

NEST SUCCESS, HABITAT UTILIZATION AND NEST-SITE SELECTION OF LONG-BILLED CURLEWS IN THE COLUMBIA BASIN, OREGON¹

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Abstract. Breeding ecology of Long-billed Curlews (*Numenius americanus*) in north-central Oregon was studied during spring and summer, 1978-1979. Five habitats were used by territorial curlews, and habitat selection by adults with and without broods was studied. Both adults and adults with broods used habitats significantly different from availability. A preference for habitats of low vertical profile and low vertical density (plant parts/volume/height) was observed; habitats with tall, dense shrubs or weedy annual vegetation were generally avoided. Nest density varied from 0-9 nests/40 ha. Highest nest density occurred in cheatgrass habitats. Nest success as computed by the Mayfield method was 0.69 in 1978 ($n = 40$) and 0.65 in 1979 ($n = 61$). Predators destroyed 10 (4) and 16% (10) of the nests in 1978 and 1979, respectively. Eight of 14 (57%) nests over both years were destroyed by mammalian predators; at least three (21%) were taken by crows (*Corvus brachyrhynchos*) or magpies (*Pica pica*). Nest predation rate was significantly lower in annual grass habitats. Differences between nest sites and randomly selected habitats were related to vertical stratification of vegetation. Vegetative cover was important in only the bunchgrass habitat. Overall, nest sites were less complex above 5 cm than surrounding areas. Significant differences in nest-site structure between habitats were observed for five of six paired comparisons, indicating some plasticity in nest-site selection by breeding curlews.

Key words: Long-billed Curlew; *Numenius americanus*; habitat use; nest-site selection; nest success; Columbia Basin; Oregon.

INTRODUCTION

The Long-billed Curlew is the most southerly breeding curlew in North America, and it nests in several habitats. Nesting habitat for the species is usually described as mixed-grass and short-grass communities (Davis 1949, Bailey and Neidrach 1965, Graul 1971, Sadler and Maher 1976, Bicak 1977, McCallum et al. 1977, King 1978, Redmond and Jenni 1986). In the Columbia and Great Basins, curlews breed in mixed-grass meadows, annual grassland (cheatgrass or medusahead [*Taeniatherum asperum*]) associations and occasionally in agricultural or crested-wheatgrass habitats (Allen 1980).

Agricultural development of prairies has reduced breeding habitat for Long-billed Curlews, which resulted in declines in breeding numbers over the last century (Wickersham 1902, Dawson 1923, Sugden 1933, Jewett 1936, Bent 1962). Extensive agricultural development occurred in the Columbia Basin during the 1970s with over

100,000 ha of shrubsteppe vegetation converted to circle-pivot irrigation systems in a five-county area alone (Muckleston and Highsmith 1978). During this time, the status of breeding curlews in the Columbia Basin was unknown, although many long-time residents believed that a drastic reduction in the breeding population occurred as a result of the agricultural development (H. Curtis, pers. comm.). These historical changes in community physiognomy probably changed the abundance and distribution of Long-billed Curlews, because avian habitat preferences and utilization patterns are often intimately tied to structural features of the habitat (Hilden 1965, Cody 1968, Wiens 1973, Eiserer 1980).

Intensive livestock grazing in the late 1800s deteriorated range conditions throughout the Columbia Basin. Large tracts of native bunchgrass were stressed beyond recovery, and the invasion of exotic cheatgrass (*Bromus tectorum*) significantly changed the vegetative structure of shrubsteppe communities. Many sites formerly dominated by the sagebrush (*Artemisia tridentata*)-bluebunch wheatgrass (*Agropyron spicatum*) association were burned or heavily grazed, with

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fire killing the sagebrush. Cheatgrass, along with other seral species, replaced bunchgrass.

We examined the habitat relationships of Long-billed Curlews and general features of the habitat available to predict how changes in habitat structure and overall availability might influence their populations. Herein, we report on nest success, habitat utilization, and nest-site selection of long-billed curlews in the Columbia Basin of north-central Oregon.

STUDY AREA

The study was conducted in the Columbia Basin of northern Umatilla and Morrow Counties, Oregon. The area is characterized by hot, dry summers and moderately cold, moist winters. The 30-year mean annual precipitation for the study areas was 21.67 cm (Ruffner 1978), most of which falls during winter and early spring. Sandy soil occurs along the Columbia River, grading into more loamy soils to the south. Most native vegetation has been drastically changed by intensive grazing, burning, and cultivation on the sandy soils in the areas. In general, the study area was comprised of two habitats; sagebrush/western-needle-and-thread (*Stipa comata*) on the sandy soils grading into a sagebrush/bluebunch wheatgrass habitat on the southern end of the study area (Daubenmire 1970). The study area was dominated by a gray rabbitbrush (*Chrysothamnus baysisus*)/cheatgrass association with lesser amounts of needle and thread, snowy buckwheat (*Eriogonum niveum*) and patchy Jim Hill mustard (*Sysimbrium altissimum*). On more loamy sites, some patches of sagebrush/bluebunch wheatgrass were extant with snakeweed (*Gutierrezia sarothrae*)/gray rabbitbrush-Sandberg's bluegrass (*Poa sandbergi*)/cheatgrass dominating the more disturbed sites.

Five habitats were chosen for intensive investigation, because Long-billed Curlews used them in varying degrees, and they were each structurally unique and contiguous with each other. The five habitats included cheatgrass grassland, bunchgrass grassland, bitterbrush shrubland, open-low shrub, and dense forb (see Pampush 1981, Green and Anthony 1989 for detailed descriptions).

METHODS

Upon arrival of the earliest returning curlews in mid-March, observations were initiated to determine the distribution and abundance of cur-

lews on the study area. Behavior was observed throughout the prenesting phase of the breeding cycle to determine habitat use of breeding curlews. Most observations were conducted from a vehicle with 7 × 35 binoculars and a 20 × spotting scope so as not to disturb them.

Systematic nest searches were initiated in early April of both years. Nest searching was conducted by people roughly 5 m apart and walking slowly, in a line, across the study plots. This approach assured complete coverage of the plots and detection of most all of the active nests. In 1979, 40-ha plots were established in each of five habitats with at least four replicates of each habitat (24 plots total). These study plots were searched from 7 April to 2 May using the technique described above with the aid of 1,300 volunteer, high-school students. Each of the five habitats was searched sequentially with the replicate plots being searched under the same scheme. This scheme was adopted to avoid sampling bias toward a particular habitat since the onset of nesting could vary over a six-week period. Nest density per plot, clutch size, fate of nest, type of predator depredated nest, number of addled eggs, and number of eggs hatched per clutch were recorded for all nests.

CENSUSING AND HABITAT UTILIZATION

A modified strip transect technique (Hayne 1949) was employed to determine habitat utilization and preference patterns of adults with and without broods. Four large transects were sampled by foot from 1 April to 1 August on the Umatilla National Wildlife Refuge, US Army Ammunition Depot, and the US Navy Bombing Range (two transects on the North and South sectors). Transects were sampled during the early morning hours when curlews were most active. The assumption was made that all adult curlews within 50 m of the transect (except incubating adults) were included in the sample. Curlews flying over the transect were not included unless they were males performing "display flights." Because "display flights" were performed over relatively fixed areas, the males performing them within the 100-m transect were included in the sample and assigned to the habitat that they were observed flying over. Since adult curlews attending young exhibit a strong defensive response by flying toward and swooping down on intruders (predator, vehicle, or human on foot), the census strip was widened to 150 m on either side of the

transect when adults with broods were surveyed. This is approximately the maximum distance at which curlews with broods responded to humans. All of the area included within the transect strip was classified into one of the five habitats, and the percentage of each habitat occurring along the transects was calculated.

VEGETATIVE MEASUREMENTS

The importance of vegetative structure in nest-site selection was determined by comparing vegetative characteristics of nest sites to those of the general habitat. In each of the 40-ha study plots ($n = 24$), ten 100-m transects were established randomly, and subsample points were selected randomly within each 10 m interval for vegetative measurements. To measure vegetative characteristics at nest sites, we established four 100 m transects at 90° angles and originating from the nest cup. Subsample points along each of the transects were established randomly within each 10 m interval, providing a total of 40 sample points for each nest. At each of the sample points for nests and the general habitat, a number of vegetative characteristics were measured. Vertical density was described as the number of touches of plant parts within 5-cm height intervals on a 6-mm diameter vertical rod (Wiens 1973). Effective height was the height at which 90% of a white, 30-cm wide, board, was obscured by vegetation when viewed from 10 m at eye level (Wiens 1973). Percent cover of grasses, herbs, and bare ground was estimated using a 10 × 50 cm (0.1 m²) plot as described by Dabemire (1959). Shrub cover was estimated by the line-intercept method along each transect (Piper 1973). Foliage height evenness and diversity were computed from the vertical density measurements according to Pielou (1975). Nineteen vegetative characteristics plus eight computed variables (Table 1) were used to compare nest sites with general habitat characteristics.

STATISTICAL ANALYSES

Data on habitat utilization were analyzed at two levels. First, a χ^2 test was used to determine whether habitats were utilized in proportion to their availability. Secondly, confidence intervals were constructed around the theoretical proportion to determine whether observed use of each habitat was significantly different from expected. Because several parameters were being estimated

TABLE 1. List and description of variables measured in characterizing the habitat of occupied and potential nest sites of Long-billed Curlews in the Columbia Basin.

Variable	Description
Percent bare ground	Percentage estimate of cover of bare ground, forbs, annual and perennial grasses.
Percent forb	
Percent grass	
Shrub intercept	Meters of shrubs intercepted along 100 m transects divided by 100 (Piper 1973).
Shrub volume	Shrub intercept multiplied by the mean height of the intercepted shrubs.
Effective height	Height at which 90% of a white board is obscured by vegetation when viewed 1 m from the ground at a distance of 10 m (Wiens 1973).
Vertical density, grasses	Number of touches by plants within 25 cm height intervals (0–25, 26–50, 50+) along a thin vertical rod (Wiens 1973).
Vertical density, forbs	
Vertical density, shrubs	
Vertical density, all vegetation	
Vertical density total	
Foliage height diversity of grasses, forbs, shrubs and all vegetation	Indices computed from vertical density measurements according to Pielou (1975:8–15)
Foliage height evenness for grasses, forbs, shrubs and all vegetation	Indices computed from vertical density measurements according to Pielou (1975:8–15)

simultaneously, a “family” of confidence intervals with an α of 0.10 was used (Neu et al. 1974).

Nest-site characteristics were analyzed in two ways. First, discriminant function analysis was used to describe differences in vegetative characteristics between nest sites and habitats in general. Discriminant functions were generated for four of the habitats, nest sites within habitats, and one with all nests and habitats combined. One discriminant function was generated in each comparison, and variables were added stepwise with a minimum α of 0.15 to enter the model ($F = 4.0$). A varimax vector rotation was used because it highlights the variable that explains the most variability in the data without change in variable composition of the model (Nie et al. 1975). Secondly, nest-site characteristics were compared with Hotelling’s T^2 test to determine whether or not nest sites were structurally dif-

ferent between pairs of habitats. Factor analysis was employed to generate linear combinations of variables used for T^2 analysis. After factor analysis, univariate t -tests were conducted to determine which variables contributed most to the significant differences between habitats.

Normality of the data was checked, and non-normal data were transformed. All coverage data were recorded as percent and thus were arcsine transformed; vertical density data were log transformed. All differences were considered significant at the 0.05 level unless stated otherwise.

RESULTS

Ninety percent of the observed nests ($n = 112$) had a clutch size of four eggs, 9% contained three eggs, and one nest (1%) contained two eggs. A mean incubation period of 29 days \pm 12 hr was observed (range: 28–31 days) for 10 nests of known history. Mean hatching dates were 14 May 1978 ($n = 45$, range = 1 May–2 June) and 15 May 1979 ($n = 66$, range = 3 May–4 June).

NEST DENSITY AND SUCCESS

Nest density varied considerably among habitats and plots within habitats. Highest nest density (3.6 nests/40 ha, range = 2–9 nests) occurred in the cheatgrass habitat. Density of nests in the other habitats was low; density in bunchgrass habitats was 1.4 nest/40 ha (range = 0–3 nests), dense forb was 1.3 nests/40 ha (range = 0–2 nests); open low shrub was 1.0 nests/40 ha (range = 0–2 nests), and bitterbrush was 0.5 nests/40 ha (range = 0–1 nest). The greatest density observed in any plot, other than cheatgrass, was (3.0 nests/40 ha) in the bunchgrass habitat. This particular plot adjoined several hundred hectares of annual-grass habitat, and the distribution of nest sites within the plot was along the edge of the shortgrass-bunchgrass interface.

Nest success as computed by Mayfield (1975) was 0.69 in 1978 ($n = 40$) and 0.65 in 1979 ($n = 61$). Predators destroyed 10 (4) and 16% (10) of the nests in 1978 and 1979, respectively. Four nests were abandoned in 1978 and two in 1979. Nest predation rate was significantly higher than expected in habitats other than annual grass ($\chi^2 = 6.36$, $P < 0.05$), suggesting that predators were more dense or nests were more vulnerable in these habitats. Eight of 14 nests (57%) depredated over the two years were destroyed by mammalian predators, primarily badgers (*Taxidea taxus*) and coyotes (*Canis latrans*). Corvids

(crows and magpies) were responsible for at least three of 14 (21%) nest predations.

HABITAT UTILIZATION: ADULTS WITHOUT BROODS

Adult curlews without broods utilized habitats in proportions different from availability on all four transects ($P < 0.05$) (Table 2). The cheatgrass habitat was highly preferred along the two transects which had the highest density of curlews (1.88 and 2.48/40 ha) and was used roughly in proportion to availability along the other two transects.

Cropland was highly preferred along the Umattilla Refuge transect, although the particular field utilized varied with changes in vegetative structure. Curlews used cropland as long as the crop was low in profile (or the ground fallow) and moved elsewhere when it was > 30 cm tall. Wheat, potatoes, and alfalfa comprised the major crops, and alfalfa was available recurrently depending on haying schedule.

Bunchgrass on one portion of the study area and open-low shrub on another were both preferred ($P < 0.05$). However, the bunchgrass tract was contiguous with an irrigated pasture and annual grass habitat in which two nests were located. The proximity of these two habitats may have influenced use of the bunchgrass habitat. The open low shrub habitat comprised 59% of the available habitat on the Bombing Range South and was used significantly more than other habitats. Snakeweed dominated the open-low shrub habitat and was much shorter than rabbitbrush or bitterbrush with mean effective height (EFHT) of 16 cm.

Dense forb and bitterbrush habitats were used less than expected along the transects. Bunchgrass was used less than expected on the Bombing Range North and South transects, as was the open-low shrub on the Bombing Range North. In general, curlews selected habitats of low vertical profile or low mean vertical density and avoided habitats of greater vertical profile or high mean vertical density.

HABITAT UTILIZATION: ADULTS WITH BROODS

Females generally abandon their mates and brood prior to fledging of the young, and males generally remain with the brood until the young are able to fly (Pampush 1981). Habitat utilization of adults with and without broods were similar

TABLE 2. Habitat utilization of adult Long-billed Curlews without broods along four transects in north-central Oregon during spring and summer 1979.

Transect	Habitat	No. of adults obs.	% use	% avail.	Confidence limits
Bombing Range South ($\chi^2 = 20.4, P < 0.05$)	Cheat grass	10	0.09	0.08	0.03–0.15
	Bunchgrass	9	0.08 ^a	0.17	0.02–0.14
	Dense forb	2	0.02 ^a	0.15	0.00–0.05
	Open-low-shrub	74	0.70 ^a	0.59	0.60–0.80
Bombing Range North ($\chi^2 = 53.4, P < 0.05$)	Cheat grass	122	0.55 ^a	0.33	0.47–0.63
	Bunchgrass	14	0.06 ^a	0.12	0.02–0.10
	Dense forb	77	0.35 ^a	0.44	0.27–0.43
	Open-low-shrub	7	0.03 ^a	0.11	0.00–0.06
Army Depot ($\chi^2 = 500.3, P < 0.05$)	Cheat grass	177	0.76 ^a	0.20	0.70–0.82
	Bitterbrush	26	0.11 ^a	0.39	0.06–0.16
	Bunchgrass	27	0.12 ^a	0.05	0.07–0.17
	Dense forb	4	0.02 ^a	0.36	0.00–0.04
Umatilla Refuge ($\chi^2 = 176.5, P < 0.05$)	Cheat grass	26	0.11	0.09	0.07–0.15
	Dense forb	27	0.12 ^a	0.54	0.08–0.16
	Cropland	177	0.77 ^a	0.37	0.73–0.81

^a Denotes statistically significant difference in use of habitat from availability.

(Tables 2–4, respectively). Along three of four transects, adults with broods used habitats significantly different from availability ($P < 0.05$) (Table 3). Cheatgrass habitat was selected along all three transects. Habitats of greater height and vertical density were used less than available by broods. Bitterbrush was avoided even though the interstices between shrubs were very similar structurally to the adjacent annual-grass habitat. The vertical component of this habitat appeared to influence habitat utilization. Dense forb was

avoided on all three transects, even though grasshopper (a common food) densities appeared as high in this habitat as in cheatgrass. Dense forb had the highest mean vertical density of all five habitats and second greatest effective height (behind bitterbrush habitat). Curlew chicks often struggled to get through the dense annuals (*Symsbrium*, *Amsinckia*), and adults probably had limited visibility when in this habitat.

Cropland was used by broods on a periodic basis on the Umatilla Refuge, and medium

TABLE 3. Habitat utilization of adult Long-billed Curlews with broods along four transects in north-central Oregon during spring and summer 1979.

Transect	Habitat	No. of adults obs.	% use	% avail.	Confidence limits
Bombing Range South ($\chi^2 = 10.3, P < 0.05$)	Cheat grass	2	0.06	0.08	
	Bunchgrass	4	0.12	0.17	
	Dense forb	6	0.18	0.15	
	Open-low-shrub	22	0.65	0.59	
Bombing Range North ($\chi^2 = 81.9, P < 0.05$)	Cheat grass	99	0.64 ^a	0.33	0.55–0.73
	Bunchgrass	4	0.02 ^a	0.12	0.00–0.05
	Dense forb	27	0.17 ^a	0.44	0.10–0.24
	Open-low-shrub	24	0.16	0.11	0.09–0.23
Army Depot ($\chi^2 = 400.1, P < 0.05$)	Cheat grass	159	0.74 ^a	0.20	0.67–0.81
	Bitterbrush	37	0.17	0.39	0.11–0.23
	Bunchgrass	10	0.05	0.05	0.02–0.08
	Dense forb	8	0.04 ^a	0.36	0.01–0.07
Umatilla Refuge ($\chi^2 = 17.0, P < 0.05$)	Cheat grass	8	0.28 ^a	0.09	0.11–0.45
	Dense forb	7	0.24 ^a	0.54	0.08–0.40
	Cropland	14	0.48	0.37	0.29–0.67

^a Denotes statistically significant difference in use of habitat from availability.

TABLE 4. Summary of habitat utilization patterns by adults with and without broods of Long-billed Curlews along four transects in north-central Oregon.^a

Transect	Adults without broods		Adults with broods	
	Preferred	Avoided	Preferred	Avoided
Army Depot	Cheatgrass Bunchgrass	Dense forb Bitterbrush Bunchgrass Dense forb	Cheatgrass Bunchgrass	Bitterbrush Dense forb Bunchgrass Dense forb
Bombing Range North	Cheatgrass	Open-low-shrub	Open-low-shrub	
Bombing Range South	Open-low-shrub	Bunchgrass	(χ^2 insignificant, $P > 0.05$)	
Umatilla Refuge	Cropland (alfalfa)	Cheatgrass	Cheatgrass	Cropland (alfalfa) Dense forb

^a Preference determined with "family" of confidence intervals (Neu et al. 1974).

hatching date roughly coincided with the first alfalfa cutting. Immediately prior to swathing, alfalfa fields were not used by curlews. Swathing created a habitat of low vertical profile and curlews used the alfalfa fields for some period of time following cutting. When the alfalfa grew taller than 30 cm tall, curlew use ceased until the next swathing. On the Umatilla Refuge, adults with broods used an alfalfa field for up to three weeks, although the cheatgrass habitat was nearby.

Bunchgrass habitats were avoided by adults with broods on the Bombing Range North and used in proportion to availability on the Army Depot. The patchiness of western-needle-and-thread grass along the Army Depot transect provided a microhabitat of annual grass interspersed with bunchgrass. Use of bunchgrass habitat was restricted to stands that were contiguous with cheatgrass. Extensive stands of bunchgrass habitat were avoided by adults with broods.

Open-low-shrub habitat was used in proportion to availability. This habitat comprised 11% of the available habitat and occurred in close proximity to annual-grass (33%) and dense forb (44%) habitats. This habitat and the annual grass habitat may be particularly important before the young fledge for thermal cover during hot days.

NEST-SITE SELECTION

Structural differences in vegetation between nest sites and randomly selected plots were statistically significant ($P < 0.05$) in four of the five habitats and for all habitats combined (Table 5). Differences between vegetation at nest sites and the general habitat were not statistically significant for the bitterbrush habitat ($P > 0.05$), which was probably the result of small numbers of nests found in that habitat ($n = 2$). The bitterbrush habitat was avoided for nesting and other uses by curlews (Tables 2-4).

For the cheatgrass habitat, the discriminant function selected effective height (EFHT), overall foliage height evenness (FHETOT), and vertical density of herbs from 0 to 25 cm high (HH25) in distinguishing between nest sites and the general habitat. All three are measures of vertical structure of the habitat. Effective height and foliage height evenness (FHETOT) were greater in randomly selected plots than at nest sites, which indicated that vegetation at nest sites was shorter and vertically patchier than the habitat in general. Mean vertical density of herbaceous plants

in the 0–25 cm height interval was greater at the nest sites than along random transects, reflecting the occurrence of standing dead tumbleweed plants and live *Opuntia* cactus that were associated with nest sites on sandy soil.

For bunchgrass habitats, total grass cover (TOTGR), bare ground cover (BRGD), and herb cover (HERB) were significantly different between nest sites and the general habitat. Total grass cover was significantly ($P < 0.05$) higher at nest sites (67%) as compared to random plots (55%). Herbaceous cover was slightly higher at nest sites than random plots (6.0 versus 4.0%) due primarily to the occurrence of *Phlox* and *Lupinus*. Bare-ground cover was included in the model, but the difference in means at nest sites versus random plots was not significant (mean: 0.296 vs. 0.297; SD: 0.067 vs. 0.081, respectively), so these results appear spurious.

For the dense forb habitat total grass cover, effective height, and foliage height diversity discriminated between nest and random plots. Effective height was the most important variable in the model, and nest sites had lower mean values than random plots ($\bar{x} = 23.7$ and 32.0 cm, respectively). Total grass cover and foliage height diversity of herbs were lower for nest sites than random plots.

The dense forb habitat was compositionally similar but structurally quite different from the annual-grass habitat. Mean effective height at nest sites was very similar for both habitats, but mean effective height for random plots among the habitats (Table 5) differed significantly ($P < 0.05$). Curlews chose nest sites away from the taller, denser cover as evidenced by the inclusion of effective height and foliage height diversity of herbs in the discriminant model. Nest sites were generally located in patches where the soil was more stabilized and cheatgrass-Sandberg's bluegrass dominated. Cheatgrass grew in dense patches in some areas within the dense forb habitat. Generally, the open cheatgrass-dominated areas, where curlews nested, were of lower plant biomass than the dense forb habitat.

For open-low shrub habitat, the discriminant function selected only effective height. Mean effective height for nests and random plots was 22.0 and 28.0 cm, respectively. The dominant vegetative element contributing to the difference in effective height was snakeweed. The open-low shrub habitat supported a low nesting density, even though its mean effective height was higher

than that of the cheatgrass habitat by only 3.2 cm. Nest sites in open-low shrub habitat were characterized by lower shrub cover than random plots ($\bar{x} = 8.0$ vs. 11.0%), but the difference was not statistically significant ($P > 0.05$).

For the habitats combined, five variables were important in discriminating between nest versus random plots (Table 5). Effective height explained most of the variability in the data followed closely by foliage height diversity of grass. This model indicated that curlews selected nest sites with shorter and structurally less complex vegetation than available in the habitats in general. Also, the vertical distribution of vegetation at nest sites was "patchier" than in the pooled habitats, as indicated by the inclusion of foliage height evenness in the model.

COMPARISONS OF NESTS AMONG HABITATS

Comparisons of nest sites among habitats revealed statistically significant ($P < 0.05$) differences for five of six paired habitat comparisons. Seven variables in the cheatgrass/bunchgrass comparison contributed significantly to the differences ($P < 0.0001$). All seven variables were related to vertical stratification of the vegetation with effective height, diversity, and vertical density all higher at nest sites in the bunchgrass habitat (Table 6). For nest sites in the cheatgrass/dense forb comparison, mean values for bare-ground cover and grass foliage height diversity were statistically different ($P < 0.001$). Bare ground cover was higher at nests in cheatgrass habitat, whereas foliage height diversity of grasses was higher at the dense forb nest sites. Percent bare ground and vertical density of annual herbs were significantly different ($P < 0.05$) in the cheatgrass/open-low-shrub comparison. Mean bare ground cover and annual herb vertical density in the 0- to 25-cm height interval were greater at cheatgrass nest sites. For the bunchgrass/dense forb comparison, three variables were significantly ($P < 0.0001$) different and all were related to vertical stratification and diversity. Grass was denser and more diverse at the bunchgrass nest sites, whereas annual forb density at the 0–25 cm high was greater at the dense forb nest sites. For the bunchgrass/open-low-shrub nest comparison, three variables were significantly ($P < 0.001$) different between habitats. All three variables were measures of mean vertical density of vegetation, and nests in the bunchgrass habitat had a higher vertical density of grasses from 0–50 cm

TABLE 5. Discriminant function coefficients for comparison of nest sites and randomly selected plots of Long-billed Curlews in north-central Oregon. Means and standard deviations for variables at nest sites and habitats are given in parentheses.

Habitat	Variables in the discriminant models				
	TOTGR	BRGD	HERB	EFHT	FHDG
Cheatgrass				-0.52	
Nest sites (<i>n</i> = 25)				(22.2 ± 2.8)	
Habitat (<i>n</i> = 70)				(24.8 ± 3.3)	
Bunchgrass	1.48	0.86	0.97		
Nest sites (<i>n</i> = 9)	(67 ± 0.16)	(0.30 ± 0.07)	(0.06 ± 0.08)		
Habitat (<i>n</i> = 50)	(55 ± 0.12)	(0.30 ± 0.08)	(0.04 ± 0.05)		
Dense forb	-0.51			-1.25	
Nest sites (<i>n</i> = 7)	(0.32 ± 0.08)			(23.7 ± 3.5)	
Habitat (<i>n</i> = 40)	(0.40 ± 0.09)			(32.7 ± 4.0)	
Open-low-shrub				1.00	
Nest sites (<i>n</i> = 4)				(22.0 ± 3.5)	
Habitat (<i>n</i> = 40)				(28.0 ± 2.9)	
Habitats Combined				-0.89	0.80
Nest sites (<i>n</i> = 45)				(23.8 ± 3.8)	(0.60 ± 0.12)
Habitat (<i>n</i> = 240)				(28.9 ± 5.1)	(0.62 ± 0.16)

* TOTGR = Total grass cover, BRGD = Bare ground cover, HERB = Herbaceous cover, EFHT = Effective height, FHDG = Foliage height diversity of grasses, FHDH = Foliage height diversity of herbs, FHETDT = Total from 0-25 cm, HG50 = Vertical density of grasses from 26-50 cm, HSTALL = Vertical density of all vegetation.

and a higher overall vertical density. The results of these pairwise comparisons indicated that curlews selected nest sites with considerable structural variability among habitats, which was a reflection of inherent differences between habitats.

DISCUSSION

Hubbard (1973) speculated that the evolutionary origin of Long-billed Curlews was in one of several North American refugia resulting from the extensive Pleistocene glaciation. The center of geographic origin of Long-billed Curlews is not known, although the Great Plains (Johnsgard 1978) seems likely, because they breed in short-grass habitats throughout their range. The Columbia Basin historically was dominated by tall bunchgrass (Daubenmire 1970), but curlews preferred cheatgrass habitats and avoided the bunchgrass habitats in this study. In addition, they were observed infrequently in bunchgrass habitats in a breeding survey by the senior author in the Columbia and Great Basins.

NEST DENSITY AND SUCCESS

Long-billed Curlews had highest nest success and density in cheatgrass habitats in this study. The mean nest density of 3.57 nests/40 ha in this habitat is similar to the highest density (4.10

nests/40 ha) observed by Skeel (1983) for Whimbrels near Churchill, Manitoba. She attributed the high density and nesting success in her habitat to the advantages of greater cryptic coloration in denser vegetation. In contrast, Long-billed Curlews in this study nested in highest densities and were most successful in the simplest, most open habitats. Because 57% of depredated nests were destroyed by mammalian predators and nest predation was significantly higher in habitats other than cheatgrass, it appears that Long-billed Curlews in northcentral Oregon are adapted to breeding in habitats of low shrub cover and of low vegetative profile. This phenomenon may be an adaptation for predator detection and avoidance, because coyotes, badgers, crows, and magpies are common nest predators throughout their breeding range. Similarly, Redmond and Jenni (1986) found that most nest losses in western Idaho were a result of canids, badgers, or corvids.

HABITAT UTILIZATION PATTERNS

In this study, an overall preference for habitats of low vertical profile and low vertical density was evident. Nesting adult curlews often foraged away from their territory when they were not incubating. Adults with and without broods foraged in cropland on the study areas and adjacent to them. Short or freshly swathed alfalfa was used

TABLE 5. Continued.

Variables in the discriminant models					Correctly classified
FHDH	FHETOT	HH25	HG50	HSTALL	
	-0.64 (0.68 ± 0.16) (0.76 ± 0.07)	0.55 (0.50 ± 0.31) (0.38 ± 0.22)			74
					84
0.58 (0.62 ± 0.08) (0.72 ± 0.26)					87
					82
	-0.54 (0.70 ± 0.12) (0.76 ± 0.08)		-0.50 (0.80 ± 0.12) (0.15 ± 0.18)	-0.31 (0.02 ± 0.09) (0.05 ± 0.15)	76

extensively as a foraging area even though no nesting behavior was observed in this habitat. Redmond (1986) observed curlews flying to undefended foraging sites on agricultural land within 10 km of their territories in western Idaho. Redmond (1986) also observed Long-billed Curlews to forage away from their defended territories in years when dense residual vegetation covered most of their territories, and this resulted in lower clutch size. Skeel (1983) observed Whimbrels regularly foraging away from defended territories, and monogamous calidridine sandpipers often exhibit similar foraging patterns during the incubation period (Holmes 1971, Jehl

1973, Miller 1979). Although foraging often occurred at a distance from the defended territory in this study, curlews regularly foraged in the cheatgrass habitat throughout the breeding season. Both 1978 and 1979 were years of high grasshopper (Orthoptera) numbers, and curlews were often observed foraging on them.

NEST-SITE SELECTION

Comparison of nest-site characteristics in different habitats in this study indicated that Long-billed Curlews were relatively plastic in nest-site selection, although a preference for structurally short (low vertical profile) habitats was evident.

TABLE 6. Comparison of nest-site characteristics between habitats for Long-billed Curlews in north-central Oregon.

Habitats compared	Results of Hotelling's <i>t</i> ² test between groups (<i>P</i> < 0.05)	Variables contributing to significant univariate <i>t</i> -tests ^a
Cheatgrass/Bunchgrass	(<i>P</i> < 0.0001)	EFHT, FHDG, FHDTOT, HGWE, HTOT-25, HGTO, HTOVRL
Cheatgrass/Dense forb	(<i>P</i> < 0.0001)	BRGD, FHDG
Cheatgrass/Open-low-shrub	(<i>P</i> < 0.05)	BRGD, HH25
Bunchgrass/Dense forb	(<i>P</i> < 0.0001)	FHDG, HG25, HH25
Bunchgrass/Open-low-shrub	(<i>P</i> < 0.001)	HG25, HG50, HTOVRL
Dense forb/Open-low-shrub	Nonsignificant	

^a EFHT = Effective height, FHDG = Foliage height diversity of grasses, FHDTOT = Foliage height diversity of all vegetation, HG25 = Vertical density of grasses from 0-25 cm., HTOT = Vertical density of all vegetation from 0-25 cm, HG50 = Vertical density of grasses from 0-50 cm, HTOVRL = Vertical density of all vegetation overall, BRGD = Bare ground cover, HH25 = Vertical density of herbaceous plants from 0-25 cm.

Grassland ecosystems are characterized by climatic variability and unpredictability (Wiens 1974), and yearly variation in precipitation and temperature may result in varying structure of an annual grassland. Comparison of nest-site and general habitat characteristics indicated that vertical structure of vegetation was an important factor in nest-site selection. Vegetative height and foliage height diversity were lower at nest sites than surrounding habitats in all cases except one. The importance of overall foliage height evenness in the cheatgrass habitat and all habitats combined indicated that curlews selected nest sites with vertically patchier vegetation than occurred in the general landscape. Cryptic coloration of eggs and plumage suggest that predation has been a strong selective force, and the vertically uneven distribution of vegetation around nest sites may enhance adult survival or nest success. Mortality of nesting adults was low over the two years; only six of 101 nests were abandoned and mortality was possible only in three of these cases. Bicak (1977) found that Long-billed Curlew nest sites in Nebraska had greater vertical biomass at the 5–10 cm height interval than did the shortgrass in general, but he did not examine relative vertical dispersion (evenness) of vegetation.

Long-billed Curlews avoided bitterbrush and bunchgrass habitats in this study even though these habitats were contiguous with cheatgrass habitats in which a high breeding density occurred. Avoidance of native bunchgrass habitat is interesting because it was the dominant climax community prior to the arrival of Europeans in the area (Poulton 1955). Historically, curlews either did not use native bunchgrass habitats for nesting, or these habitats are different now than they were 200 years ago. In addition, intensive grazing likely reduced the abundance of bunchgrass and left prime conditions for the subsequent invasion of exotic cheatgrass. Curlews currently breed in high densities in cheatgrass-dominated areas, which were formerly dominated by bunchgrass. Various habitats probably supported curlews prior to the advent of European people, including areas dominated by Sandberg's bluegrass and saltgrass around playas. These habitats may have supported breeding curlews prior to the invasion of cheatgrass, and the distribution of breeding curlews may have changed after cheatgrass became well established. Similarly, wild fires may have played an

important role in the evolution of habitat and nest-site selection of this species, because fires kill most shrubs and create open habitats. Such changes would create more favorable habitat conditions for Long-billed Curlews; Burrowing Owls, *Athene cunicularia* (Green and Anthony 1989); and Loggerhead Shrikes, *Lanus ludovicianus* (Poole 1993). All three species are prominent breeders in shrubsteppe communities of the Columbia Basin of Oregon and Washington.

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