-flights throughout the nesting period, but we believe that the frequency declined as hatching approached.

It seems likely that the large size of the prairie territories we studied was a function of both limited wetland foraging habitat and the possible advantage gained by spacing nests to reduce the risk of predation. We do not rule out the contribution of an anticuckoldry selection force in nest area defense.

Willets showed strong and consistent selection for certain wetland conditions. Shallow wetlands, including alkali lakes, characterized by relatively sparse shoreline cover were preferred throughout our study, despite substantial between-year changes in wetland availability and conditions as a result of drought. Within used wetlands, Willets showed preference for lightly vegetated sites. Willet preference for shorter, sparser cover may be related to easier prey capture, higher prey densities, better surveillance for predators, or easier escape flight.

TABLE 7

MEAN PERCENTAGE AVAILABILITY OF UPLAND LAND-USE TYPES AND PERCENTAGE USE BY WILLET BREEDING PAIRS AND BROODS WITH PREFERENCE SCORES FOR 1979–1981 COMBINED

Land use	Use		Availability	Preference score[a]	
	Pairs	Broods		Pairs	Broods
	(33)[b]	(13)[b]	(3)[c]		
Pasture	60.6	61.5	28.2	−0.4A	−0.8A
Idle grassland	12.1	15.3	10.3	−1.4A	−1.3A
Hayfield	15.2	15.3	24.9	0.0AB	−0.3A
Tilled	12.1	7.7	36.8	+1.8B	+2.3B

[a] Use vs availability analysis (Johnson 1980). Scores with the same letter are not significantly different ($P > 0.05$).
[b] Number of pairs or broods observed.
[c] Number of years; 368 quarter sections sampled each year.

Willets defended territories with higher densities and greater diversity of wetlands than generally available across our study area. In a highly variable environment, defense of large areas with a high diversity of possible foraging sites may be a hedge against unpredictable changes. Semipermanent wetlands may play an important role in this regard. Although our analysis suggests low preference by Willets for these wetlands, this may be an artifact of their widespread abundance. During dry years, or late in summer, semipermanent wetlands may provide vital habitat for adults and broods. Ryan et al. (1984) suggested that a similar habitat selection strategy has evolved in Marbled Godwits (*Limosa fedoa*), which exploit the same prairie environment. The possible importance of different components of wetland complexes at different stages of the breeding cycle of waterfowl also has been noted frequently (Patterson 1976, Swanson et al. 1979, Duebbert and Frank 1984, Mulhern et al. 1985).

With the exception of a strong avoidance of tilled areas, Willets showed little selection for upland land-use types. Breeding pairs did select upland areas with substantially greater amounts of short, sparse cover than were available across the study area. Such sites allowed for easy surveillance for predators by adult Willets. The preference shown for native vegetation, which was typically short to moderate in height, may reflect avoidance of introduced grasses and legumes that exhibited tall, dense growth forms. Willets constructed nests in very short, sparse cover.

Howe (1982) suggested that Willet internest distances, territorial behavior, and predator densities were interrelated. In a seemingly predator-free environment, he reported high nest densities, implied a lack of nest area defense, and recorded no antipredator behavior. At a second Willet nesting area with predators, Howe reported greater internest distances,

TABLE 8

MEAN PERCENT AVAILABILITY OF UPLAND VEGETATION HEIGHT CATEGORIES AND PERCENT USE BY WILLET PAIRS AND BROODS, 1979–1981 COMBINED

Vegetation height	Use	Availability	
		Used sites	Unused sites
Pairs	(32)[a]	(32)[b]	(756)[b]
<15 cm	81.3	72.0	46.6
15–60 cm	18.7	26.6	47.7
>60 cm	0.0	1.5	5.6
	$P > 0.25$[c]	$P = 0.003$[d]	
Broods	(13)	(13)	(360)
<15 cm	0.0	15.7	29.6
15–60 cm	84.6	62.3	52.5
>60 cm	15.4	22.0	17.9
	$P > 0.1$	$P = 0.39$	

[a] Number of pairs or broods observed.

[b] Number of upland sites sampled.

[c] Probability of greater χ^2 value; Goodness-of-fit test, use vs availability within used wetlands.

[d] Probability of greater F-statistic; MANOVA, comparison of availability in used and unused wetlands.

low-level nest area defense, and predator mobbing by Willets. In the Prairie Pothole region where we worked, predation on ground nests is frequent (Miller 1971, Duebbert and Kantrud 1974, Kirsch and Higgins 1976, Sargeant et al. 1984). In North Dakota, Willet defense of large upland nesting areas resulted in long internest distances. In our area, nesting Willets did not mob predators, or us, unless the nest was approached to within a few meters. Instead, the incubating adults seemingly relied on their cryptic coloration for concealment in the large blocks of homogeneous upland habitat. That spacing of nests can affect predation rates has been demonstrated by numerous avian studies (e.g., Tinbergen et al. 1967). Page et al. (1983) presented experimental evidence that low nest density was an important antipredator strategy for Snowy Plovers (*Charadrius alexandrinus*) nesting in homogeneous beach habitat.

We saw few broods in uplands, but our data are probably biased by the greater difficulty of seeing chicks in upland habitats versus wetlands. We strongly suspected that broods made frequent use of uplands during the first 2 weeks after hatching. The broods we observed used taller upland cover than adults alone, presumably gleaning invertebrates from the vegetation and using the taller vegetation as escape cover. Use of wetland habitats by young chicks may be limited by their small size, which results in reduced foraging efficiency, or by their inability to avoid predators in wetland habitats.

The Prairie Pothole ecosystem has been substantially altered by land-use changes associated with the arrival of European culture in the late 1800s. The major environmental changes have been the drainage of wetlands, conversion of native grasslands to small grain and row-crop agriculture, replacement of native grazers with domestic livestock, and suppression of wildfires. No data on Willet population levels in the pristine prairie ecosystem are available, but substantial reductions in historical times are suspected, probably as the result of habitat destruction. The Willet has been extirpated from Iowa and Minnesota (AOU 1983), and range reductions are known in North Dakota (Stewart 1975).

The drought of 1980 and 1981 disproportionately reduced the availability of shallow, less permanent wetlands (Ryan et al. 1984) (Table 1). The temporary loss of these preferred feeding habitats probably was the primary cause of the observed decline in breeding Willets from 1979 to 1981. Small shallow ponds are the most easily drained for agricultural development. As wetland drainage continues in the northern prairie region, Willet populations likely will decline.

Our data suggest that Willets avoid intensively tilled lands. Agricultural development undoubtedly has had a negative impact on the Willet population in the northern Great Plains. Continued conversion of native grass habitats to croplands or nonnative vegetation likely will reduce Willet densities and distribution in this region. Such development will increase the role that publicly managed lands must play in the conservation of Willets and other prairie fauna.

In the Prairie Pothole region, Willets are adapted to exploit short, sparse cover in wetland and upland habitats. In the pristine prairie, these habitat conditions were created and maintained by the interaction of soil moisture, fire, and native grazers (Ryan et al. 1984, Ryan 1986). Management of public wildlife areas in the northern prairie region has been directed primarily at species requiring tall, dense nesting cover. Elsewhere (Ryan et al. 1984, Ryan 1986), we have suggested using grazing, mowing, and prescribed burning on some public areas to assure that all components of the pristine prairie ecosystem, to which grassland wildlife have adapted, are provided. We reemphasize those recommendations.

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