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Multiscale Habitat Selection by Long-billed Curlews (*Numenius americanus*) Breeding in the United States

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Abstract.—Long-billed Curlew (*Numenius americanus*) populations have declined during the past 150 years in part due to destruction and fragmentation of grasslands used during the breeding season. Here, multiscale habitat characteristics best predicting number of Long-billed Curlews, detected during range-wide surveys conducted throughout the United States in 2004 and 2005, were determined. Long-billed Curlews were most often observed in habitats classified primarily as grassland habitat and secondarily as shortgrass or pasture/rangeland, all with low vegetation heights (i.e. 4-15 cm). Numbers of Long-billed Curlews were positively associated with wetland habitats on a local scale and hay/pasture areas on a landscape scale, but negatively associated with shrub/scrub on local and landscape scales and evergreen forests on a landscape scale. The study confirmed the importance of grassland, cropland, pasture and wetland habitats for breeding Long-billed Curlews across its geographic range in the United States. These results reinforce the need to conserve, manage, or create contiguous tracts of grasslands containing emergent wetlands for Long-billed Curlews throughout the breeding season and their range in the United States.
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Key words.—breeding, GIS, grasslands, habitat characteristics, Long-billed Curlew, nesting, *Numenius americanus.*

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During the last 150 years, population size and breeding range of Long-billed Curlews (*Numenius americanus*) have declined, especially in the eastern portion of their range in the United States and Canada (Brown *et al.* 2001; Dugger and Dugger 2002). Currently, Long-billed Curlews are considered Highly Imperiled in both the United States and Canada shorebird conservation plans due to these declines and continuing threats (Donaldson *et al.* 2000; U.S. Shorebird Conservation Plan 2004). The main cause attributed to Long-billed Curlew declines within the United States is the >30% loss and fragmentation of Great Plains grassland habitat (Fellows and Jones 2009). For example, from 1950 to 1990, grasslands west of the Mississippi River declined by 11 million ha, with approximately 36% converted to uses other than cropland (Conner *et al.* 2001). Threats to grasslands and ultimately to breeding grassland birds such as Long-billed Curlews include: conversion of native grasslands to agriculture or suburban development; introduction of nonnative plant species, particularly forbs (e.g. knapweeds [*Centaurea* spp.]); unmanaged grazing pressure; and fire suppression leading to invasion of woody plants (Pampush and Anthony 1993; Hill 1998; Cannings 1999; Dugger and Dugger 2002). Therefore, the importance of proactive management has become magnified for breeding Long-billed Curlew habitat conservation.

Within the United States, Long-billed Curlews breed primarily in shortgrass or mixed-grass prairie habitats of the central and western Great Plains, Great Basin and intermontane grasslands of the western United States (Dugger and Dugger 2002). Historically, Long-billed Curlews bred over a much larger range, including some records in the 1800s documenting Long-billed Curlews within historic tallgrass prairies of the midwestern United States (Dugger and Dugger 2002). Within their current range, Long-billed Curlews use agricultural fields, tame pastures, and native grasslands for nesting and foraging throughout the breeding season (Dechant *et al.* 1999) and place nests in a variety of grasses including: buffalograss (*Buchloe dactyloides*; Clarke 2006), junegrass (*Koeleria macrantha*; Clarke 2006), cheatgrass (*Bromus tectorum*; Allen 1980; Pampush and Anthony 1993), and Sandberg's bluegrass (*Poa sandbergii*; Allen 1980; Pampush and Anthony 1993). However, structural characteristics may be more important than specific plant species in which nests are placed, as Long-billed Curlews nest in grasslands with short vertical profiles (< 10 cm) and low densities (< 50% cover; Pampush 1980; Pampush and Anthony 1993; Dugger and Dugger 2002), with few trees or shrubs, and avoid areas with taller, denser grass, shrubs and weedy vegetation (Pampush and Anthony 1993; Dechant *et al.* 1999; Dugger and Dugger 2002).

Within the generalized grassland habitats described above, Long-billed Curlews may make subtle adjustments in local habitat selection throughout the breeding season (Fellows and Jones 2009). For example, Long-billed Curlews may select brood-rearing habitat based upon vegetation structure (Pampush and Anthony 1993), as well as prey availability (e.g. low stature grasslands and croplands; Pampush 1980; Foster-Willfong 2003; Clarke 2006). However, few data exist concerning habitat selection and characteristics used during courtship, nest site selection (King 1978; Allen 1980; Pampush and Anthony 1993; Shackford 1994; Clarke 2006), foraging (Stenzel *et al.* 1976) or brood rearing (Pampush and Anthony 1993).

Habitat selection is also a result of local vegetation structure and habitat availability that may vary unpredictably and annually (King 1978; Pampush 1980; Foster-Willfong 2003; Fellows and Jones 2009). For example, within grassland habitats, proximity to surface water in natural wetlands may be a relevant determinant of breeding season habitat use (Gratto-Trevor 2006), but Long-billed Curlews tend to exhibit strong nesting site fidelity even when surface water presence varies annually (see McCallum *et al.* 1977; Redmond and Jenni 1982). Breeding habitats may be prone to both natural (e.g. drought, fire, flooding, etc.) and anthropogenic (e.g. conversion, development, etc.) disturbances that may influence the suitability of an area for nesting Long-billed Curlews. Because of this, range-wide Long-billed Curlew habitat requirements are poorly defined (but see Fellows and Jones 2009). Consequently, successful conservation of range-wide Long-billed Curlew populations requires detailed examination of breeding habitat(s) at multiple spatial scales to develop sound management strategies under which Long-billed Curlews and humans can coexist. Our objective was to determine multiscale habitat characteristics best predicting number of Long-billed Curlews detected during the arrival and pre-incubation periods in breeding regions throughout the western United States.

METHODS

Survey

The research was conducted as part of a range-wide survey to estimate Long-billed Curlew breeding population size throughout the United States and Canada in 2004 and 2005 (Stanley and Skagen 2007; Jones *et al.* 2008). Although the survey was range-wide, we used only habitat data collected in the United States (Jones *et al.* 2008). Townships (an approximately 9,324 ha square unit of land as designated by the Public Land Survey System), within the geographic range of breeding Long-billed Curlews, were used as sampling units in which survey routes were selected (Stanley and Skagen 2007; Jones *et al.* 2008). Initially, proportions of townships consisting of unsuitable habitat were estimated (e.g. high elevation, area developed, large water bodies, etc.; see Stanley and Skagen 2007 for censoring approaches). Townships possessing ≥30% suitable habitat were classified into one of three strata based upon % grassland habitat (Stanley and Skagen 2007; Jones *et al.* 2008) calculated from the National Land Cover Data (National Land Cover Database 2001; Homer *et al.* 2004). Strata 1-3 were defined using Saunders' (2001) grassland criteria (i.e. stratum 1 = 0-5% grassland, stratum 2 > 5-50%

grassland and stratum 3 > 50-100% grassland). Stratum 4 consisted of townships that contained <30% suitable Long-billed Curlew habitat. Townships were selected using simple random sampling without replacement within each stratum for each survey year (Jones *et al.* 2008). Samples were allocated among strata using estimated variances from Saunders (2001), resulting in 42, 53, 45 and 15 townships sampled from stratum 1, 2, 3 and 4 respectively, in 2004 and 26, 64, 50 and 15 townships sampled from stratum 1, 2, 3 and 4 respectively, in 2005 (Stanley and Skagen 2007). Within each selected township, a 32-km survey route was delineated along roads excluding interstate highways or roads with two or more lanes, following Saunders (2001).

Survey execution was designed to correspond with Long-billed Curlew arrival and preincubation periods, a time when detection probability was greatest because they were exhibiting behaviors to attract mates and establish breeding territories and had not yet begun incubation (Jones *et al.* 2008). Because this period varies geographically, the study area was divided into temporal periods representing the average breeding period for Long-billed Curlews within a specific region. This was accomplished by creating a breeding chronology map that correlated the First Lilac Leaf Date data (Cayan *et al.* 2001) with Long-billed Curlew breeding records from the literature and local area specialists (S. L. Jones, pers. comm.). Surveys were conducted from 21 March-15 May during both years, with southern latitudes surveyed earlier than northern latitudes (see Jones *et al.* 2008 for survey periods). During each survey, observers traveled the 32-km route by vehicle, stopping at points 0.8 km apart and recording all Long-billed Curlews seen or heard during a 5-min sample window. The distance from the observer to each Long-billed Curlew seen or heard was determined by laser rangefinder or ocular estimation and grouped into one of three categories (i.e. 0-400 m, >400-800 m, and >800 m; Jones *et al.* 2008). As very few Long-billed Curlews were detected > 800 m away from the route (<15% of all Long-billed Curlews detected; Stanley and Skagen 2007), habitat and detection of Long-billed Curlews > 800 m from each route were not included in this study.

Local Habitat

Local habitat analysis was performed on a stop-level. When a Long-billed Curlew was seen, observers recorded the following habitat variables immediately surrounding each individual bird (5-m radius): vegetation height (categorized from 1-6 estimated based on visual relationship between vegetation and standing Long-billed Curlew; category 1 = bare ground-4 cm [can see foot of standing Long-billed Curlew], category 2 = 4-10 cm [covers foot to "knee" of standing Long-billed Curlew], category 3 = 10-15 cm [up to base of belly of standing Long-billed Curlew], category 4 = 15-45 cm [up to back of standing Long-billed Curlew], category 5 = 45-65 cm [up to eye level of standing Long-billed Curlew], category 6 = >65 cm [above head of standing Long-billed Curlew]) and all relevant primary, secondary, tertiary and habitat condition codes (Appendix 1). Additionally, within 400 m of each stop, regardless of Long-billed Curlew detection (i.e. seen or heard), observers estimated percent cover of up to four primary habitat codes (i.e. recorded primary codes that comprised ≥25% of the area in decreasing order of abundance until 100% classification or four primary codes were estimated) and all appropriate secondary, tertiary and habitat condition codes by quadrant (i.e. NE, NW, SE, SW). These data were used to estimate percent cover for each habitat category for each stop on each route. All habitat data were recorded after each 5-min survey period was completed. In some instances, primary habitat was not recorded or only partially recorded for a stop (100% of habitat was not recorded if not all habitat was observable [e.g. topography blocked line of sight] or classifications that comprised <25% of the area were present). In this study, we included stops in which observers classified ≥50% of the habitat (487 out of 9860 stops [5%] resulted in <50% habitat classification).

Landscape Habitat

Landscape habitat analysis was performed on a route-level. We delineated 32-km survey routes by tracing roads along which surveys were conducted using Street Maps USA for use with ArcGIS 9.2 (ESRI 2005). To correspond with maximum observation distances (i.e. 800 m; see above), we placed 800 m distance habitat plots (i.e. buffers) around each route using ArcGIS 9.2. Within each plot, we used the 2001 National Land-Cover Data to determine any habitat associations with number of Long-billed Curlews seen or heard along a route. These data provide relevant, standardized land cover classifications for the entire sampling region measured in close temporal proximity to surveys. Although there were three to four years between land cover data classification (2001) and data collection (2004 and 2005), land cover data correctly classified the majority of stop level habitat (i.e. when field classifications from a subset of stops [237 stops located on different routes] was compared to land cover classifications within a 400 m radius of each stop, 65% of field classifications were correctly classified by the land cover data). We determined percentage of each habitat (Appendix 1) within plots for each route using Thematic Raster Summary in Hawth's Analysis Tools in ArcGIS (Beyer 2004). As habitat along routes were representative of Long-billed Curlew habitat in general (Stanley and Skagen 2007), it is unlikely that any bias occurred from only sampling habitat around roads.

Data Analyses

Distribution Selection. Because our response variables were count data, we modeled number of Long-billed Curlews detected on local and landscape scales using the Poisson distribution (PROC GENMOD; SAS Institute 2002). However, when using this distribution, overdispersion was high (i.e. deviance/degrees of freedom [df] >4), especially among landscape models. Therefore, we used the negative binomial distribution (PROC GENMOD; SAS Institute 2002) to model number of Long-billed Curlews detected on both the local and landscape scales. In all instances, using the negative binomial distribution, we concluded that the models fit the data well (i.e. deviance/df ≈ 1).

Local Scale. To determine local habitat variable(s) best predicting number of Long-billed Curlews detected 0-400 m from a stop, we developed a set of candidate models, *a priori*, consisting of biologically relevant combinations of primary habitat categories (see Appendix 1). In all models, correlated ($P \leq 0.05$) variables were excluded from entering the same model. To account for spatial autocorrelation of stops along the same route, we used generalized estimating equations (GEE) repeated among stops for a given route. GEEs are an extension of generalized linear models that account for the covariance structure of response variables (Hardin and Hilbe 2003). We used the quasi-likelihood criterion (QIC_u) to select the best model(s) from the candidate set. QIC_u is a modified version of Akaike's Information Criterion corrected for small sample size (AIC_c) that can be used with GEEs, where QIC_u replaces the likelihood in AIC_c with the quasi-likelihood (Pan 2001). An individual model was considered plausible when $\Delta QIC_u < 2$ (Burnham and Anderson 2002). We present parameter estimates, standard errors, confidence intervals, and *P*-values from the top model(s). Number of Long-billed Curlews within 0-400 m from a stop point was also modeled using secondary, tertiary and habitat conditions when grassland or cropland was the primary habitat (see Appendix 1) using negative binomial regression with same methodology as above.

Landscape Scale. To determine landscape habitat variable(s) best predicting number of Long-billed Curlews detected within 800 m of a route, irrespective of strata, we developed a set of candidate models, *a priori*, consisting of biologically relevant combinations of landscape habitat variables (see Appendix 1). In all models, correlated ($P \leq 0.05$) variables were excluded from entering the same model. Because our landscape habitat analysis corresponded to the route-level, we did not account for the covariance structure of the response variable with the use of GEEs. We used AIC_c to select the best model(s) from the candidate set of models. An individual model was considered plausible when $\Delta AIC_c < 2$ (Burnham and Anderson 2002). We present parameter estimates, standard errors, confidence intervals and *P*-values from the top model(s). Number of Long-billed Curlews within 800m of a route was also modeled using landscape habitat variable(s) (see Appendix 1) within each strata (i.e. stratum 1, 2 or 3) using negative binomial regression with same methodology as above.

RESULTS

In 2004 and 2005, 9,860 stops along 285 routes were surveyed in the United States (139 routes in 2004 and 146 in 2005). There was at least one Long-billed Curlew detected 0-800 m from an observer on 112 of these routes (60 routes in 2004 and 52 in 2005; see Stanley and Skagen [2007] for figure of routes in which Long-billed Curlews were detected) and at least one Long-billed Curlew 0-800 m from an observer on 14, 43 and 55 routes within stratum 1, 2 and 3, respectively (no Long-billed Curlews were detected within stratum 4). Of the 1,026 Long-billed Curlews observed within 0-800 m during 2004 and 2005, the majority occurred in Montana (23.5%), Nebraska (13.1%), Oregon (12.3%) and South Dakota (12.3%). However, Texas (17.8 Long-billed Curlews/route), South Dakota (9.0 Long-billed Curlews/route), New Mexico (8.6 Long-billed Curlews/route), Nebraska (7.4 Long-billed Curlews/route) and Oklahoma (6.6 Long-billed Curlews/route) had the greatest mean number of Long-billed Curlews detected per route.

Local Scale

The majority (63%) of Long-billed Curlews detected 0-800 m from a stop were located in grassland habitat (most occurring in shortgrass prairie [52%] and pasture grasslands [37%]), followed by cultivated crops (22.2%; an almost equal percent occurring in dry [52.3%] and irrigated [47.7%] lands). Additionally, most (71.5%) Long-billed Curlews detected 0-800 m from a stop occurred within vegetation 4-15 cm tall (categories 2 and 3).

Among 15 candidate primary habitat models (Table 1), the model best predicting number of Long-billed Curlews within 400 m of a stop was the additive model of % shrub/scrub and % wetland (Table 1). The largest

Table 1. Generalized estimating equation models using the negative binomial distribution for primary local habitat data predicting number of Long-billed Curlews 0-400 m from survey stops in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Model	No. parameters	ΔQIC_u[a]	QIC_w[b]
% EMWL + % SHRB	3	0.00	1.00
% SHRB	2	73.71	0.00
% EMWL + % GRAS	3	138.28	0.00
% EMWL	2	143.09	0.00
% EMWL + % STEP	3	160.85	0.00
% OWWL	2	180.41	0.00
% WOOD	2	183.15	0.00
% CROP	2	187.33	0.00
% GRAS	2	214.25	0.00
Intercept	1	217.93	0.00
% WEED	2	220.89	0.00
% STEP	2	231.81	0.00
% OTHR	2	232.09	0.00
% RCWS	2	252.57	0.00
% BARE	2	262.98	0.00

[a]Difference between model's quasi-likelihood criterion and the lowest QIC_u value.

[b]QIC_u relative weight attributed to model.

coefficient in the model was associated with % wetland with a positive coefficient, followed by % shrub/scrub with a negative coefficient (Table 2). Within the grassland primary habitat, among the seven candidate secondary habitat models (Table 3), the model best predicting number of Long-billed Curlews within 400 m of stop was the single variable model containing % planted pasture and rangelands (Table 3), which had a positive model coefficient (Table 4). Within the grassland primary habitat, among the four candidate tertiary habitat models (Table 3), the model best predicting number of Long-billed Curlews within 400 m of stop was the single variable model containing % short grass (i.e., <12 cm; Table 3), which had a positive model coefficient (Table 4). Within the cropland primary habitat, among the three candidate tertiary models (Table 3), the model best predicting number of Long-billed Curlews within 400 m of stop was the single variable model containing % medium crop (i.e. 12-38 cm; Table 3), which had a negative model coefficient (Table 4). Within the cropland primary habitat, there was no top model (i.e. not sufficient evidence to reject the intercept as a plausible model [$\Delta AIC_c < 2$]) of habitat condition associated with number of Long-billed Curlews detected within 400 m of a stop (Tables 3 and 4).

Landscape Scale

Among 19 candidate models (Table 5), the model best predicting number of Long-billed Curlews within 800 m of a route, irrespective of strata was the additive model of % evergreen, % hay and % shrub (Table 5). The largest coefficient in the model was associated with % evergreen forest with a negative coefficient, followed by % hay with a positive coefficient and % shrub/scrub with a negative coefficient (Table 6). Goodness of fit statistic from the top model indicated that the model fit the data well (deviance/df = 0.806). Among 27 candidate models within stratum 1 (i.e. 0-5% grassland), the first four models should be considered plausible (i.e. ΔAIC_c < 2; Table 7). In these models, % herbaceous had the greatest model coefficient and was negative in the top three models (Table 8), followed by % shrub/scrub in the top model also with a negative coefficient. % crop and % hay also appear to be important variables among these models, both having a positive model coefficient when they were present. Goodness of fit statistic from the top model indicated that the model fit the data well (deviance/df = 0.595). Among the 20 candidate models within stratum 2 (i.e. 5-50% grassland), the model best predicting number of Long-billed Curlews 0-800 m from a route was the additive model of % evergreen, % hay, and % shrub/scrub (Table 7). In this model, % evergreen forest had the greatest model coefficient and was negative, followed by % hay with a positive model coefficient and % shrub/scrub with a negative coefficient (Table 8). Goodness of fit statistic from the top model indicated that the model fit the data well (deviance/df = 0.769). Among the 19 candidate models within stratum 3 (i.e. 50-100% grassland), the model best predicting number of Long-billed Curlews within 800 m of a route was the single variable model containing % shrub/scrub (Table 7), which had a negative model coefficient (Table 8). Goodness of fit statistic from the top model indicated that the model fit the data well (deviance/df = 1.090).

Table 2. Characteristics of top-ranked generalized estimating equation model using the negative binomial distribution for local habitat data predicting number of Long-billed Curlews 0-400 m from survey stops in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Parameter	Estimate	SE	Wald 95% CI		Chi-square	*P*
Intercept	-2.605	0.137	-2.874	-2.336	-18.97	<0.001
% EMWL	3.647	1.423	0.859	6.435	2.56	0.010
% SHRB	-1.991	0.575	-3.118	-0.864	-3.46	<0.001

Table 3. Generalized estimating equation models using the negative binomial distribution for secondary, tertiary and habitat condition for grassland and cropland primary habitat data predicting number of Long-billed Curlews 0-400 m from survey routes in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Model	No. parameters	ΔQIC_u[a]	QIC_w[b]
Grassland secondary habitat			
% PAST	2	0.00	1.00
% NTPA	2	34.69	0.00
% SHTG	2	38.15	0.00
% MIXG	2	74.20	0.00
Intercept	1	89.90	0.00
% TALG	2	96.51	0.00
% CRPC	2	173.64	0.00
Grassland tertiary habitat			
% SHRT	2	0.00	1.00
Intercept	1	157.89	0.00
% MEDM	2	157.91	0.00
% TALL	2	366.47	0.00
Cropland tertiary habitat			
% MEDM	2	0.00	1.00
% SHRT	2	15.98	0.00
Intercept	1	545.60	0.00
Cropland habitat conditions			
Intercept	1	0.00	0.54
% IR	2	0.63	0.39
% DY	2	4.09	0.07

[a]Difference between model's quasi-likelihood criterion and the lowest QIC_u value.
[b]QIC_u relative weight attributed to model.

Table 4. Characteristics of top-ranked generalized estimating equation models using the negative binomial distribution for secondary, tertiary and habitat condition for grassland and cropland habitat data predicting number of Long-billed Curlews 0-400 m from survey routes in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Parameter	Estimate	SE	Wald 95% CI		Chi-square	*P*
Grassland secondary habitat						
Intercept	-2.535	0.196	-2.920	-2.151	-12.92	<0.001
% PAST	0.868	0.476	-0.064	1.800	1.83	0.068
Grassland tertiary habitat						
Intercept	-2.509	0.295	-3.088	-1.930	-8.50	<0.001
% SHRT	0.582	0.707	-0.804	1.967	0.82	0.411
Cropland tertiary habitat						
Intercept	-0.591	0.537	-1.643	0.461	-1.10	0.271
% MEDM	-4.203	2.239	-8.591	0.185	-1.88	0.061
Cropland habitat conditions						
Intercept	-2.536	0.244	-3.014	-2.059	-10.41	<0.001

DISCUSSION

During the range-wide Long-billed Curlew survey in the United States, Long-billed Curlews were most frequently observed in low stature (i.e. 4-15 cm), shortgrass prairie and pasture grasslands as well as cultivated crops. Additionally, secondary and tertiary local habitat analysis of grasslands revealed that Long-billed Curlews within 0-400m of a

Table 5. Negative binomial regression models for landscape habitat data predicting number of Long-billed Curlews 0-800 m from survey routes in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
% EVGR + % HAY + % SHRB	4	0.00	0.93
% EVGR + % SHRB	3	5.17	0.07
% HAY + % SHRB	3	20.09	0.00
% SHRB	2	26.18	0.00
% CROP + % HERB	3	36.67	0.00
% EVGR	2	38.30	0.00
% EVGR + % HAY	3	39.06	0.00
% HERB	2	48.85	0.00
% DECD	2	53.42	0.00
% CROP + % HAY	3	53.80	0.00
% CROP	2	55.19	0.00
% EMRG	2	56.90	0.00
Intercept	1	58.56	0.00
% MIXD	2	58.78	0.00
% HAY	2	59.05	0.00
% WATR	2	59.70	0.00
% DEVL	2	60.24	0.00
% WDWT	2	60.48	0.00
% BARN	2	60.60	0.00

[a]Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.
[b]AIC_c relative weight attributed to model.

Table 6. Characteristics of top-ranked negative binomial regression model for landscape habitat data predicting number of Long-billed Curlews 0-800 m from survey routes in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Parameter	Estimate	SE	Wald 95% CI		Chi-square	*P*
Intercept	1.908	0.187	1.543	2.274	104.59	<0.001
% EVGR	-8.378	2.367	-13.017	-3.739	12.53	<0.001
% HAY	3.972	1.737	0.567	7.376	5.23	0.022
% SHRB	-2.921	0.403	-3.711	-2.131	52.54	<0.001
Dispersion	3.707	0.495	2.737	4.676		

route were positively associated with short grass (i.e. <12 cm) and planted pasture and rangelands. These results are consistent with other studies throughout their range, where Long-billed Curlews use low stature (i.e. <10 cm; Dugger and Dugger 2002) agricultural fields, tame pastures, and native grasslands for nesting and foraging throughout the breeding season (Dechant *et al.* 1999). However, if planted pastures and rangelands are providing adequate breeding/nesting habitat or are simply used because they are the most available grassland habitat in these areas is unclear. Future work should focus specifically upon quantifying and comparing Long-billed Curlew selection functions and reproductive success in planted pastures and rangelands with other grassland habitats. Nearly two-thirds of all Long-billed Curlews were detected in grassland habitats. Some evidence indicates that number of Long-billed Curlews detected during the preincubation period accurately reflects the number nesting in an area (Saunders 2001; Gratto-Trevor 2006). Additionally, during the pre-incubation period, Long-billed Curlews are on nesting territories and conducting courtship activities, indicating that nest placement will occur within the individual territory of the observed bird (Saunders 2001). Because of this, these results substantiate the need for conservation and management of existing

Table 7. Negative binomial regression models for landscape habitat data predicting number of Long-billed Curlews 0-800 m from survey routes within strata 1-3 in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Model	No. parameters	ΔAIC_c [a]	AIC_w [b]
Stratum 1 (0-5% grassland)			
% HERB + % SHRB	3	0.00	0.23
% CROP + % HAY + % HERB	4	0.28	0.20
% CROP + % HERB	3	1.74	0.10
% CROP + % HAY	3	1.89	0.09
% EVGR + % HERB + % SHRB	4	2.31	0.07
% CROP + % EVGR + % HAY + % HERB	5	2.79	0.06
% SHRB	2	3.45	0.04
% CROP	2	3.70	0.04
% CROP + % EVGR + % HERB	4	4.15	0.03
% CROP + % EVGR + % HAY	4	4.30	0.03
% HERB	2	4.77	0.02
% EVGR + % SHRB	3	5.73	0.01
% CROP + % EVGR	3	6.04	0.01
% DEVL	2	6.34	0.01
% HAY + % HERB	3	6.39	0.01
% EVGR + % HERB	3	6.42	0.01
Intercept	1	7.45	0.01
% DECD	2	7.83	0.00
% EVGR + % HAY + % HERB	4	8.03	0.00
% EMRG	2	8.13	0.00
% HAY	2	8.73	0.00
% WDWT	2	8.78	0.00
% EVGR	2	9.10	0.00
% BARN	2	9.62	0.00
% WATR	2	9.70	0.00
% MIXD	2	9.70	0.00
% EVGR + % HAY	3	10.34	0.00
Stratum 2 (> 5-50% grassland)			
% EVGR + % HAY + % SHRB	4	0.00	0.46
% HAY + % SHRB	3	2.00	0.17
% EVGR + % SHRB	3	2.02	0.17
% DECD	2	3.07	0.10
% SHRB	2	4.35	0.05
% EVGR + % HERB	3	7.33	0.01
% EVGR	2	8.22	0.01
% WATR	2	9.16	0.00
% HERB	2	9.35	0.00
% EVGR + % HAY	3	9.68	0.00
Intercept	1	10.17	0.00
% CROP + % HAY	3	10.31	0.00
% CROP + % HERB	3	10.43	0.00
% MIXD	2	10.43	0.00
% BARN	2	10.83	0.00
% CROP	2	11.00	0.00
% HAY	2	11.48	0.00
% DEVL	2	11.67	0.00
% WDWT	2	11.76	0.00
% EMRG	2	12.11	0.00
Stratum 3 (> 50-100% grassland)			
% SHRB	2	0.00	0.50

[a]Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b]AIC_c relative weight attributed to model.

Table 7. (Continued) Negative binomial regression models for landscape habitat data predicting number of Long-billed Curlews 0-800 m from survey routes within strata 1-3 in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Model	No. parameters	ΔAIC_c[a]	AIC_w[b]
% HAY + % SHRB	3	2.20	0.16
% EVGR	2	3.96	0.07
% EMRG	2	4.10	0.06
% CROP + % EVGR	3	5.21	0.04
% EVGR + % HAY	3	5.86	0.03
% EVGR + % HERB	3	5.94	0.03
% WATR	2	6.19	0.02
Intercept	1	6.92	0.02
% CROP + % EVGR + % HAY	4	7.03	0.01
% CROP	2	7.53	0.01
% BARN	2	7.61	0.01
% DECD	2	7.90	0.01
% DEVL	2	8.33	0.01
% HAY	2	8.95	0.01
% HERB	2	9.02	0.01
% WDWT	2	9.05	0.01
% MIXD	2	9.07	0.01
% CROP + % HAY	3	9.51	0.00

[a]Difference between model's Akaike's Information Criterion corrected for small sample size and the lowest AIC_c value.

[b]AIC_c relative weight attributed to model.

native grasslands for breeding Long-billed Curlews.

We also detected Long-billed Curlews in cropland areas. Several studies have documented Long-billed Curlews nesting within native and tame grasslands (e.g. Dechant *et al.* 1999), while few found Long-billed Curlews occurring in croplands during the breeding season (Pampush 1980; Shackford 1994; Saunders 2001). In Oklahoma, Shackford (1994) documented 14 territories and two Long-billed Curlew nests in cultivated fields, but both nests were destroyed by human activities prior to hatching. Although it is unclear how Long-billed Curlews are utilizing croplands (i.e. for foraging, display or nest placement), use of these areas during the breeding season may result in increased risk to nests and/or juveniles (Shackford 1994). Results that may be exacerbated in areas where little overall grassland habitat is available (i.e. strata 1 with 0-5% grassland).

Habitat descriptions for grassland nesting shorebirds such as Long-billed Curlews rarely emphasize wetland or standing water presence during the breeding season (but see Dechant *et al.* 1999). For example, Pampush and Anthony (1993) do not mention wetlands when describing Long-billed Curlew nest site selection in Oregon; and Gratto-Trevor (2006) suggested that (managed) wetland presence may not benefit nesting Long-billed Curlews in Alberta. Long billed Curlews have been observed within 400 m from standing water during the breeding season in Colorado and Texas (McCallum *et al.* 1977; King 1978), but strong site fidelity among years may dampen breeding habitat selection plasticity in response to variation in surface water presence in emergent wetlands (McCallum *et al.* 1977). As such, necessity of wetlands in close proximity to Long-billed Curlew nesting habitat is poorly understood, but was clearly important in this study, as percentage of wetlands at survey stop-level had a strong effect on number of Long-billed Curlews detected. Although brood-rearing Long-billed Curlews typically forage in upland areas (Pampush and Anthony 1993), Long-billed Curlew chicks move toward wetland areas as they grow (Foster-Willfong 2003). Proximity to wetlands may influence nest site selection as chick mortality may be reduced via shorter travel times to wetland

Table 8. Characteristics of top-ranked negative binomial regression models from landscape habitat data predicting number of Long-billed Curlews 0-800 m from survey routes within strata 1-3 in the United States during 2004-2005 surveys (variable abbreviations found in Appendix 1).

Parameter	Estimate	SE	Wald 95% CI		Chi-square	*P*
Stratum 1 (0-5% grassland)						
Top-ranked model						
Intercept	2.610	1.004	0.642	4.579	6.76	0.009
% HERB	-27.538	23.213	-73.034	17.958	1.41	0.236
% SHRB	-3.207	1.252	-5.661	-0.754	6.578	0.010
Dispersion	4.590	1.904	0.859	8.32		
Second-ranked model						
Intercept	-0.782	0.581	-1.920	0.356	1.81	0.178
% CROP	3.389	1.253	0.934	5.844	7.32	0.007
% HAY	17.638	11.412	-4.729	40.004	2.39	0.122
% HERB	-30.924	28.665	-87.106	25.257	1.16	0.281
Dispersion	4.299	1.743	0.882	7.716		
Third-ranked model						
Intercept	-0.073	0.504	-1.061	0.914	0.02	0.884
% CROP	2.759	1.262	0.286	5.233	4.78	0.029
% HERB	-26.721	23.564	-72.904	19.463	1.29	0.257
Dispersion	5.111	2.080	1.035	9.187		
Fourth-ranked model						
Intercept	-1.239	0.542	-2.301	-0.176	5.22	0.022
% CROP	3.511	1.246	1.069	5.953	7.94	0.005
% HAY	18.357	11.583	-4.344	41.059	2.51	0.113
Dispersion	4.958	2.006	1.028	8.889		
Stratum 2 (>5-50% grassland)						
Intercept	1.821	0.352	1.132	2.511	26.78	<0.001
% EVGR	-7.105	3.202	-13.380	-0.830	4.93	0.027
% HAY	4.325	2.479	-0.534	9.183	3.04	0.081
% SHRB	-2.850	0.747	-4.315	-1.385	14.55	<0.001
Dispersion	5.181	1.071	3.082	7.279		
Stratum 3 (>50-100% grassland)						
Intercept	2.145	0.217	1.719	2.570	97.76	<0.001
% SHRB	-4.943	1.493	-7.870	-2.016	10.96	<0.001
Dispersion	2.254	0.435	1.402	3.106		

foraging sites, but how Long-billed Curlews assess future habitat (i.e. brood rearing) conditions during the prelaying period remains unknown. Nonetheless, presence of emergent wetlands positively influenced the number of Long-billed Curlews observed in this study, and habitat management prescriptions for breeding Long-billed Curlews clearly need to incorporate emergent wetland conservation, an element heretofore generally overlooked.

The number of Long-billed Curlews detected was negatively influenced by the percentage of evergreen forests and shrub/scrub habitats. Encroachment of woody vegetation into potential breeding areas for Long-billed Curlews reduces availability of habitat characteristics (i.e. low vegetation cover) important for nesting, predator detection, feeding behavior and intraspecific communication (Bicak *et al.* 1982; Dechant *et al.* 1999). Grassland management through controlled grazing, prescribed fire and mowing are frequently recommended for maintaining suitable Long-billed Curlew nesting and brood-rearing habitat (Bicak *et al.* 1982; Cannings 1999; Dechant *et al.* 1999; Dugger and Dugger 2002). When properly timed and executed at the right intensity, these practices reduce shrub/scrub and evergreen forest cover and extent and decrease vegetation height, which should improve breeding habitat for Long-billed Curlews.

Habitat variables associated with number of Long-billed Curlews detected varied in strength and importance among varying amounts of grassland habitat present within the landscape. Within stratum 1, where little overall grassland habitat was available, we found a positive association with crop and hay areas and a negative association with herbaceous and shrub/scrub habitats. Although Long-billed Curlews seem to select areas with similar structural quality as suitable grassland habitats (e.g. low vertical profile and reduced woody vegetation), they appear to select against stratum 1 grasslands. Perhaps Long-billed Curlews were selecting croplands and hay production areas as foraging sites within this stratum, especially if grassland areas are of poor quality. Moreover, small or highly fragmented grasslands in these areas may be unsuitable for breeding Long-billed Curlews, as is frequently reported for other grassland birds that possess specific breeding area requirements (Herkert 1994; Helzer and Jelinski 1999). For example, Long-billed Curlew territories range from 6-20 ha depending upon habitat quality and geographic location (Dechant *et al.* 1999) and minimum habitat patches should be three times the available territory size (18-60 ha; Redmond *et al.* 1981). Similarly, Ohanjanian (2002) suggested suitable habitat should be ≥250 m across for breeding Long-billed Curlews in British Columbia. Therefore, we suspect that grassland patch size may have limited Long-billed Curlew use of grasslands in this stratum.

Similarly, within stratum 2, Long-billed Curlews were negatively associated with evergreen forests and shrub/scrub habitats, but positively associated with hay production areas. Within stratum 2, grasslands are more abundant and Long-billed Curlews appear to select habitats with similar structure as grassland areas, although percentage of grasslands was not a significant predictor of Long-billed Curlew numbers. Within stratum 3, Long-billed Curlews were negatively associated with shrub/scrub habitat. Because grassland habitat is abundant within this stratum (50-100%), it is not surprising that grassland cover would not be a useful predictor when analyses were constrained to this stratum. However, assuming that stratum 3 reflects the best grassland coverage available at a township scale, it is clear that Long-billed Curlew habitat selection was most related to encroachment of woody vegetation. Stanley and Skagen (2007) found no differences in Long-billed Curlew density among the three strata, indicating that Long-billed Curlews were present in areas with little to no grassland habitat in the landscape. One possible explanation for these results is that Long-billed Curlews are highly site faithful and maybe returning to the same area each year to nest, despite habitat alterations that decrease suitability (McCallum *et al.* 1977). In areas of little to no grassland habitat, however, we have demonstrated the Long-billed Curlews were selecting areas of similar structural quality to grasslands (e.g. low vertical profile and reduced woody vegetation).

Our study determined breeding habitat associations of Long-billed Curlews in the United States from one of the most comprehensive and large-scale range-wide surveys available. Although we confirmed the relative importance of grassland, cropland, pasture, and wetland habitats to breeding Long-billed Curlews, this study also clearly provides some guidance for range-wide habitat conservation and management strategies. For example, grassland habitats are clearly important at both local and landscape scales in this study, although the relative importance of planted pasture and rangelands as compared to native grassland habitat needs to be examined further. Additionally, in all grassland areas, shrub and woody plant reduction should be a priority. Our results also reinforce the need to conserve, manage or create (large) contiguous tracts of relatively woody-plant free grasslands containing emergent wetlands for Long-billed Curlews throughout the breeding season and their range in the United States.

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Appendix 1. Codes and code descriptions for local and landscape habitat designations during 2004-2005 surveys for breeding Long-billed Curlews in the United States (2001 National Land Cover Dataset definitions accessed from <http://www.mrlc.gov/nlcd_definitions.php>).

Code	Code description
Local primary code	
GRAS	grasslands
CROP	cropland, planted growing crops, post-harvest stubble
RCWS	rural cultivated woodlands, scattered farm buildings, shelterbelts, orchard tree farms
BARE	barren ground, plowed not yet replanted, planted not yet growing
WEED	weedy fields: former grasslands, forb dominated fields
SHRB	clumped shrubs
STEP	steppe: widely dispersed shrubs with ≥50% grass
WOOD	woodlands
EMWL	wetlands/wet meadows
OWWL	open water wetlands, rivers, lakes, reservoirs, irrigation canals
OTHR	urban residential, industrial, miscellaneous
NREC	not recorded, skipped
UNKN	cannot see due to topography or other visual obstructions
Grassland secondary code	
CRPC	Conservation Reserve/Permanent Cover Program
SHTG	shortgrass prairie: blue grama (*Bouteloua gracilis*)—buffalo grass (*Buchloe dactyloides*), include cactus and small shrubs
MIXG	mixed-grass prairie: wheatgrass (*Agropyron cristatum*)—needlegrass (*Stipa* spp.)
TALG	tallgrass prairie: wheatgrass—bluestem (*Andropogon* spp.), needlegrass
NTPA	native prairie
PAST	non-native, tame pasture/rangelands
TUND	alpine tundra, montane grasslands
Grassland/Cropland tertiary code	
SHRT	short grass, <12 cm
MEDM	mid grass, 12-38 cm
TALL	tall grass, >38 cm
Management tools	
IR	irrigated grassland, cropland, etc.
DY	dryland cropland, tame pastures
Landscape code	
BARN	Barren land—vegetation accounts for <15% of total cover
CROP	Cultivated crops—>20% crop vegetation
DECD	Deciduous forest—>20% trees >5 m tall with >75% of species shedding foliage
DEVL	Developed—mixture of constructed materials and vegetation
EMRG	Emergent herbaceous wetlands—>80% perennial herbaceous vegetation and substrate periodically saturated or covered with water
EVGR	Evergreen forest—>20% trees >5 m tall with >75% of species maintaining leaves
HAY	Pasture/hay—>20% grasses and/or legumes planted for livestock, grazing, or production of seed or hay crops
HERB	Grasslands/herbaceous—>80% grammanoid or herbaceous vegetation
MIXD	Mixed forest—>20% trees >5 m tall, with neither deciduous nor evergreen species comprising >75% of total tree cover
SHRB	Shrub/scrub—>20% shrubs <5 m tall
WATR	Open water—open water with <25% cover of vegetation or soil
WDWT	Woody wetlands—>20% forest or shrubland vegetation and soil or substrate is periodically saturated with or covered with water