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Long-Billed Curlew Nest Site Selection and Success in the Intermountain West

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Abstract

Grassland birds have experienced steeper population declines between 1966 and 2015 than any other bird group on the North American continent, and migratory grassland birds may face threats in all stages of their annual cycle. The grassland-associated long-billed curlew (*Numenius americanus*) is experiencing population declines in regional and local portions of their North American breeding range. The nesting period is an important portion of the annual cycle when curlews may face demographic rate limitations from a suite of threats including predators and anthropogenic disturbance. We compared nest sites to random sites within breeding territories to examine nest site selection, and modeled correlates of nesting success for 128 curlew nests at 5 Intermountain West sites. Nest sites were 6 times more likely than random sites to be situated adjacent to existing cowpies. Additionally, curlews selected nest sites with shorter vegetation, and less bare ground, grass, and shrub cover than at random sites within their territories. Nest success varied widely among sites and ranged from 12% to 40% in a season with a mean of 27% for all nests during the 2015 and 2016 seasons. Higher nest success probability was associated with higher curlew densities in the area, greater percent cover of conspicuous objects (cowpies, rocks) near the nest, and higher densities of black-billed magpies (*Pica hudsonia*) and American crows (*Corvus brachyrhynchos*) at the site. We also found increased probability of nesting success with increased distance from a nest to the nearest potential perch in that territory. Given the central role of working lands to curlews in much of the Intermountain West, understanding limitations to nesting success in these diverse landscapes is necessary to guide adaptive management strategies in increasingly human-modified habitats. We suggest some grazing and irrigation practices already provide suitable nesting conditions for curlews, and others may require only minor temporal shifts to improve compatibility.

Keywords: breeding, Idaho, Intermountain West, long-billed curlew, nest site selection, nest success, *Numenius americanus*, SamplePoint, Wyoming.

Waders within the Numeniini tribe are globally recognized as imperiled and in need of conservation (Pearce-Higgins et al. 2017). In North America, grassland birds are experiencing steeper population declines than any other group of birds (Sauer et al. 2017). As grasslands-associated members of the Numeniini tribe, long-billed curlews (*Numenius americanus*; curlews) are a shared element between these vulnerable groups, and their successful conservation could provide a blueprint for affiliated species. Curlews breed in North America across much of the Intermountain West and Great Plains (Dugger and Dugger 2002, Fellows and Jones 2009). Population declines recorded in some breeding areas (e.g., >90% in 1 southwest Idaho, USA, site; Pollock et al. 2014) and significant habitat alterations range-wide have led to concern for the species across most areas in which they breed (Fellows and Jones 2009, U.S. Geological Survey 2017).

The decline of curlew numbers has generally been attributed to extensive habitat loss, degradation, and fragmentation primarily through development and conversion to agriculture across the grasslands of North America where curlews nest (Conner et al. 2001, Fellows and Jones 2009). Curlew pairs have strong breeding territory fidelity, with males exhibiting high natal philopatry, and females only occasionally moving to new breeding territories (Redmond and Jenni 1982). Therefore, emigration by adults is not thought to explain negative population trends from specific breeding ground populations. For closely related Eurasian curlews (*Numenius arquata*), observed declines in the breeding population could be accounted for by decreased nest success alone (Grant et al. 1999), highlighting the importance of understanding threats to curlew nest success.

Although many habitat features may influence nesting success, the most common direct cause of nest failure is predation (Ricklefs 1969), and ground-nesting grassland birds are especially susceptible to this threat (Best et al. 1997). Birds may minimize predation risk by selecting nest sites where vegetation structure provides protection from predators (Winter et al. 2005) or through broader scale site characteristics such as nesting in areas with a high density of conspecifics to facilitate communal defense (Macdonald and Bolton 2008). Curlews use distraction displays and engage in predator mobbing, traits that benefit from enhanced visibility of their surroundings to allow advanced detection of approaching predators and facilitate recruitment of conspecifics to fend off threats (Götmark et al. 1995). Alternatively, curlews can rely on nest crypsis as a predator defense, which could perhaps explain why nest placement near conspicuous objects such as cowpies and rocks is often reported (Dugger and Dugger 2002). If the shape and coloration of an incubating curlew from above mimics conspicuous objects, as one of many hypothesized reasons for the practice suggests, it may provide camouflage from aerial nest predators. Anthropogenic features and disturbances across spatial scales also pose risks to nest success, and similarly may be countered through nest site selection (Carney and Sydeman 1999, Beale and Monaghan 2004). Roads may serve as predator corridors, coincide with perches for avian predators (i.e., fences, utility poles), or function as ecological traps, and generally have negative effects on a variety of bird species (Fahrig and Rytwinski 2009). Adding to the complexity of nest site selection, some birds exhibit adaptive plasticity in response to perceived predation risk, selecting nest sites with higher concealment when the predation pressure warrants (Forstmeier and Weiss 2004). These fine balances suggest nest site selection is scale-dependent and subtle. Moreover, knowledge of curlew nest success in relation to proximity to anthropogenic features is important when considering road or structure development in breeding areas.

Habitat structure and composition at curlew nest sites has been studied (Fellows and Jones 2009), but we propose 2 reasons why further research is needed. First, existing habitat selection studies have reported contradictory findings, which may be a product of study designs that compared used versus unused habitat (Jones 2001), or inconsistent ground cover estimates (Booth et al. 2015). Male curlews defend breeding territories and the pair selects a nest site within their territory (Dugger and Dugger 2002). Thus, comparing nest sites to unused sites may not be an adequate measure of nest site selection because habitat outside of the territory is not technically available to the curlew pair, nor is it always definitively unused (Jones 2001). Second, research efforts to date have rarely evaluated how nesting success relates to habitat variables (Clarke 2006 and Gregory et al. 2011 are exceptions), and none have evaluated a comprehensive list of biologically meaningful variables at multiple spatial scales. Few studies go beyond descriptive measurements of habitat immediately surrounding curlew nest sites by examining associations between nest success and breeding-area characteristics (Cochran and Anderson 1987, Pampush and Anthony 1993). Examinations of nest success in relation to finer-scale nest site characteristics are even more sparse and often have contradictory results, such as Clarke (2006) and Gregory et al. (2011) finding opposing effects of vegetation height on nest success, and may contain aforementioned problematic elements with study design. Given that the average nesting success of curlews is reported at 31% to 69% (Pampush and Anthony 1993, Hartman and Oring 2009) and may fluctuate between years and within the same land cover type (e.g., 40% nest success in 1977 vs. 17% in 1978 in the same annual grassland study area; Redmond and Jenni 1986), it is not enough to simply know which land cover types are associated with higher nesting success. Instead, research that explains the link between nesting success and biologically relevant conditions across multiple scales, including habitat characteristics at the nest site, is important to more comprehensively guide conservation efforts for declining populations of curlews.

We conducted a wide-scale study of curlew nesting success, recognizing the connections between habitat selection at nest sites and other external influences on nesting success. We predicted that curlews selectively choose nest sites with greater visibility from the nest (i.e., lower vegetation height), higher concealment from predators via denser vegetation or visual obstruction from surrounding topography, and near conspicuous objects that might provide

camouflage from aerial predators. We also predicted that nesting success would be lower in breeding areas that had higher predator density and where anthropogenic features (e.g., roads) were closer to the nest site, and that success would be elevated in areas with higher conspecific density.

Study Area

We conducted our study at 3 study sites located in Idaho and 2 sites in Wyoming, USA, that encompassed a range of land cover types and different land management scenarios (Appendix A). At most study sites we worked within geographically distinct subsites where we observed curlews during early-season point counts that we conducted. We accessed all sites with landowner or land manager permission.

The Long-billed Curlew Habitat Area of Critical Environmental Concern (ACEC) was managed by the Bureau of Land Management (BLM; Fig. 1A). The climate was semi-arid, with hot summers, cold winters, and low precipitation year-round (Kottek et al. 2006). Upland, rolling grasslands (~730 m elevation) were dominated by invasive annual grasses including cheatgrass (*Bromus tectorum*), the invasive forb tumble mustard (*Sysimbrium altissimum*), and some native grasses, such as Sandberg's bluegrass (*Poa secunda*). Piute ground squirrels (*Uroditellus mollis*) were abundant throughout and other dominant fauna included American badgers (*Taxidea taxus*), coyotes (*Canis latrans*), common ravens (*Corvus corax*), and raptors such as Swainson's hawks (*Buteo swainsonii*), red-tailed hawks (*B. jamaicensis*), and northern harriers (*Circus hudsonius*). Public use of the land that was concurrent with curlew nesting included recreational shooting, cattle grazing, and off-highway vehicle (OHV) recreation. We focused nest searching in 2 subsites: Emmett A (~3,360 ha) and Emmett B (~5,420 ha). Both subsites had human recreational use, but ease of public access varied. Emmett B was bisected by a paved road and the area was frequently used for OHV activities, whereas Emmett A received less use because accessing most of the area required more travel time via an unimproved dirt road and passing through several pasture gates.

Between the Lost River and the Lemhi mountain ranges, the Pahsimeroi Valley site (~1,550 m elevation; Fig. 1B) was comprised of 2 small private parcels: Goldburg (~370 ha) and Big Creek (~340 ha). Alfalfa crops irrigated by center pivots were the dominant vegetation at Big Creek, and Goldburg was a flood-irrigated wet meadow that abutted sagebrush steppe and a separately owned agricultural field. The wet meadow had diverse grasses, sedges, and forbs, but rushes (*Juncus* spp.), Timothy (*Phleum pratense*), clover (*Trifolium* spp.), and dandelion (*Taraxacum officinale*) were most abundant. Coyotes, deer (mainly *Odocoileus virginianus*), American crows (*Corvus brachyrhynchos*), black-billed magpies (*Pica hudsonia*), and raptors including short-eared owl (*Asio flammeus*) were among the dominant fauna. Cattle grazing was designed to mimic historical bison grazing and occurred on a multi-year cycle, leaving vegetation with varied heights throughout the area. Timing of the grazing was also such that it was not concurrent with curlew breeding in the subsites. The climate in the Pahsimeroi Valley was warm in the summer, cold in the winter, with low precipitation (Kottek et al. 2006) that, in summer months, mostly came in the form of rainfall from thunderstorms.

In the Island Park area of eastern Idaho, we worked in 2 subsites (~1,920 m elevation; Fig. 1C). The first, the Nature Conservancy's Flat Ranch (~2,830 ha), had flat, wet meadows similar to the Pahsimeroi Valley. The climate was characterized by long, cold winters, and short, mild summers. The area had low humidity throughout the year and received precipitation in the form of rainfall or snow, often during thunderstorms (Kottek et al. 2006). Managed grazing included quick rotations of cattle among fenced pastures and was timed to avoid overlapping the curlew nesting season. Flood-irrigation occurred after the nesting season had concluded. Public access was limited, but people were permitted to cross through the area on a dirt 2-track. A second subsite southwest of Flat Ranch, the Shotgun Valley (~4,830 ha), had mixed land ownership (BLM, state, private ownership), and cattle grazing occurred on portions of the subsite. The area was mostly sagebrush steppe with scattered pockets of wet grassland, and sometimes large flocks of gulls (*Larus* spp.) would descend on the wet grasslands to feed. Other dominant fauna included coyotes and ravens.

The National Elk Refuge (4,130 ha) in Jackson, Wyoming is within a high elevation valley (~1,950 m) bounded by the Teton Mountains to the northwest and the Gros Ventre Wilderness area to the east (Fig. 1D). Winters were long and cold in Jackson, summers were short and mild, and there was relatively little precipitation throughout the year (Kottek et al. 2006). The land was managed by the United States Fish and Wildlife Service (USFWS), and public access was restricted to roads only. The refuge used above-ground irrigation pipes for habitat restoration and maintaining forage for large numbers of wintering ungulates, especially elk (*Cervus canadensis*). Other mammalian fauna included pronghorn (*Antilocapra americana*), coyotes, and wolves (*C. lupus*). Many corvids were present,

including ravens, crows, and black-billed magpies. Primary vegetation in curlew nesting areas included Sandberg's bluegrass, needle-and-thread grass (*Stipa comata*), crested wheatgrass (*Agropyron* spp.), dandelion, spiny phlox (*Phlox hoodii*), and green rabbitbrush (*Chrysothamnus vicidoflorus*).

The subsites within the Upper Green River Basin (Fig. 1E), Horse Creek (~3,540 ha) and New Fork (~3,210 ha), were privately owned by different individuals. The landscape was characterized by flat topography, high-elevation (~2,200 m), flood-irrigated pastures and hayfields composed of diverse grasses, forbs, and rushes. Timothy, wire grass (*Jucus balticus*), sedges (*Carex* spp.), and red-top (*Agrostis palustris*) were most abundant, with willows (*Salix* spp.) and other shrubs often at the edges of fields and along riparian corridors. Raptors (e.g., red-tailed hawk, northern harrier), corvids, coyotes, and striped skunk (*Mephitis mephitis*) were abundant in the area. In early spring, many landowners dragged their fields to break up cowpies, and cattle grazing was concurrent with curlew nesting in some pastures.

Methods

We collected data during April to July breeding seasons in 2015 and 2016, following Institutional Animal Care and Use Committee guidelines and authorized under federal permit number 22929, Idaho permit number 990121, and Wyoming permit numbers 33-943-2015 and 33-943-2016. We compared used nest sites to random sites within the same territory as each nest to examine nest site selection, and further explored how nesting success was associated with finer-scale characteristics (e.g., vegetation structure and composition around the nest cup) and broader-scale site characteristics (e.g., predator density in nesting areas and distance from nests to roads).

Nest-Searching and Monitoring

We conducted nest searching in areas where we observed male territory displays, courtship behavior, or curlew pairs during early-season curlew point counts. Some individuals were marked with green leg flags with white alpha-numeric codes, but we predominately delineated territories through extensive observation of male territory displays (undulating circular flights above nesting territory) and agonistic behaviors at territory boundaries. We capitalized on behavioral cues to locate nests. Curlews spend several days selecting and preparing a cupped scrape on the ground where they will usually lay 4 eggs over the course of 4.5 days while continuing to add pieces of grass to the nest cup (Hartman and Oring 2006). After this period, biparental incubation is inconspicuous, and lasts approximately 28–29 days from the time the last egg is laid (Pampush and Anthony 1993, Dugger and Dugger 2002, Hartman 2008). We used binoculars and spotting scopes to watch for nest-building, incubation switches, or predator mobbing from vantage points usually ≥ 100 m from the observed curlews. Once we located a nest, we marked its position with a hand-held global positioning system (GPS) unit and estimated age with egg floatation (Liebezeit et al. 2007). Every 3 to 5 days thereafter we viewed nests from the farthest vantage point from which we could confirm nest status, usually at a distance between 25 m and 300 m. To reduce the potential of our presence or scent trails leading predators to nests, we made efforts to avoid trampling vegetation, did not leave dead-end trails at nests, checked our surroundings for nest predators such as ravens and coyotes before we approached nests, and minimized the number and proximity of all visits. We traveled by foot in all nesting areas for various aspects of the study and assumed our scent would be most heavily associated with distant vantage points and transects where we spent most of our time, rather than curlew nests. We increased visitation frequency to 1 check per day beginning 2 days prior to predicted hatch date. We considered a nest successful if ≥ 1 egg hatched.

As soon as we became aware of a nest failure, we systematically searched for egg remains and predator sign in a 25-m radius from the nest, or up to a 50-m radius if we found nothing in the 25-m radius. We conservatively assigned an avian or mammalian predator identification but often avoided more specific identification because of considerable overlap among species in observable sign left by predators (Larivière 1999, Pietz and Granfors 2000). For example, digging at the nest bowl and cached eggs is characteristic of mammalian depredation, whereas smaller, inward puncture holes on eggs are characteristic of avian predators, and missing eggs are often associated with common raven, coyotes, or a number of other predators (Larivière 1999).

Characterizing the Breeding Area

At the start of the breeding season, we conducted 1 repetition of point counts in all study sites to determine curlew density. We based survey timing on standardized curlew survey windows for regions outlined in Jones et al. (2008). Our earliest surveys occurred in southwest Idaho (28 Mar–17 Apr survey window) and the latest surveys were at high-elevation sites in eastern Idaho and western Wyoming (21 Apr–15 May survey window). These survey windows

capture the period when curlews are most likely to be detected because incubation has not been initiated and males perform conspicuous territory displays more frequently. We repeated historical survey routes when possible and plotted new road routes in many areas. We expanded surveys to include off-road points to account for possible road bias, though some research suggests road presence and associated vegetation differences do not bias abundance estimates for curlews (Wellicome 2014). We spaced points approximately 800 m apart to minimize potential for double counting and to follow standard curlew survey protocols (Jones et al. 2003). We traveled between road points in a vehicle and between off-road points on foot. Beginning 30 minutes after sunrise, 2 observers recorded the distance to curlews detected aurally or visually during 5-minute counts at designated points as in Jones et al. (2003). Both observers scanned for curlews and 1 observer recorded data. The role of data recorder alternated at each point. Observers recorded distance to the curlew using a rangefinder, sex of the curlew based on bill morphology or territory display, the number of curlews detected, behavior (e.g., flying over, displaying), wind intensity using the Beaufort scale, temperature at the start and end of the survey, and other behavioral and directional notes to help avoid double-counting. In addition to estimating curlew density, we used point count observations, particularly observations of courting pairs, to focus nest-searching efforts.

With increasing latitude and elevation, curlews returned to breeding areas and initiated nesting at later dates. Timing of nest initiation relative to the start of the breeding season in each area could be important for effective communal defense through synchronized nesting chronology, or for avoiding predictable patterns of temperature extremes. Small sample sizes at some sites and bimodal initiation date medians prevented us from using median initiation dates as a relative breeding season start date. We instead used green-up date as a proxy. To determine a coarse estimate of the green-up date at each breeding subsite, we selected the midpoint of green-up date range windows in each subsite from long-term (2000–2013) MODIS Phenological Parameters produced by the United States Department of Agriculture Forest Service (2017). Satellite-derived green-up dates allowed for finer spatial resolution ($\leq 500 \text{ m}^2$) but captured similar temporal phenomena as were used to develop the standardized survey windows for curlews (Jones et al. 2008).

We used line transect distance sampling to assess relative levels of predator density and anthropogenic disturbance among nesting areas (Buckland 2001). We followed a stratified random transects design and placed transects at a density of approximately 1 transect/ km^2 within areas of the subsites where we planned to nest search based on point count surveys. We used binoculars to aid identification of avian predators. To reduce the likelihood of double-counting, we separated parallel transect lines by a minimum of 800 m. We repeated each 500-m-long transect 3 times per season, with varied diurnal timing. We paced walking speed on transects to attain a minimum duration of 30 minutes, and recorded duration as a control variable. For any animal that was a potential nest predator (e.g., badgers, coyotes, and corvids) and for any anthropogenic activity or feature that could be a potential disturbance for nesting curlews (e.g., dirtbikes, OHV trails, target shooting, roads), we recorded measured distances using a rangefinder and sighting angles with a compass. The sighting angle was the difference in degrees from the bearing of the transect line to the sighted predator or anthropogenic disturbance.

Characterizing the Nest Site and Territory

We assessed smaller-scale habitat parameters during a single visit at the nest site and at 4 random sites within the same territory. We standardized timing of data collection by visiting nests sites approximately 1 week (7 ± 0.35 [SE] days) post-hatching, or a week after projected hatch date if the nest failed, to minimize measurement bias introduced by temporal factors (McConnell et al. 2017). If nest age was unknown, we excluded the nest from further analyses. Curlew territories may vary from approximately 6 ha to 14 ha in size and the boundaries are somewhat loosely defined through aerial territory displays and agonistic behaviors (Allen 1980, Jenni et al. 1981). We assumed that we could discern approximate territory boundaries through behavior-based nest searching and extended observation. Using a random number chart of compass bearings between 1° and 360° and a separate random number chart of distances between 25 m and 125 m, we plotted selected bearing and distance combinations relative to the nest site on a handheld GPS to locate random sites. We chose a 125-m maximum because our past field work with curlews and previously estimated territory size (Allen 1980) suggested this would keep random sites within the same territory as the nest. We re-selected random sites if they appeared to be outside observed territory boundaries of the nest, or if they were in a location where nesting was not possible (e.g., in a river) because those locations were unavailable as nest sites.

The ability to detect approaching predators while incubating could be advantageous for curlews because they often use distraction displays to lead predators from nests (Allen 1980). Visibility from a nest site is affected by vegetation structure and topography. For a biologically meaningful quantification of visibility, we measured the height at which a 215.9×279.4 -mm white board set 10 m away from the nest cup was 90% obscured, when viewed from the eye-

level of an incubating curlew (~25 cm). This is a slight modification of Wiens' (1973) effective height where the white board is viewed from a height of 1 m, and similar to the protocol used by Bicak (1982) in a curlew grazing study. We termed this measurement effective visible height and recorded the value in each cardinal direction. To assess the relative level of concealment a curlew would be afforded while incubating, we used a 20 × 25-cm red and white checkered cube (20 4 × 4-cm squares/side), viewed from 10 m away and 75 cm high (to approximate coyote eye-level) in each cardinal direction. If a square was ≥50% visible, we did not consider it concealed. We averaged effective visible height measurements from each cardinal direction and divided the sum of concealed squares on each face of the cube by the number of squares to create 1 measurement of effective visible height and percent concealed, per nest site or random site. Given that cowpies may also provide a level of camouflage or other structural advantages (Dugger and Dugger 2002, Hood and Dinsmore 2007), we counted the number of cowpies (≥10 cm diameter) in a 3-m radius of nests and random sites and measured the distance from those sites to the nearest edge of the closest cowpie. Because anthropogenic features could pose potential direct and indirect risks to curlew nests, we used a rangefinder to measure the distance from nests and random sites to features such as buildings or roads, and to potential perches for avian predators, such as fences or utility poles.

To reduce observer bias in percent ground cover estimates, we digitized the process using the program SamplePoint (Booth et al. 2006), and quantified percent cover of vegetation categories. We used a 2-m-tall pole and a downward-facing camera mounted at the end of a 75-cm boom that was parallel to the ground to take pictures on each side of the nest and random sites. In SamplePoint, we calculated percent cover in an ~2-m² area using 84- or 100-point grids overlaid on each image. Two individuals conducted the entire analysis and trained for consistent identification of bare ground, grass, forb, shrub, litter or debris, conspicuous object, water, equipment, or unknown if the grid point was unidentifiable. The conspicuous objects category was a combination of points marked as cowpies or other conspicuous objects such as larger stones. It was necessary to broaden the conspicuous object category to include more than cowpies because not all study sites had cattle, and we observed curlews nesting next to other conspicuous objects such as rocks during the first season of the study. With SamplePoint results, we divided the number of grid points identified as a given category by the number of identifiable grid points in the image to calculate percent cover of each category.

Model Development and Analysis

Nest Site Selection Modeling.—We used a conditional logistic regression to compare nest site to random site characteristics with the survival package in R (Therneau 2015, R Core Team 2017). With each set of sites in a territory divided into strata, we coded nest sites as case locations and the 4 random sites as control locations. We eliminated variables for which occurrence was extremely rare and did not include highly correlated variables in the same model (Pearson's correlation; $|r| \geq 0.7$; Ratner 2009). We created a binomial category for the presence or absence of a cowpie within 50 cm to test whether nest placement adjacent to cowpies was non-random. Because we only measured and selected variables for which we hypothesized influenced site selection, we explored all possible combinations of the selected variables. Variables included presence of a cowpie within 50 cm, effective visible height, percent concealed, and ground cover estimates such as percent grass, forb, bare ground, debris, and shrub. We ranked and evaluated models using Akaike's Information Criterion framework adjusted for small sample size (AIC_c) and Akaike weights (Burnham and Anderson 2002). The resulting candidate set contained several models within 2 AIC_c of the top-supported model. To refine the candidate set, we followed suggestions by Arnold (2010) to remove models with redundant parameters because they are not competitive. The procedure to remove uncompetitive models was as follows: if a model within 2 AIC_c was simply the nested top model plus 1 additional parameter, we considered the additional parameter redundant when removal of that parameter failed to change coefficient estimates of remaining parameters by >20% (Hosmer et al. 2013), and if the associated P -value of the parameter was >0.15 (Arnold 2010). Following the removal of non-competitive models, we derived parameter estimates from the top-ranked model.

Curlew Density Estimation.—We used the R package Distance (Miller 2017, R Core Team 2017) to estimate curlew density in subsites based on early season point counts. Our survey routes extended beyond subsites and covered more area than we could nest search. Thus, for fitting detection curves, we used all data, but post-stratified to estimate curlew density within each subsite, each year. We designated points as being within a subsite if a monitored nest that was included in the analysis was within approximately 1,600 m of a point count location. We excluded observations of curlews recorded as fly-overs and included only individuals that were in breeding territories. As recommended for point counts by Buckland (2001), we truncated data by 10% which eliminated distant sightings (mainly observations

≥800 m). We used Kolmogorov-Smirnov and Cramer-von Mises tests to check goodness-of-fit for hazard rate and half-normal key functions and then ran models for all combinations of covariates that may affect detectability, including sex of the curlew and wind intensity. We ranked competing models with AIC_c (Akaike 1981).

Predators and Anthropogenic Disturbance Estimation.— We calculated the perpendicular distances between sighted predators or disturbances and the transect line using recorded sighting angles and distance, and estimated predator density using the package *Distance* in R (Miller 2017, R Core Team 2017). Following Buckland et al. (2001), we did not fit models for predators or disturbances with fewer than approximately 60 detections across subsites and years. Additionally, we found that most sites were associated with specific types of human disturbance (e.g., target shooting, recreational OHVs, jogging) with little overlap, which prevented us from making comparisons among sites with gradients of disturbance levels. These factors limited our analyses only to avian predators. We split the avian predators into groups based on detectability characteristics. Groups included diurnal raptors, most commonly Swainson's hawks, red-tailed hawks, and northern harriers; and corvids, which included only common ravens, American crows, and black-billed magpies.

We included all sightings of each avian group in respective modeling sets because detectability characteristics were similar within groups and an increased number of detections allowed us to improve precision of density estimates. We compared goodness of fit for different detection key functions using Kolmogorov-Smirnov and Cramer-von Mises tests, and then ran models for all possible combinations of detectability covariates including species, time duration of transect, year, site, and subsite. Initial models had poor goodness-of-fit results, likely because of rounding during data collection. We improved model fit by binning distances into 50-m increments (Buckland 2001) and re-evaluating model covariates. We used an information criterion framework to rank competing models (Akaike 1981), and estimated raptor and corvid species density for every subsite, during both years by post-stratifying the results. Though different raptor species may pose different threats to curlews, we did not post-stratify raptor density by species because some species occurred only at 1 or 2 sites and many observations were recorded as unknown raptor species, which would have limited the analysis to only the most common and easily identifiable species.

Nest Success Modeling.— We modeled nest success using a generalized linear model with a logistic exposure link to account for variation in exposure days (Shaffer 2004) using the package *lme4* in R (Bates et al. 2015, R Core Team 2017). We used nest success as the binomial response variable and selected predictor variables as fixed effects. We included only nests with known fate in the analysis. Nest success predictor variables fell into 5 categories: 1) communal defense capacity (curlew density [birds/km²] in the subsite), 2) nest timing (initiation date, and initiation date relative to the start of the breeding season), 3) concealment or visibility (% concealed, effective visible height, and % conspicuous object), 4) avian predator density (raptors, common ravens, American crows, black-billed magpies, and non-raven corvids per km²), and 5) disturbance or anthropogenic features (road distance, perch distance, site, and subsite). We also ran models using site, subsite, and year as random effects.

We used percent cover by conspicuous object acquired from *SamplePoint* analyses for nest success models instead of presence of cowpie within 50 cm because we were interested in the relationship of conspicuous objects near the nest site and success, and nests at some sites had conspicuous objects but not cowpies because of absence of cattle. Nests with and without cowpies in a 50-cm radius differed in percent cover of conspicuous objects (Welch's $t_{64.57} = -5.39$, $P \leq 0.001$), and cowpie density was strongly correlated (Pearson's correlation; $r = 0.72$, $df = 125$, $P \leq 0.001$) with percent cover of conspicuous objects. We concluded that percent conspicuous object was an appropriate metric that accounted for cowpie presence or absence within 50 cm.

We had complete data for all selected variables except perch distance because of inconsistency in perch data collection. We conducted 2 analyses: in the main (full) analysis, we did not include perch distance as a covariate ($n = 128$), and the second (perch) analysis used a subset of the data that had complete perch information ($n = 100$). We ran exploratory models for all possible covariate combinations in model sets that did not include highly correlated pairs (Pearson's $|r| \geq 0.7$) in the same model. Following methods used in our nest site selection analysis, we ranked models using AIC_c .

For comparisons of nest success, we used the Mayfield method (Mayfield 1961, 1975) because Mayfield estimates are directly comparable with logistic exposure models (Shaffer 2004) and commonly used in existing curlew literature. Both methods account for differences in exposure time, but logistic exposure models can additionally account for continuous predictor variables, whereas the Mayfield method simply calculates a constant daily survival rate (Shaffer

2004). We used a 33-day nesting period, which included approximately 4.5 days for laying and 28–29 for incubation. We also used Pearson's correlation for several follow-up analyses examining breeding area and nest site or territory relationships.

Results

Nest Site Selection

The top-ranked model for nest site selection by curlews was >2 AIC_c units from the second-ranked model, and nest site selection was best approximated by the model that included presence of ≥ 1 cowpie within 50 cm, effective visible height, percent bare ground, percent grass, and percent shrub (Table 1). Nest sites were 6 times more likely to have a cowpie within 50 cm than random sites (Table 2). Relative to random sites within the territory, there was greater visibility of surroundings from curlew eye-level at nest sites. The odds that the site was a nest site rather than a random site decreased by 4.2% for every 1 cm increase in effective visible height from curlew eye-level (Table 2). Nest site ground cover composition also varied from random sites; nest sites had less bare ground, grass cover, and shrub cover than nearby random sites. The odds that a site was a nest site versus a random site decreased by 3.9%, 2.3%, and 4.8% for every 1% increase in bare ground, grass, and shrub cover, respectively (Table 2). Bare ground at our study sites occurred at dirt roads, in slick spots (small areas where water accumulates in sagebrush-steppe ecosystems), interspersed among bunchgrass and other vegetation, and at excavated badger burrows. A moderate, negative correlation (Pearson's correlation; $r = -0.54$, $df = 126$, $P \leq 0.001$) between grass and forb cover suggested that increasing percent cover by forbs made up for decreasing percent cover by grass at our study sites.

Overall Nest Success and Causes of Failure

Overall curlew nesting success at our sites was 27.1% (Mayfield method; $n = 128$; Table 3). Nest success was lowest at the National Elk Refuge breeding site in Jackson, Wyoming, with an estimated nest success of 12.2% in 2016 ($n = 6$), and highest at 2 sites in 2015: the Upper Green River Basin, Wyoming (40.0%; $n = 25$) and the Pahsimeroi Valley, Idaho (39.1%; $n = 17$). At the ACEC in southwest Idaho, nest success for 2015 and 2016 combined was 18.8% ($n = 46$).

Of 74 unsuccessful nests, 52 (70%) had evidence of nest depredation, and 9 (12%) failed from unknown causes. Of the remaining 13 failures (18%), 2 nests flooded and were subsequently abandoned (found with intact eggs in nest cup), 3 nests flooded and the nest cups were empty before predicted hatch date so we suspected flooding followed by depredation, 2 nests were abandoned after predicted hatch date suggesting infertile eggs, 2 nests appeared to have failed because of cattle trampling, 2 nests showed signs of cattle trampling and flooding, and 2 nests with intact eggs were abandoned for unknown reasons. Of 52 depredated nests, we suspected corvid predators at 12 nests, mammalian predators (badger and coyote primarily, and rarely striped skunk) at 21 nests, and we were unable to identify the predator for 17 of the depredations. Two nests suffered adult mortalities due to predators, leading to nest failure, which we also categorized as a depredation failure.

Re-nesting attempts by individuals marked with alpha flags occurred only after unsuccessful nesting attempts. Based on continuous territory monitoring, we suspected unmarked birds also re-nested, and curlews generally did so more frequently after failures that occurred early in the breeding season and early in the nesting process. A wider range of nest initiation dates at sites with longer breeding seasons further supports re-nesting after early failure occurs, and generally nest initiation dates became later with increasing latitude and elevation of the breeding site (Appendix B). For 2 confirmed re-nesting attempts by marked curlews in southwest Idaho, egg-laying began again approximately 7–10 days after failure.

Correlates of Nest Success

The final candidate set of the full nest analysis included 5 competitive models within 2 AIC_c , with the parameters non-raven corvid density and percent conspicuous object occurring in all (Table 4). Of these equally suitable models, we chose to select the most parsimonious model, which explained nest success with the fewest variables. In the perch analysis ($n = 100$), which included a subset of nests with a perch distance variable, the final candidate set included 4 competitive models within 2 AIC_c , with non-raven corvid density and perch distance occurring in all models (Table 4). Between 2 equally suitable and equally parsimonious models within this set, we selected the model that included distance to nearest road because of the management implications and relevance to our research questions. We

recognize the uncertainty in this model selection approach but chose not to model average because of associated interpretability challenges (Cade 2015, Banner and Higgs 2017). With the addition of a random effect in both analyses, parameter coefficient values remained consistent with comparable fixed effect models and the variance of the random effect was approximately zero. This indicated that the variation was accounted for by the fixed effects, and inclusion of random effects did not improve explanatory power.

In the selected model for the full analysis, 3 predictor variables (i.e., curlew density, non-raven corvid density, % cover of conspicuous objects) best explained curlew nest success for the full dataset ($n = 128$; Table 4). Probability of nesting success was positively associated with curlew density in nesting areas, and the odds a nest successfully hatched increased by 7.5% for every additional curlew/km² (Table 5; Fig. 2A; Appendix C). Though common raven density was not an important correlate of nest success, the combined density of the other corvids present, American crows and black-billed magpies, was positively associated with nesting success. The probability of nest success increased by 11.1% for every additional non-raven corvid/km² (Table 5; Fig. 2B). Percent cover of conspicuous objects was also positively associated with nest success. The odds of nest success increased by 15.8% for each additional 1% of cover of cowpies and large rocks (Table 5; Fig. 2C).

In the second analysis with the perch distance variable dataset ($n = 100$), our selected model included 3 parameters: the density of non-raven corvids at the subsite, the distance from the nest to the nearest perch, and the distance from the nest to the nearest road (Table 4). The distance from the nest to the nearest perch had a positive relationship with nest success. Nests were 3.9% more likely to be successful for every 10 m of additional distance to a perch (Table 5; Fig. 3A). As in the full model, nest success was positively associated with density of non-raven corvids at the subsite (Table 5; Fig. 3B). Increasing distance from the nest to the nearest road also had a positive effect on nest success. Nests were 16.8% more likely to survive for every 100-m increase in distance away from a road (Table 5; Fig. 3C).

We further explored predictor variable relationships through correlation analyses. There was a weak, positive correlation between percent cover of conspicuous objects at the nest and the density of all corvids (common ravens, American crows, and black-billed magpies) by year at the subsite level (Pearson's correlation; $r = 0.23$, $df = 126$, $P < 0.01$). Conversely, there was no correlation between percent cover of conspicuous objects at random sites and corvid density (Pearson's correlation; $r = 0.16$, $df = 126$, $P = 0.07$). We also found a negative correlation between crow and raven density (Pearson's correlation; $r = -0.36$, $df = 126$, $P < 0.001$).

Discussion

Long-billed curlews breeding in the Intermountain West demonstrate flexibility for nesting habitat, and the varied nest success we observed emphasizes the complicated and location-specific nature of the factors influencing nest success. Though we attributed most nest failures to predators and report that curlews do select for certain habitat features at nest sites, our prediction that structural vegetation features (e.g., effective visible height and concealment) would reduce depredation risk was not supported. Instead, a combination of other nest site and breeding area characteristics, including the potential for communal defense by conspecifics, appear to be influencing nest success.

We predicted that curlews would balance a trade-off between visibility from the nest and concealment when incubating through selected vegetation structure at nest sites. This was partially supported because nest sites did afford better visibility of the surrounding area from the nest. Research using other metrics of visibility, such as vertical density, reported similar trends of lower vegetation height at curlew nest sites (Pampush and Anthony 1993). Our measure of how well an incubating curlew was concealed did not differ between nests and random sites. This suggests visual obstruction provided by vegetation or topography may be relatively unimportant for curlews. Nesting where visibility of surroundings is high and concealment is minimal is consistent with other cryptically colored shorebirds that use distraction display tactics that require advanced detection of approaching predators (Walters 1990, Koivula and Rönkä 1998, Amat and Maserò 2004).

Our research confirms that curlews selectively place nests adjacent to conspicuous objects such as cowpies and rocks at a territory scale. Many Charadriiform waders exhibit a similar tendency, including mountain plovers (*Charadrius montanus*; Graul 1975, Knopf and Miller 1994) and snowy plovers (*C. alexandrinus*; Hood and Dinsmore 2007). At times, birds exhibit adaptive plasticity in response to perceived predation pressure by selecting nest sites with higher concealment when there is increased predator presence (Forstmeier and Weiss 2004). There was a positive correlation between corvid density in an area and percent cover of conspicuous objects at nest sites but not at random sites, which could suggest adaptive plasticity for curlew nest placement and warrants further exploration.

Curlew nest success generally fell within the expected range for the species but was lower than expected at 2 sites. In other curlew nesting studies with multiple years and large sample sizes, nest success ranged from 31% ($n = 215$ in NV, USA, hay fields; Hartman and Oring 2009) to 69% ($n = 40$ in annual grasslands in north-central OR, USA; Pampush and Anthony 1993), whereas we measured nest success to be 12% to 40%. Where nest success was lowest, the National Elk Refuge, small sample size and only 1 season of data prevented us from drawing in-depth inferences. Low nest success in southwest Idaho does not appear to be an anomaly; Pollock et al. (2014) reported similar results in recent years. This contrasts with research in 1977–1979 in the same southwest Idaho study area (Redmond and Jenni 1986), which reported nest success of 39.7% (Mayfield method; $n = 119$), more than double that of success in 2015 and 2016 (Mayfield method; $n = 50$). In comparison, nest success in the Upper Green River Basin during this study was slightly higher (Mayfield method; 40%; $n = 25$) than was found by Cochran and Anderson (1987) within most of the same nesting area (Mayfield method; 33.6%; $n = 21$). Additionally, the evidence of re-nesting that we observed contrasts with the findings of Redmond and Jenni (1986), who did not observe re-nesting in the same southwest Idaho study area, and those of Paton and Dalton (1994) at the Great Salt Lake in Utah, USA, but matches the findings of Hartman and Oring (2009) in northeastern Nevada. Taken together, the baseline data for some sites and additions to long-term datasets reported in this study provide a coarse overview of the current status of curlew nesting success across the Intermountain West.

Depredation was the main proximate cause of nest failure at our study sites. In relatively homogenous environments such as grasslands, predator search-strategies are often opportunistic (Vickery et al. 1992, Martin 1993). Nest depredation by specific predators has been demonstrated to occur in proportion to the density of those predators (Angelstam 1986), which suggests some level of incidental depredation. Furthermore, incidental depredation has been implicated in other nesting studies where researchers supplemented alternative prey (Cortés-Avizanda et al. 2009), and physically altered nest concealment levels (Howlett and Stutchbury 1996). A common practice of ground squirrel shooting in southwest Idaho leaves an abundance of easily scavenged carrion, and a spillover effect could apply to curlews if mammalian and avian predators are attracted to the area by live ground squirrels or carrion, and then incidentally encounter curlew nests. Though we were able to estimate avian predator density, the inability to assess mammalian predator density was a limitation in our study. Considering the challenges associated with density estimates of mammalian, primarily nocturnal, predators in grasslands, we propose future studies use an index of abundance or, with more substantial funding, camera traps following a random encounter model (Wilson and Delahay 2001, Rowcliffe et al. 2008).

Nest success was explained primarily by covariates measured at the breeding-area scale, but we also found 1 nest site habitat variable to be important. At high-density breeding areas, curlews commonly recruit ≥ 6 conspecifics to fend off predators (Pampush 1980). In support of 1 of our predictions, there was a positive association between nest success and curlew density in the breeding area. Though most research that has examined nest success in this context has used nest density rather than conspecific density, the proposed mechanism influencing increased nest success is the same: increased capacity for communal defense (Macdonald and Bolton 2008). We used curlew density as a proxy for nesting density because curlews establish territories upon arriving at the breeding grounds, maintain them throughout the season, and often will join in mobbing predators regardless of nesting status. Similar to our study, Pampush and Anthony (1993) documented highest curlew nesting success in an area with the highest nest density, though they did not incorporate density as a predictor variable in nest success models. Alternatively, strengthened effectiveness of nest defense for some biparental shorebirds is associated with nest age, rather than nest density (Smith and Wilson 2010, Freeman and Miller 2018). We also acknowledge the possibility that, rather than influencing nest success, increased curlew density may be a consequence of nest success, characteristic natal philopatry, or habitat conditions that promote more densely arranged territories and may indirectly increase probability of nest success.

Nest success was positively associated with non-raven corvid density in both selected nest success models, and in almost every other competitive model, despite crows and magpies being potential nest predators of curlews. We offer 2 potential explanations for this counterintuitive result. First, the relationship may be linked to the habitat characteristics and biotic community at 2 subsites: New Fork in the Upper Green River Basin of Wyoming, and Goldburg in the Pahsimeroi Valley, Idaho. At Goldburg, there was a known roost and nesting area for crows in some nearby willows, and at New Fork magpies nested in abundant large shrubs along the edges of meadows where curlews nested, leading to high crow and magpie densities, respectively. These areas had relatively high curlew density and nesting success, and avian depredation did not appear to be the cause of any of the nest failures that occurred. Non-raven corvid density may have been low enough that there was a negligible effect on nests, and simultaneously associated with other predictors of nest success that we did not measure. Second, curlews, crows, and magpies have

shared nest predators, and there is interspecific competition among corvids for similar resources. Interactions between crows and ravens are asymmetric, with crows much more likely to attack ravens (Freeman and Miller 2018). There was a negative correlation between crow and raven density in our study and this potentially suggests a protective effect by crows from nest predation by ravens if crows are suppressing raven presence. Similar protective effects have been observed with other nesting shorebirds including Hudsonian godwits (*Limosa haemastica*) by mew gulls (*Larus canus*; Swift et al. 2017) and semipalmated plovers (*Charadrius semipalmatus*) by arctic terns (*Sterna paradisaea*; Nguyen et al. 2006). In sum, anti-predator mobbing by crows or corvids in general may have acted to moderate other avian and mammalian predators in curlew breeding areas.

Interactive effects of predators and anthropogenic features alter predation risk across a number of landscapes (Evans 2004). We found that the probability of nest success decreased with decreasing distance from each nest to potential perches. Similarly, nest proximity to roads was also negatively correlated with nest success. In contrast to our study, perch distance had no effect on the nest success of other Charadriiform waders (Wallander et al. 2006), and road distance had no effect on nest success for Hudsonian godwits (Swift et al. 2017) or lesser prairie chickens (*Tympanuchus pallidicinctus*; Pitman et al. 2005). Curlews in some Intermountain West breeding areas, however, face additional threats from roads, which may not be present in other studies. Specifically, the threats include direct mortality to adults by illegal shooting or vehicle impact, which could then cause nest failure. Though shot adults have mostly been found adjacent to roads (e.g., 9 suspected shot illegally in 1977 and 1979 [Jenni et al. 1981], and from 2013–2017, 6 of 15 adults with transmitters were illegally shot [Carlisle et al. 2017]) and we documented 1 potential vehicular mortality of a tagged adult during our study, neither of these threats were directly connected to causes of nest failure for the nests we monitored.

Curlews selectively sited nests adjacent to cowpies and rocks, and nest success was positively correlated with the percent cover of these conspicuous objects. Shape and coloration similarities of cowpies and incubating birds has been hypothesized to further enhance camouflage, and relatively low profiles of the objects could maintain visibility of surroundings or provide a clear route for quick departures from the nest (Dugger and Dugger 2002, Hood and Dinsmore 2007; Fig. 4). In cases where conspicuous objects are relatively rare, however, predators may learn to associate these objects with nests. For example, snowy plover nests near conspicuous objects had increased daily survival rates in areas where similar conspicuous objects were common (Hood and Dinsmore 2007) but lower success when the objects were relatively scarce (Page et al. 1985). Cowpies and rocks were common throughout our study sites. Most nest sites had <5% ground cover by conspicuous objects, but several were sited in >10% cover by conspicuous objects, leading to wide confidence intervals for predicted probability of nest success around this extreme. Though other structural vegetation features, such as increased visibility, were selected by curlews at nest sites, this did not appear to influence nest success. Similarly, vegetation height did not influence nest success of Eurasian curlew, where nest predation was also the main proximate cause of nest failures (Grant et al. 1999).

Our top models for nest success only had moderate Akaike weights, which is a value that can be directly interpreted as the conditional probabilities for each model (Wagenmakers and Farrell 2004). These model weights may be partially explained by variability of importance of predictor variables at our study sites across the Intermountain West. Conversely, we may have been unable to identify or properly quantify ≥ 1 parameters that are important for explaining nest success of curlews in our region. This is certainly possible when considering predation risk because we were unable to derive an estimate of mammalian predator densities, and we did not include time-dependent variables such as weather that are more commonly used in daily survival rate modeling. We maintain, however, that the inherent uncertainty in model selection does not detract from improved study design and analyses, nor does it diminish the significance of our findings regarding the ecology of curlews.

Management Implications

Nest success at our Intermountain West field sites indicates that curlew nesting is compatible with a range of vegetation types and conditions, including some working lands, but modifications may improve nesting success. Maintaining the preferred nest site characteristic of visibility could be achieved through habitat improvement efforts that establish vegetation with low vertical profiles. Cowpies left over from cattle grazing may provide dual benefits of creating preferred nest site characteristics and increasing probability of nest success. Because we found nest success was negatively associated with proximity to roads and perches, possible management options could include removal of unnecessary structures, or refraining from constructing new roads or perches in curlew breeding areas. Grazing and irrigation strategies tailored to curlew nesting ecology appear to be effective for minimizing nest failure by trampling or flooding, and further research could better define management guidelines on working lands. We suggest a slight

delay of flood-irrigation, perhaps by ≥ 1 week, which could reduce temporal overlap with nesting and increase nest success. Alternatively, in the absence of early snowmelt in the spring, flood irrigation timed to occur when curlews are establishing nests could discourage nesting in flood-prone low spots from the onset.

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Figure Captions

- Figure 1. Study sites of breeding long-billed curlews in April to July of 2015 and 2016 in Idaho and Wyoming, USA, at A) the Long-billed Curlew Habitat Area of Critical Environmental Concern (ACEC) with subsites Emmett A and Emmett B, B) the Pahsimeroi Valley, with subsites Big Creek and Goldberg, C) Island Park area with subsites Flat Ranch and Shotgun Valley, D) the National Elk Refuge, and E) the Upper Green River Basin with subsites Horse Creek and New Fork.
- Figure 2. Predicted probability of long-billed curlew nest success shown with 85% confidence intervals (gray shading) and based on the full dataset ($n = 128$) in Idaho and Wyoming, 2015–2016. In the selected model, probability of nest success varied with A) conspecific density in the nesting area, B) density of non-raven corvids including American crow (AMCR) and black-billed magpie (BBMA) at the subsite, and C) percent cover of conspicuous objects near the nest. Jittered dots represent success or failure of a nest (y -axis), and associated x -axis value.
- Figure 3. Predicted probability of long-billed curlew nest success shown with 85% confidence intervals (gray shading) based on a subset of the data with perch information ($n = 100$) in Idaho and Wyoming, 2015–2016. In the selected model, probability of nest success varied with A) distance from the nest to the nearest perch, B) density of non-raven corvids including American crow (AMCR) and black-billed magpie (BBMA) at the subsite, and C) distance to the nearest road. Jittered dots represent success or failure of a nest (y -axis), and associated x -axis value.
- Figure 4. Incubating long-billed curlew with adjacent cowpies at the Long-billed Curlew Habitat Area of Critical Environmental Concern in southwest Idaho, USA, 2016.

Tables

Table 1. Model selection table of conditional logistic regression models that best described selection of nest sites used by long-billed curlews, Idaho and Wyoming, USA, compared to random sites within the same territory as the nest during 2015 and 2016.

Nest site selection model parameters ^a	K^b	ΔAIC_c^c	ω_i^d
Cowpie+visibility+% bare ground+% grass+% shrub	5	0.00	0.571
Cowpie+visibility+% bare ground+% grass	4	2.92	0.133
Cowpie+visibility+% grass+% shrub	4	3.14	0.119
Cowpie+visibility+% shrub	3	3.92	0.080
Cowpie+visibility+% bare ground+% shrub	4	5.41	0.038
Cowpie+visibility	2	6.35	0.024
Cowpie+visibility+% grass	3	6.79	0.019
Cowpie+visibility+% bare ground	3	7.17	0.016
Cowpie+% bare ground+% grass+% shrub	4	26.35	0.000

^aCowpie within 50 cm (cowpie), effective visible height from the nest (visibility), percent ground cover by bare ground (% bare ground), percent ground cover by grass (% grass), percent ground cover by shrubs (% shrub).

^bNumber of model parameters.

^cDifference in Akaike's Information Criterion adjusted for small sample size.

^dAkaike weight.

Table 4. Competitive models for correlates of long-billed curlew nest success in Idaho and Wyoming, USA, in 2015 and 2016 using generalized linear models and a logistic exposure link. We present models within 2 Akaike's Information Criterion adjusted for small sample size (AIC_c) of the top model for the full dataset of 128 nests, where Akaike weights are based on the set of 5 competitive models and the perch subset of 100 nests, where Akaike weights are based on the set of 4 competitive models.

Nest success model selection ^a	df ^b	ΔAIC_c^c	ω_i^d
Full dataset			
NRcorvids/km ² +%conspicuous object+curlew/km ²	4	0.00	0.334
NRcorvids/km ² +%conspicuous object+curlew/km ² +road dist	5	0.74	0.231
NRcorvids/km ² +%conspicuous object+curlew/km ² +%concealed	5	1.50	0.158
NRcorvids/km ² +%conspicuous object+road dist+%concealed	5	1.73	0.141
NRcorvids/km ² +%conspicuous object+road dist+%concealed+raptors/km ²	6	1.78	0.137
Perch subset			
NRcorvid/km ² +perch dist+curlew/km ² + raven/km ²	5	0.00	0.388
NRcorvid/km ² +perch dist+curlew/km ²	4	0.97	0.239
NRcorvid/km ² +perch dist+road dist	4	1.24	0.209
NRcorvid/km ² +perch dist+curlew/km ² +road dist	5	1.72	0.164

^aNon-raven corvid density (NRcorvids/km²), percent conspicuous object ground cover (%conspicuous object), curlew density (curlew/km²), distance to nearest road in meters (Road dist), percent of squares concealed from a predator's perspective (%concealed), raptor density (raptors/km²), distance to nearest perch in meters (perch dist), raven density (raven/km²).

^bDegrees of freedom.

^cDifference in AIC_c .

^dAkaike weight.

Table 2. Parameter estimates from the top-ranked conditional logistic regression model of nest site selection by long-billed curlews, Idaho and Wyoming, USA, 2015 and 2016. Log-odds coefficients are exponentiated as odds ratios, and 85% confidence intervals are associated with the odds ratios for interpretation.

Parameter	β^a	Odds ratio	SE	85% CI	Wald χ^2	<i>P</i>
Cowpie within 50 cm	1.783	5.949	0.254	4.125 to 8.581	53.947	<0.001
Effective visible height (cm)	- 0.042	0.958	0.009	0.971 to 0.941	28.009	<0.001
% bare ground	- 0.040	0.961	0.018	0.936 to 0.986	1.195	0.274
% grass	- 0.023	0.977	0.008	0.965 to 0.989	6.272	0.012
% shrub	- 0.066	0.515	0.646	0.203 to 1.306	4.953	0.026

Table 3. Nest success estimates for long-billed curlews breeding in Idaho and Wyoming, USA, 2015 and 2016. Nests with unknown fate or unknown age were not included.

Year	Site	<i>n</i>	Apparent hatch rate (%) ^a	Mayfield DSR ^b	Mayfield estimate (%) ^c
2015	ACEC, ID	26	23.08	0.944	15.55
2015	Pahsimeroi Valley, ID	17	58.82	0.972	39.10
2015	Island Park, ID	13	46.15	0.965	30.40
2015	Upper Green River Basin, WY	25	48.00	0.973	39.98
2015 Total		81	40.74	0.963	28.97
2016	ACEC, ID	24	37.50	0.958	24.06
2016	Pahsimeroi Valley, ID	17	58.82	0.964	29.93
2016	National Elk Refuge, WY	6	16.67	0.938	12.21
2016 Total		47	42.55	0.957	23.62
Overall 2015 and 2016		128	41.41	0.961	27.08

^aPercent of nests hatched of total nests found.

^bMayfield daily survival rate (DSR).

^cMayfield nest success estimate, using an estimated 33 days of nesting (~4.5 days laying, 28–29 days incubating).

Table 5. Parameter estimates for correlates of long-billed curlew nest success, Idaho and Wyoming, USA, 2015 and 2016, from the selected generalized linear model with logistic exposure link and derived from the full dataset (*n* = 128) and perch subset (*n* = 100). Log-odds coefficients are exponentiated as odds ratios, and 85% confidence intervals are associated with the odds ratios for interpretation.

Parameter	Units	β^a	Odds ratio	85% CI	<i>P</i>
Full dataset					
Curlew density	birds/km ²	0.073	1.075	1.036 to 1.119	0.015
Non-raven corvids	birds/km ²	0.106	1.112	1.056 to 1.183	0.012
% conspicuous object	% cover	0.146	1.158	1.054 to 1.298	0.054
Perch subset					
Non-raven corvids	birds/km ²	0.111	1.118	1.053 to 1.196	0.021
Perch distance	m	0.004	1.004	1.002 to 1.006	0.007
Road distance	m	0.002	1.002	1.001 to 1.003	0.036

^aLog-odd coefficients.

Appendix A. Characteristics of Long-Billed Curlew Study Areas in 2015 and 2016

Site name	Subsite	Nearest town, state lat, long elevation (m)	Land ownership	Dominant vegetation	General habitat and land use during nesting season
Long-billed Curlew Habitat Area of Critical Environmental Concern (ACEC)	Emmett A	Emmett, ID 43.8N, -116.6W 820	Bureau of Land Management (BLM)	Cheatgrass, Sandberg's bluegrass, Medusahead (<i>Taeniatherum caput-medusae</i>), squirreltail (<i>Elymus elymoides</i>), tumble mustard, fiddleneck (<i>Amsinckia</i> spp.)	Arid annual grassland with dispersed cattle grazing, some off-highway vehicle (OHV) recreation, frequent target and ground squirrel shooting.
ACEC	Emmett B	Emmett, ID 43.7N, -116.6W 810	BLM	Cheatgrass, Sandberg's bluegrass, squirreltail, tumble mustard, fiddleneck	Arid annual grassland with dispersed cattle grazing, frequent OHV recreation, frequent target and ground squirrel shooting, trash dumping.
Pahsimeroi Valley	Big Creek	May, ID 44.5N, -113.7W 1,780	Private	Alfalfa (<i>Medicago sativa</i>), wheat (<i>Triticum</i> spp.), dandelion, cheatgrass, <i>Poaceae</i> , <i>Brassicaceae</i>	Center-pivot agriculture adjacent to sagebrush steppe and cattle pastures.
Pahsimeroi Valley	Goldburg	May, ID 44.4N, -113.6W 1,900	Private	<i>Carex</i> spp., <i>Juncus</i> spp., <i>Poaceae</i> , clover, dandelion, American bistort (<i>Polygonum bistortoides</i>), willows.	Sub-irrigated pasture (irrigation begins near end of nesting season) with cattle grazing after nesting season.
Island Park	Shotgun Valley	Island Park, ID 44.4N, -111.6W 1,950	Private, state, and BLM	Kentucky bluegrass (<i>Poa pratensis</i>), sagebrush (<i>Artemisia tridentata</i>), mule's ear (<i>Wyethia</i> spp.), yarrow (<i>Achillea millefolium</i>), <i>Aster</i> spp., dandelion, lupines (<i>Lupinus</i> spp.)	Sagebrush steppe with pockets of irrigated wet meadows. Occasional access by landowners via OHV, and some grazing.

Island Park	Flat Ranch	Island Park, ID 44.6N, -111.3W 1,960	The Nature Conservancy	Timothy, foxtail (<i>Alopecurus pratensis</i>), Kentucky bluegrass, dandelion, slender cinquefoil (<i>Potentilla gracilis</i>), yarrow, mule's ear, clover, blue-eyed grass (<i>Sysyrinchium montanum</i>), <i>Carex</i> spp.	Wet meadow with flood-irrigation (after nesting season), public access by foot only for nature-watching, fishing, and some grazing after the nesting season
Jackson	National Elk Refuge	Jackson, WY 43.5N, -110.7W 1,940	Federal	Smooth brome (<i>Bromus inermis</i>), needle-and-thread grass, crested wheatgrass (<i>Agropyron cristatum</i>), pale madwort (<i>Alyssum alyssoides</i>), dandelion, slender wheatgrass (<i>Elymus trachycaulus</i>), Idaho fescue (<i>Festuca idahoensis</i>), Poaceae, alfalfa, yellow salsify (<i>Tragopogon dubius</i>), spiny phlox, green rabbitbrush	Grassland with native ungulate grazing, weed-control pesticide application, pipe-fed irrigation, jogging and bicycling recreation on packed gravel road.
Upper Green River Basin	Horse Creek	Daniel, WY 42.9N, -110.3W 2,300	Private	Timothy, red-top, Kentucky bluegrass, <i>Carex</i> spp., <i>Juncus</i> spp., dandelion, cinquefoil, clovers	Flood-irrigated hay pasture, bullpens, cattle grazing
Upper Green River Basin	New Fork	Pinedale, WY 42.9N, -109.9W 2,200	Private	Timothy, red-top, Kentucky bluegrass, <i>Carex</i> spp., <i>Juncus</i> spp., dandelion, clovers.	Flood-irrigated hay pasture, bullpens, cattle grazing

Appendix B. Nest Initiation Date Summary for Long-Billed Curlews in the Intermountain West, USA, 2015 and 2016

Year	Site	<i>n</i>	Initiation date		
			\bar{x}	Median	Range
2015	ACEC ^a , ID	26	1 May	25 Apr	11 Apr–27 May
	Upper Green River Basin, WY	25	10 May	7 May	27 Apr–03 Jun
	Island Park, ID	13	6 May	4 May	25 Apr–16 May
	Pahsimeroi Valley, ID	17	2 May	28 Apr	20 Apr–27 May
2016	ACEC, ID	24	1 May	29 Apr	14 Apr–22 May
	National Elk Refuge, WY	6	14 May	21 May	28 Apr–27 May
	Pahsimeroi Valley, ID	17	5 May	30 Apr	19 Apr–01 Jun

^aLong-billed Curlew Habitat Area of Critical Environmental Concern (ACEC).

Appendix C. Long-Billed Curlew Density in 2015 and 2016 by Nesting Area

Subsite	Nesting area	2015		2016	
		Curlews/km ²	SE	Curlews/km ²	SE
ACEC, ID ^a	Emmett A	1.231	0.316	0.389	0.199
ACEC, ID	Emmett B	0.908	0.356	0.141	0.096
Pahsimeroi Valley, ID	Big Creek	2.740	1.085	2.297	0.938
Pahsimeroi Valley, ID	Goldburg	7.288	2.617	6.225	2.613
Island Park, ID	Flat Ranch	14.431	2.258		
Island Park, ID	Shotgun Valley	2.702	0.933		
Jackson, WY	National Elk Refuge			1.273	0.617
Upper Green River Basin, WY	Horse Creek	9.691	1.751		
Upper Green River Basin, WY	New Fork	2.722	0.742		

^aLong-billed Curlew Habitat Area of Critical Environmental Concern (ACEC).

Summary for online Table of Contents: Long-billed curlew nest success was positively correlated with the presence of conspicuous objects (e.g., cowpies, rocks), increasing distance between the nest and the nearest potential perch, higher densities of magpies and crows, and higher density of curlews near the nest territory. Curlews selected nest sites with increased visibility of their surroundings and that were near existing cowpies. Our results suggest that nesting curlews may benefit from some aspects of cattle grazing, and nesting success might be improved through reduction of potential perches for avian predators and preserving breeding areas with high curlew density.







