BUILDING THE FULL ANNUAL CYCLE PICTURE FOR LONG-BILLED CURLEWS: CORRELATES OF NEST SUCCESS IN THE BREEDING GROUNDS AND SPATIAL DISTRIBUTION AND SITE FIDELITY IN THE WINTERING GROUNDS

by

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The following individuals read and discussed the thesis submitted by student Stephanie E. Coates, and they evaluated her presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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ABSTRACT

Migratory birds face threats throughout the annual cycle, and cumulative effects from linkages between the breeding and non-breeding grounds may impact species at the population level. Long-billed Curlews (*Numenius americanus*) are a migratory shorebird of conservation concern associated with grasslands that show breeding population declines at some regional and local scales. Curlews exhibit high site fidelity to breeding territories, but also spend approximately 75% of the year on the wintering grounds. Therefore, localized population declines could indicate localized threats, in the breeding or wintering grounds. However, little information is available regarding the spatial distribution of curlews on the wintering grounds, especially for Mexico. Furthermore, breeding ground studies which examine habitat selection and nest success in the context of predator and anthropogenic pressures are lacking. We add critical information that could help pinpoint conservation issues, including understanding limitations to nesting success and mapping spatial distribution and habitat use patterns during the non-breeding season. On the breeding grounds, we used a conditional logistic regression model to compare used nest-sites to available random sites and examine habitat selection within territories. We also studied correlates of nesting success with a generalized linear model for 128 curlew nests at five sites in the Intermountain West. During the non-breeding season, we attached satellite transmitters to track 21 curlews that bred in the Intermountain West and wintered in California and Mexico and quantified 95% home range and 50% core use size via utilization distributions created with dynamic Brownian

Bridge Movement Models. For 14 individuals, we tracked multiple winter seasons and compared inter-annual site fidelity among winter areas, sexes, and habitat type with a Utilization Distribution Overlap Index. We documented four main wintering areas: (1) Central Valley of California, (2) the adjoining Imperial and Mexicali Valleys of California and Mexico, (3) the Chihuahuan Desert of inland Mexico, and (4) coastal areas of western Mexico and the Baja Peninsula. Curlews wintering in coastal areas had significantly smaller home ranges and fewer core use areas than inland-wintering curlews. Home ranges in the Central Valley were larger than other inland areas, and Central Valley females had larger home ranges than Central Valley males. Inter-annual site fidelity for wintering curlews was high, regardless of habitat type or sex. On the breeding grounds, curlews selected habitats for nest-sites with lower vegetation height and lower percent cover of grasses, bare ground, and shrubs than available sites. Nest-sites were six times more likely to have a cowpie within 50 cm than random sites. Higher probability of nest success was associated with higher curlew density in the nesting area, increasing percent cover of conspicuous objects such as cowpies within approximately two meters of the nest, and – surprisingly – higher densities of American Crows and Black-billed Magpies in the breeding area. In a separate analysis with a subset of nests (n = 100), we found nests had higher probability of success when they were farther from roads and perches. Given the central role of working lands to breeding curlews in much of the Intermountain West, an understanding of limitations to nesting success in these diverse landscapes is necessary to guide adaptive management strategies in increasingly human-modified habitats. Similarly, foundational understanding of winter spatial ecology is essential for understanding population declines which may be related to linkages between breeding and non-breeding seasons. Overall, these findings provide valuable information for full annual cycle conservation and will be particularly constructive for conservation planning once range-wide migratory connectivity is mapped.

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LIST OF ABBREVIATIONS

BSU	Boise State University
GC	Graduate College
TDC	Thesis and Dissertation Coordinator

INTRODUCTION: LONG-BILLED CURLEWS IN CONTEXT

Migratory grassland birds face threats in all parts of their annual cycle (Sillett and Holmes 2002, Webster et al. 2002, Newton 2004, Holmes 2007), but timing and intensity of negative pressures may vary by species and across populations. Consequently, conservation efforts for such species need to consider reproductive success, winter mortality, as well as migration risks and more subtle indirect threats (Sutherland 1996, Norris 2005). Foundational information for many migratory birds, such as the location of key wintering areas, spatial use and distribution in those areas, and links between segments of the annual cycle remains unknown, however. A better understanding of the complete annual cycle is important for identifying causal factors of declining populations because habitat quality and fine-scale conditions experienced by wildlife in one stage of the annual cycle may induce carry-over effects, where fitness consequences emerge in subsequent portions (Norris and Taylor 2006, Norris and Marra 2007, Harrison et al. 2011). In addition, although the amount of research taking place on breeding grounds generally outweighs efforts in other portions of the annual cycle (Faaborg et al. 2010), for many species important limitations are occurring on the breeding grounds and still warrant further research (Sherry and Holmes 1995). Further identifying limitations to reproductive success, especially in the context of threats at different scales, is a critical component of developing effective conservation plans for many declining bird species (Orians and Wittenberger 1991). Equally important is understanding spatial distribution throughout the range of a species because both areas of research provide a framework for identifying habitat requirements and can pinpoint threats to a population.

Grassland birds experienced steeper population declines from 1966 to 2015 than any other avian group in North America (Sauer et al. 2017). The current conservation status designated by the State of the Birds Watchlist for the group is ‘Steep Declines’, one level below the most critical ‘In Crisis’ category. Notably, there have been 70% population losses since 1970 of grassland species migrating between the Great Plains and the Chihauhuan Desert of Mexico (NABCI 2016). North American grasslands have undergone rapid and drastic habitat changes in a similar period. Once comprising half of the lower 48 states, conversion to agriculture or rangeland, invasion by non-native vegetation (Steidl et al. 2013), development, and anthropogenic disturbances have led to the loss or conversion of approximately 28% of all grassland from 1850 to 1990 (Conner et al. 2001). In the Great Plains, approximately half of grasslands remain intact, with 8% converted to agriculture between 2009 and 2017 alone (Plowprint Report 2017). Since 1950, more than a third of the losses represent conversion to habitat types other than agriculture (Conner et al. 2001). Grassland alterations may catalyze population-level changes in avian communities by affecting reproductive success. Nesting success for some grassland breeders is influenced by vegetation structure and composition (Winter et al. 2005), and habitat conditions are often correlated with nesting success because they are associated with foraging resource quality (Pärt 2001), predator density (Whittingham and Evans 2004), and anthropogenic disturbances (Carney and Sydeman 1999, Beale and Monaghan 2004).

The *Numeniini* are a tribe of wading shorebirds globally recognized as imperiled and in need of collaborative conservation action; of 13 species, seven are critically endangered, endangered, or near threatened (Pearce-Higgins et al. 2017). *Numeniini* share life history traits which cumulatively increase susceptibility to extinction, including long-distance migrations (Sanderson et al. 2006), late age of reproductive maturity, and low fecundity (Piersma and Baker 2000). One member of the *Numeniini* are long-billed Curlews (*Numenius americanus*), a migratory shorebird of conservation concern that breed in grasslands, pastures, some agricultural croplands across the Intermountain West and much of the Great Plains in the U.S. and Canada (Dugger and Dugger 2002, Fellows and Jones 2009). Two subspecies are sometimes recognized: the larger-bodied *N. a. americanus* in more southern parts of the breeding range, and the northern, smaller-bodied *N. a. parvus* (Dugger and Dugger 2002). In relation to some *Numeniini*, curlews have more generalist habitat requirements, selectively occupying a range of grasslands, including pastures, rangelands, wetlands, and some types of agriculture (Saalfeld et al. 2010), a characteristic which may have shielded curlews so far from more serious population declines.

On the breeding grounds, Breeding Bird Surveys (BBS) from 1966 to 2015 suggest curlews have range-wide population stability, where population decreases in some portions of the range are balanced by population increases in others (Sauer et al. 2017). However, while BBS provides the most thorough account of long-term relative population trends available for curlews, population estimates for the species may be unreliable because data are sparse, detections are infrequent in many states, and surveys are conducted during or after incubation – after the display period when curlews are most conspicuous (Stanley and Skagen 2007, Fellows and Jones 2009, Sauer et al. 2017). State Wildlife Action Plans in 16 states in which curlews occur list them as a Species of Greatest Conservation Need (USGS SWAP 2017). Federally, curlews are designated a Bird Species of Conservation Concern by the USFWS, ‘sensitive’ by the BLM in most breeding states, and ‘highly imperiled’ by the U.S. Shorebird Conservation Plan (Brown et al. 2001). Internationally, the Committee on the Status of Endangered Wildlife in Canada considers curlews of ‘Special Concern’ (COSEWIC 2002, 2011). These concerns stem from uncertainty in population status as well as significant habitat alterations and other potential threats range-wide.

Although curlew populations occur in a variety of grassland habitats, past studies indicate that individuals have high site fidelity to breeding areas (Redmond and Jenni 1982), which may limit plasticity for home range shifts following habitat degradation or loss. Further limiting options for curlews displaced by habitat loss, the habitat in areas to which they are displaced may also be degraded or disappearing. For example, in a key curlew wintering area, the Central Valley of California, more than 30% percent of wetlands were lost between 1939 and the mid 1980’s (Frayer et al. 1989). Wintering ground site fidelity research is limited but has shown variation at different spatial scales; high fidelity to winter home ranges, but lower fidelity to small-scale foraging patches (Sesser 2013). Habitat loss and degradation is widespread, non-discriminatory, and a concern even for generalist species, such as the Long-billed Curlew.

In 2009 the US Fish and Wildlife service published a conservation action plan for Long-billed Curlews (Fellows and Jones 2009). The outlined conservation actions fall into four groups: 1) population monitoring and assessment; 2) habitat assessment and management; 3) research; and 4) education and outreach. Since the publication of the plan, curlew research has filled existing gaps in each of these categories, especially with regards to assessing nesting success and breeding habitat in areas where information was lacking (Hartman and Oring 2009, Gregory et al. 2011, 2012), tracking migratory routes (Page et al. 2014), mapping wintering range and habitat (Sesser 2013, Page et al. 2014, Kerstupp et al. 2015) and studying wintering ecology (Navedo et al. 2012, Shurford et al. 2013, Kerstupp et al. 2015). Our research addressed several of the identified knowledge gaps, but also added components beyond the scope of the plan. Specifically, we added baseline and comparative population density and nesting success information for many sites in the Intermountain West and gave context to nesting success by assessing the role of habitat, potential communal defense, nest-site selection, predator density, and anthropogenic features. We also assessed wintering range locations, and spatial distribution patterns and site-fidelity in those ranges. Our research fueled community education and outreach through public presentations, volunteer involvement, curlew naming contests for tagged birds, a live-stream satellite tracking map, and a ‘Curlews in the Classroom’ program delivered to K-12 students in southwest Idaho. Through this public engagement we aimed to reduce an identified threat to curlews in southwest Idaho, illegal shooting, and to share knowledge we gained through collaborative efforts.

CHAPTER ONE: CORRELATES OF NESTING SUCCESS AND NEST-SITE SELECTION OF LONG-BILLED CURLEWS IN IDAHO AND WYOMING

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 portions of their annual cycle. Long-billed Curlews (*Numenius americanus*) are a large, grasslands-breeding shorebird of conservation concern with identified population declines in regional and localized portions of their breeding range. Much of the landscape used by curlews is considered working land, including agriculture, rangelands, and pastures. Curlews are long-lived and exhibit high fidelity for breeding ground territories, but also spend three-quarters of the year on the wintering grounds. Thus, localized population declines could indicate localized threats on the breeding or wintering grounds. Nesting success is one critical juncture of the annual cycle at which curlews may face limitations from nest predators and anthropogenic disturbance. Nest depredation threats may be countered through selection of nest-site habitat which increases concealment, or advanced warning of predators provided by higher densities of conspecifics for communal defense. Some anthropogenic features, such as roads, fences, and other structures, may impose direct or indirect risks to curlew nests, and similarly may be countered by selection of nest-site habitat. We compared nest-sites versus random sites within the same territory 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 adjacent to conspicuous objects. Additionally, curlews selected nest-sites with shorter vegetation, and less bare ground, grass, and shrub cover, than at random sites within territories. We found nest success varied widely among sites and ranged from 12 to 40% in a season. Higher nest success probability was associated with higher curlew densities in the area, greater percent cover of conspicuous objects near the nest, and, surprisingly, higher densities of non-raven corvids at the site. In a second analysis, we also found increased probability of nesting success with increased distance between nests and the nearest potential perch. Given the central role of working lands to birds 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.

Introduction

Full annual cycle research of migratory birds is critical for conservation because species may face threats on the breeding grounds, during migration, or on the non-breeding grounds, and the timing and intensity of threats potentially vary across populations (Sillett and Holmes 2002, Webster et al. 2002, Newton 2004, Holmes 2007). Consequently, conservation efforts for such species need to consider reproductive success, winter mortality, as well as migration risks and subtle indirect threats such as carry-over effects (Sutherland 1996, Norris 2005). The amount of research taking place on breeding grounds generally outweighs efforts in other portions of the annual cycle (Faaborg et al. 2010) where more work is needed. However, for many species, important limitations are occurring on the breeding grounds that also warrant further research (Sherry and Holmes 1995). Identifying limitations to reproductive and nesting success, especially in the context of threats at different spatial scales, will be a critical component of developing effective conservation plans for many declining grassland bird species (Orians and Wittenberger 1991).

Long-billed Curlews (*Numenius americanus*) are a shorebird of conservation concern that breed in grasslands, pastures, and some agricultural croplands across the Intermountain West and much of the Great Plains in the U.S. and Canada (Dugger and Dugger 2002, Fellows and Jones 2009). Based on population estimates from the Breeding Bird Survey (BBS), increasing curlew numbers in some areas may be balancing population declines in other areas, creating range-wide stability (Sauer et al. 2017). Concerns with the BBS curlew population estimates such as wide confidence intervals due to sometimes sparse data, infrequent detections in many states, and surveys conducted during or after incubation when curlews are least conspicuous (Stanley and Skagen 2007, Fellows and Jones 2009, Sauer et al. 2011), has prompted other range-wide population assessments for the species. These more recent estimates also suggest that, across the entire range of the species, curlew numbers are likely not as low as previously thought (Stanley and Skagen 2007, Fellows and Jones 2009). However, steep declines recorded in some breeding areas (Pollock et al. 2014) as well as significant habitat alterations range-wide (see Fellows and Jones 2009) are cause for concern and curlews continue to be listed as a Species of Greatest Conservation Need by State Wildlife Action Plans in 16 states across the western and central United States – most of the states in which they breed (USGS SWAP 2017). Furthermore, several characteristics unique to curlew life history also stress the need for greater understanding of the threats for curlews at breeding grounds. Specifically, curlew pairs have strong breeding territory fidelity, with males exhibiting high natal philopatry, and females only occasionally moving to new breeding territories, likely in cases where nesting attempts the previous year failed (Redmond and Jenni 1982). Therefore, negative population trends from the breeding grounds suggest adult mortality, low nesting success, or low recruitment rather than emigration by adults. Furthermore, declining local abundance for long-lived species may be a more reliable early indicator of overall population decline than range constriction through site occupancy (Méndez et al. 2017). Unless the age structure is known in the population of a long-lived species, there may be a lag-time in the detection of declining populations (Redmond and Jenni 1986). Finally, curlews also use communal defense strategies to deter predators from nesting areas (Pampush 1981), and loss of population density in breeding areas could amplify nest failures caused by predators, creating a negative feedback loop.

The decline of curlew numbers has generally been attributed to extensive habitat loss, degradation, and fragmentation of across the grasslands of North America where curlews nest (Fellows and Jones 2009, Conner et al. 2001). Alterations of grassland may catalyze population-level changes in avian communities by affecting reproductive success. Nesting success for some grassland breeders is influenced by vegetation structure and composition (Winter et al. 2005), and habitat conditions are often correlated with nesting success because they are associated with foraging resource quality (Pärt 2001), predator density (Whittingham and Evans 2004), and anthropogenic disturbances (Carney and Sydeman 1999, Beale and Monaghan 2004).

Habitat conditions related to curlew nesting sites have been heavily studied (reviewed in Fellows and Jones 2009), but we propose two reasons why further research is needed. First, existing habitat selection studies have reported contradictory findings, which may be a product of formerly more common ‘used’ vs. ‘unused’ site comparison methodologies (Jones 2001), or inconsistent ground cover estimates (Booth et al. 2015). For example, while Cochran and Anderson (1987) found nest-sites had more grass cover and less bare ground than in surrounding fields, Pampush and Anthony (1993) found bare ground was a ‘spurious’ predictor of used and unused sites, and Paton and Dalton (1994) found curlews preferred to nest near, though not directly on, patches of bare ground. Jenni et al. (1981) suggested that vegetation structure may be more important than composition for curlew habitat selection, and this may be similar for nest-site selection. Male curlews defend breeding territories from 6 to 14 ha in size and the pair selects a location for their nest within their breeding territory (Dugger and Dugger 2002). 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 (Jones 2001).

Second, research efforts to date have rarely evaluated how habitat variables relate to nest success (but see Clarke 2006 and Gregory et al. 2011), and none have evaluated a comprehensive list of biologically meaningful variables at multiple scales. Many studies have identified and described habitat characteristics at curlew nest-sites, defined as the habitat immediately surrounding the nest (McCallum et al. 1977, King 1978, Allen 1980, Jenni et al 1981, Pampush 1981, Redmond 1986, Pampush and Anthony 1993, Paton and Dalton 1994, Saalfeld et al. 2010, Blake 2013). Fewer have examined associations between even coarser-scale habitat conditions (e.g. ‘annual grassland’ or ‘grazed field’) and nest success (Cochran and Anderson 1987, Pampush and Anthony 1993). Curlew studies which have examined nest success in relation to nest-site habitat variables focused on vegetation height and ground cover composition. Clarke (2006) found a positive association between vegetation height and nest success, despite curlews apparently selecting nest-sites with shorter vegetation than random sites in the same breeding area. Again, it should be noted that these random sites may not have been truly ‘available’, because they were not necessarily within the territory of the nesting curlews. In contrast, Gregory et al. (2011) found a negative association between nest success and vegetation height. The effect of forb cover on nest success was also incongruous in these two studies and neither study provided a potential mechanism for the influence of forb cover versus other vegetative cover on nesting success. Given that the average success rate of curlew nests is reported at 31-69 percent (Pampush and Anthony 1993, Hartman and Oring 2009) and may range widely between years and within the same habitat type, it is not enough to simply know which habitats are associated with higher nest success. Instead, research that explains the link between nest success and biologically-relevant conditions across multiple scales including habitat at the nest-site, is needed to more fully guide conservation efforts for declining bird species (Gregory et al. 2011).

Although many habitat factors may influence nest success, the most common direct cause of nest failure is predation (Ricklefs 1969), and ground-nesting grassland birds are especially susceptible to predation (Best et al. 1997). Along with cryptic coloration (Wallace 1889), birds may minimize predation risk through nesting in areas with high density of conspecifics to facilitate communal defense (Macdonald and Bolton 2008), or by selection of nest-sites based on desirable habitat features, such as vegetation structure (Winter 2005). However, habitat selection, particularly at the nest-site level, is nuanced. For example, nests which are situated in denser vegetation may be more well-concealed from predators, but if the vegetation is too tall it may hinder the visibility an incubating bird has of the surroundings. Visibility of nest surroundings may allow advanced warning of approaching predators and facilitate recruitment of conspecifics to fend off threats (Götmark et al. 1995). Furthermore, some species exhibit adaptive plasticity in response to perceived predation pressure – selecting nest-sites with higher concealment when the predation pressure warrants (Forstmeier and Weiss 2004). In relatively homogenous environments such as grasslands, nest-sites surrounded by similar habitat could decrease search-efficiency by predators (Martin and Roper 1988). These fine balances suggest habitat comparisons for nest-sites may be scale-dependent, and subtle. Furthermore, habitat selection of nest-sites by most bird species only indirectly mediates depredation threats. Concurrent data regarding common predator densities (e.g., badgers [*Taxidea taxus*], coyotes [*Canus latrans*], and corvids; Redmond and Jenni 1986, Pampush and Anthony 1993), anthropogenic features which may pose threats (e.g., roads and grazing; Pollock et al. 2014), and density of conspecifics (Macdonald and Bolton 2008) is required to obtain a more detailed picture of this complex, and potentially limiting portion of the annual cycle.

We conducted a wide-scale study of curlew nesting success, recognizing the interconnectedness of habitat selection at nest-sites and external drivers of nesting success. Two of our sites were previously studied, one in southwest Idaho (1977-1979; Redmond and Jenni 1986) and the other in western Wyoming (1982; Cochran and Anderson 1987), and we compared current and historical estimates of curlew density and nest success at these sites. We also included three other sites which lacked baseline data on nesting success but provided a diversity of grassland habitats and included private and federal government ownership. We compared used nest-sites to random sites which were available within the same territory to examine nest-site selection, and further explored how finer-scale nest habitat characteristics and broader-scale site characteristics were associated with nest survival. Our research builds on and clarifies past curlew studies on breeding-grounds by measuring densities of curlews and known predators in nesting areas, as well as considering a more comprehensive evaluation of natural and anthropogenic habitat features.

Based on our existing knowledge of curlew biology we predicted that 1) nesting success would be lower in breeding areas that had higher predator density, 2) curlews in higher density nesting areas would have greater nesting success potentially due to the greater capacity for communal defense, and 3) curlews with nest-sites closer to anthropogenic features such as roads would have lower nesting success. We also predicted that curlews selectively choose nest-sites near conspicuous objects, with greater visibility from the nest (i.e., lower vegetation height), and with higher concealment via denser vegetation or visual obstruction from surrounding habitat features such as hummocks. We examined these variables in the Intermountain West with a natural experiment.

Study Area

We conducted field work from April to July in 2015 and 2016 at breeding sites located in the Intermountain West region of Idaho (3 sites) and Wyoming (2 sites). At several breeding sites we worked within geographically distinct ‘subsites’, which were not contiguous. In southwest Idaho we worked within two nesting areas where curlews were clustered, but the habitat was not geographically distinct. We described these as ‘focal areas’ (see Appendix A.1 for site and focal area summary table). The sites, subsites and further details included:

1. The Long-billed Curlew Habitat Area of Critical Environmental Concern (ACEC), including two focal areas, near the town of Emmett, southwest Idaho (Figs. 1.1A & 1.1B).
2. The Pahsimeroi Valley near the town of May, central Idaho (Figs. 1.1A & 1.1C).
3. The Nature Conservancy’s Flat Ranch and the Shotgun Valley in the Island Park area near West Yellowstone and Island Park area in eastern Idaho (Figs. 1.1A & 1.1D).
4. Upper Green River Basin at Horse Creek and New Fork near the city of Pinedale, western Wyoming (Figs. 1.1A & 1.1D).
5. The National Elk Refuge, Jackson, western Wyoming (Figs. 1.1A & 1.1D).

The Long-billed Curlew Habitat Area of Critical Environmental Concern, hereafter the ‘ACEC’, was considered an important curlew breeding area after intensive research in the late 1970s revealed a dense breeding population (Redmond and Jenni 1986). The ACEC was managed by the Bureau of Land Management (BLM) and is an arid upland, rolling grassland (~2,400’ elevation) dominated by invasive annual grasses including cheatgrass (*Bromus tectorum*), the invasive forb tumble mustard (*Sysimbrium altissimum*), as well as some native grasses, especially Sandberg’s bluegrass (*Poa segunda*). In the pre-dust bowl era before fires and human alteration converted the area to annual grasslands, the habitat was likely composed of mostly sagebrush with grassland pockets (Jenni et al. 1981). Public use of the land included recreational shooting, cattle grazing, and off-highway vehicle (OHV) recreation. Grazing by cattle or sheep typically occurred in spring and summer, and animals were sometimes shifted between pastures during the peak of the curlew breeding season. In the 1970s, there was more grazing by sheep than cattle (Bicak et al. 1982), but the proportions have shifted and, in the study years we only observed cattle grazing in focal curlew nesting areas. Results from historical curlew research were available for comparison with current research (i.e., Jenni et al. 1981, Bicak et al. 1982, Redmond and Jenni 1982, 1986). We focused nest searching in two areas with higher curlew density than surrounding areas; focal nesting areas we named Emmett A and Emmett B. Both focal areas were similar in terms of abundant ground squirrels and human recreational use, but ease of access by the public varied. Emmett B was easily accessed via a paved road and frequently used for OHV activities, while Emmett A received less use because accessing most of the area required more travel time via an unimproved dirt road and passing through several barbed wire cattle pasture gates.

Between the Lost River and the Lemhi mountain ranges, the Pahsimeroi Valley site (~5,100’ elevation) is comprised of two small private parcels each of which we designated a subsite of the Pahsimeroi: Goldburg and Big Creek. Crops irrigated by center-pivots were the dominant vegetation at Big Creek, and Goldburg was a sub-irrigated wet meadow which abuts native sagebrush habitat as well as a separately-owned agricultural field. The wet meadow habitat had diverse grasses, sedges, rushes and forbs, but *Juncus sp.*, Timothy (*Phleum pratense*), clover (*Trifolium spp.*) and dandelion

(*Taraxacum officinale.*) were most abundant. Cattle grazing was restricted to late summer, after the curlew nesting season.

In the Island Park area of eastern Idaho, we conducted nest searching and monitoring in two subsite locations. The first, the Nature Conservancy's Flat Ranch (~6,300' elevation), had a flat, wet meadow habitat similar to the Pahsimeroi Valley. Grazing was carefully managed with quick rotations among fenced pastures and timed to avoid overlapping with the curlew nesting season. Flood-irrigation also occurred after the nesting season had concluded. Public access was limited, but people were permitted to cross through part of the study area on a dirt two track to fish at a nearby creek. A second area southwest of Flat Ranch called the Shotgun Valley, and had mixed land ownership (BLM, state, and private ownership) and different habitat types that included mostly sagebrush with scattered pockets of wet grassland and cattle grazing occurred on portions of the subsite.

The subsites within the Upper Green River Basin, named Horse Creek and New Fork, were privately owned, and we accessed each parcel with landowner permission. The landscape in the monitored area was characterized by flat topography, high-elevation (~7,200'), flood-irrigated pastures and hayfields composed of diverse grasses, forbs, and rushes. Timothy (*Phleum pratense*), wire grass (*Jucus balticus*), sedges (*Carex spp.*), and red-top (*Agrostis palustris*) were the most abundant vegetation species, with willows (*Salix spp.*) and other shrubs often at the edges of fields and along riparian corridors. In early spring, landowners drug their fields to break up cowpies, and cattle grazing was concurrent with curlew nesting in some pastures. These two study sites overlapped the study area boundaries of historical research by Cochrane and Anderson (1987) and further study site details can be found therein.

The National Elk Refuge in Jackson, Wyoming is a high elevation valley (~6,400’) bounded by the Teton Mountains to the northwest and the Gros Ventre Wilderness area to the east. The land was managed by the U.S. Fish and Wildlife Service, and public access was restricted to roads only. The refuge supported large numbers of wintering elk and other ungulates through added irrigation in the summer and supplemental feeding. Primary vegetation in curlew nesting areas included Sandberg’s bluegrass (*Poa secunda*), needle-and-thread grass (*Stipa comata*), crested wheatgrass (*Agropyron sp.*), spiny phlox (*Phlox hoodii*), and green rabbitbrush (*Chrysothamnus vicidoflorus*).

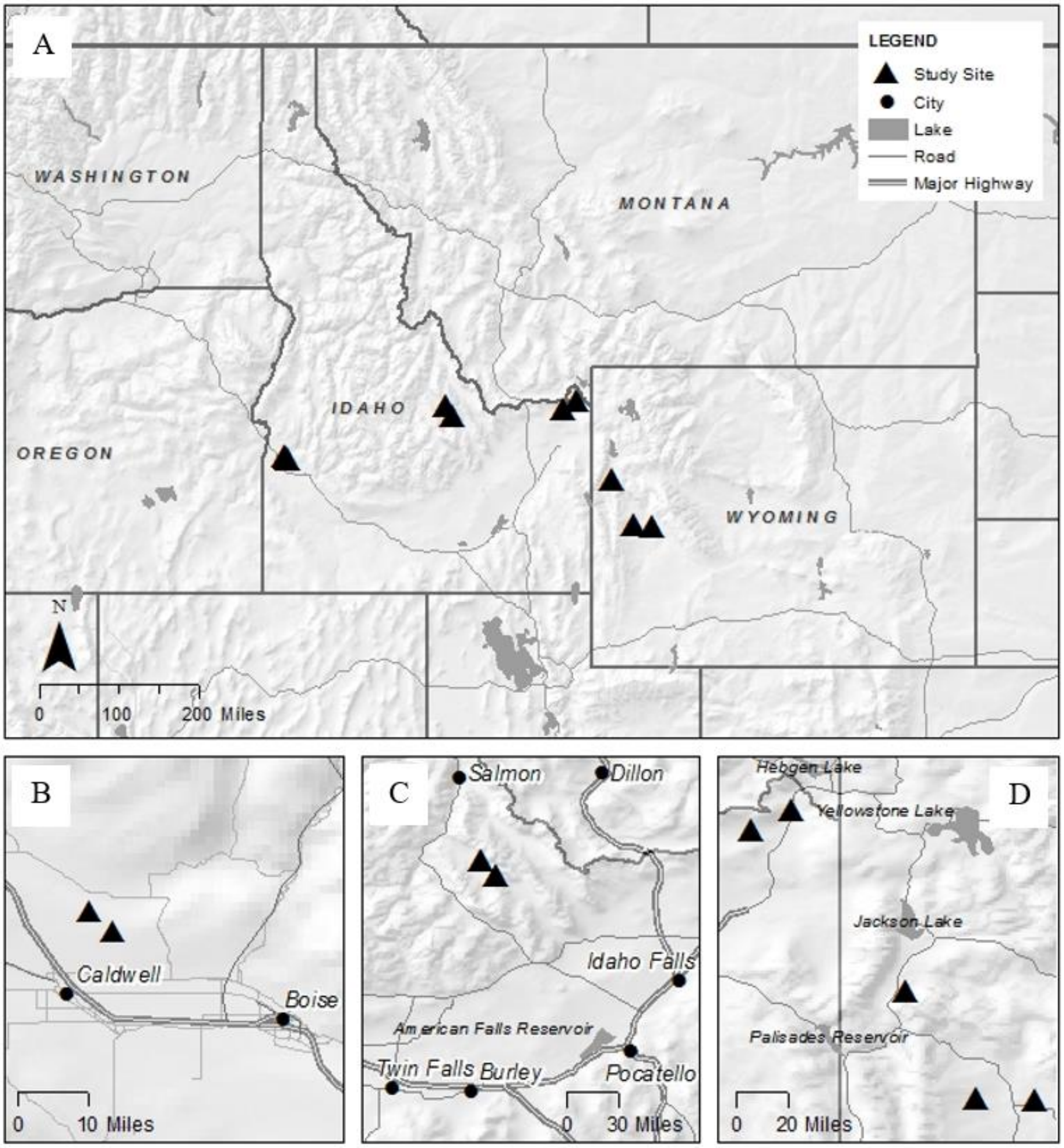

Figure 1.1 A) Long-billed Curlew study sites in 2015 and 2016. B) ACEC focal areas in southwest Idaho. C) Pahsimeroi Valley subsites in central Idaho. D) Island Park subsites in Idaho (farthest north), the National Elk Refuge site in Jackson, Wyoming, and Upper Green River Basin subsites near Pinedale, Wyoming (farthest south).

Methods

We measured nest-site selection and nest success variables at several different scales. The smallest scale, the nest-site, included the habitat within approximately 10 m or less of the nest cup. Nest-sites were within the territories of curlew pairs which are established early in the season by males through undulating flight displays and agonistic behaviors (Allen 1980, Jenni et al. 1981). While females incubate during the day, males typically remain in their territories foraging, preening, or standing guard. Territory boundaries are somewhat loose and the size may vary from approximately 6 to 14 ha (Allen 1980, Jenni et al. 1981). We were reasonably confident that through behaviorally-based nest searching and extended observation, we could discern approximate territory boundaries. At the next spatial level, we delineated ‘focal nesting areas’ where territories were clumped closely together. Subsites included larger areas of land to which we had research access. We made the distinction between subsites and focal nesting areas specifically when curlew distribution was unequal across the span of a subsite and it would have been inefficient to conduct nest-searching across the low-density areas of the subsite. When curlews were evenly distributed throughout the subsite we did not delineate separate ‘focal nesting areas’, as there was no need. Finally, we nested subsites within broader study sites, which were simply areas that were relatively distinct geographically (e.g., the Upper Green River Basin), and could be accessed on a daily basis by the same crew.

Field Methods

Early-season Curlew Point Counts

At the start of the breeding season, we conducted standardized point counts across all study areas. During this time, male curlews perform territory displays and incubation has not been initiated. We repeated historical road routes when possible, expanded surveys to include off-road points, and plotted new road transects in many areas. We spaced points a minimum of 800 m apart, and traveled between road points in a vehicle, and between off-road points on foot. Beginning 30 minutes after sunrise, two 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 one observer recorded data. The role of data recorder alternated at each point. Observers recorded distance to the curlew, sex of the bird, the number of curlews detected, behavior or status (e.g., flying over, displaying, etc.), wind intensity using the Beaufort scale, and temperature at the start and end of the survey. We used point count observations, particularly of pairs, to focus nest-searching efforts and later to estimate curlew density in specific subsites, or focal areas within sites where we located nests.

Surveying Predators and Anthropogenic Disturbance

We used distance sampling to assess relative levels of predator density and anthropogenic disturbance among nesting areas. We followed a stratified random transects design and placed transects at a density of approximately one transect per square kilometer. We separated parallel transect lines by a minimum of 800 meters to reduce the likelihood of counting a predator or disturbance from more than one transect. We repeated each 500-m-long transect three times per season, with varied timing (i.e., a transect was not surveyed in the morning during all three visits). We paced walking speed on transects for a minimum duration of 30 minutes, and recorded duration as a control variable. We recorded the distance and sighting angle to any animal that was a potential predator for curlew nests or adults and to any anthropogenic activity or feature that could be a potential disturbance for curlews (e.g., OHV recreationists and trails target shooting, vehicular traffic roads). We measured distance with a rangefinder, and used a compass to calculate sighting angle, defined as the difference in degrees from the transect line bearing and the sighted predator or anthropogenic disturbance. In addition, we recorded inanimate predator and anthropogenic disturbance signs such as crushed vegetation indicating off-road travel, abandoned shooting targets, and fresh badger burrows.

Nest-site Habitat

We standardized timing of habitat data collection by visiting nests sites approximately one 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). Within the same territory as the nest and during the same visit, we also assessed the habitat parameters at four random sites selected by randomized compass bearings and distances. We restricted the maximum distance from the nest cup to any random site to 125 m, and re-selected random sites if the selected site appeared to be outside the territory boundaries, or in a location were nesting was not possible (e.g., in a river) because we deemed those locations ‘unavailable’ as nest-sites. At nest-sites and random sites, we measured the distance to nearest anthropogenic features and distances to potential perches for avian predators with a rangefinder.

At the nest-site and random sites, the habitat parameters we measured *in situ* included effective visible height, concealment, the number of cowpies in a 3 m radius, and the distance to the nearest cowpie from the center of the nest cup or site. The ability to detect approaching predators while incubating could be advantageous (Allen 1980) and visibility from a nest-site is affected by vegetation height as well as topography. Thus, for a biologically meaningful quantification of visibility, we measured the height at which a white board set 10 m away from the nest cup was 90% obscured, when viewed from the eye-level of an incubating curlew (approximately 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 x 25 cm red-and-white checkered cube (20 4 x 4 cm squares per side), viewed from 10 m away and 75 cm high (approximately coyote eye-level) in each cardinal direction. If a square was ≥50% visible, we did not consider it concealed. We prepared the data for analysis by averaging effective visible height measurements from each cardinal direction and dividing the sum of concealed squares on each face of the cube by the total number of squares to create one measurement of effective visible height and percent concealed, per nest-site or random site.

Visual estimation of percent ground-cover can be inaccurate and difficult to standardize among a large crew. To reduce observer bias in percent cover estimates, we digitized the process using the program SamplePoint (Booth et al. 2006), and quantified percent cover of vegetation functional groups. While conducting nest habitat measurements, we used a 2 m tall pole and a downward-facing camera mounted at the end of a 75 cm boom which was parallel to the ground to take pictures on each side of the nest and random sites. In SamplePoint, we calculated percent cover using either 84- or 100-point grids overlaid on each image. Two individuals, Coates and Wright, conducted the entire analysis and trained for consistent identification of the following categories: bare ground, grass, forb, shrub, litter/debris, conspicuous object, water, equipment, or unknown. The conspicuous objects category was a combination of points marked either as cowpies or other conspicuous objects (e.g., large rocks). This designation was necessary for analyses because aerial concealment could be provided by objects other than cowpies, and because not all study sites had cattle present. With SamplePoint results, we divided the number of grid points identified as a given category by the total number of identifiable grid points in the image to calculate percent cover of vegetation groups.

Depending on latitude and elevation, the breeding season at each site began at different times. Therefore, initiation date relative to the beginning of the breeding season was a parameter of higher interest than Julian calendar dates. We examined the effect of initiation date relative to site green-up date, using green-up date as a proxy for the start of the breeding season. We used long-term (2000−2013) MODIS Phenological Parameters produced by the USDA Forest Service to determine a coarse estimate of the median green-up date window at each breeding subsite (ForWarn 2017) and then selected the midpoint of the date range window as green-up date for the breeding subsite.

Monitoring Nest Survival

Curlews are cryptic nesters and spend minimal time preparing a cupped scrape on the ground where they will usually lay four eggs. The egg-laying stage takes 4.5 days (~1.5 days between eggs), followed by an incubation stage that lasts approximately 28-29 days from the time the last egg is laid, with females incubating during the day and males during the night (Pampush and Anthony 1993, Dugger and Dugger 2002, Hartman 2008). We capitalized on behavioral cues, particularly incubation switches, to locate nests. On the initial visit after locating a nest, we floated eggs to estimate age (Liebezeit 2007) and minimize the number and proximity of future visits. Every three to five days thereafter we viewed nests from the farthest vantage point from which we could confirm status. We increased visitation frequency to one check per day in the days leading up to predicted hatch date. If at least one egg hatched, we considered a nest successful.

When nests failed, we immediately and systematically searched the area in a 50 m radius from the nest for egg remains and predator sign. 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, and missing eggs could be attributed to Common Ravens (*Corvus corax*), coyotes, or a number of other predators that are known to take eggs whole (Larivière 1999).

Analysis Methods

Quantifying Curlew Density in Focal Nesting Areas

We used the R package ‘Distance’ (Miller 2017, R Core Team 2017) to calculate curlew density in subsites and focal nesting areas. We designated points from early season point counts as being within a subsite or focal nesting area if a monitored nest which was included in the analysis was within approximately 1600 meters of a point count location. This was a conservative approach and allowed inclusion of more points for density estimates, but may have underestimated density in nesting areas where curlews are more tightly clustered. For the analyses, we included all observations except those in which the curlews did not appear to be in a home territory, such as ‘fly-over’ individuals, to avoid over-estimating density. As recommended for point counts by Buckland (2001), we truncated data by 10%. We used Kolmogorov-Smirnov and Cramer-von Mises tests to check goodness-of-fit for hazard rate and half-normal key functions. Detectability may be influenced by sex of the curlew (e.g., territory displays made by males are conspicuous), observer, wind intensity, or specifics of a subsite, so we ran models which included those covariates. To rank competing models, we used an Akaike’s Information Criterion framework adjusted for small sample size (Akaike 1981). We post-stratified density estimates from the selected model by focal nesting area and year.

Quantifying Predators and Anthropogenic Disturbances

We calculated predator density estimates within subsites using the package ‘Distance’ in R (Miller 2017, R Core Team 2017). Following the rule-of-thumb of Buckland et al. (2001), we did not fit models to predator types and anthropogenic disturbances with fewer than approximately 60 detections across sites and years, which limited our analyses to avian predators. We split the avian predators into groups based on detectability characteristics which included 1) diurnal raptors, most commonly Swainson's Hawks (*Buteo swainsoni*), Red-tailed Hawks (*Buteo jamaicensis*), and Northern Harriers (*Circus cyaneus*) and 2) corvids, which included only Common Ravens (*Corvus corax*), American Crow (*Corvus brachyrhynchos*), and Black-billed Magpie (*Pica hudsonia*). We analyzed all raptors and all corvids as groups because factors which affect detection are similar across raptor and corvid species, respectively, and increased number of detections allowed us to improve precision of estimates. We then post-stratified density estimates for corvids by species, isolating ravens from other corvids because they are often targeted for predator control, whereas crows and magpies are not. With recorded sighting angles and distances, we calculated the perpendicular distances from sighted avian predators and the transect line.

For each avian predator group, we tested multiple detection models. We first tested models with different detection key functions, compared goodness of fit with Kolmogorov-Smirnov and Cramer-von Mises tests, and then included variables that could influence detection including species, temporal variables, duration of transect, and location. Rounding observation distance and sighting angle measurements likely resulted in poor initial goodness-of-fit results. We improved model fit by binning distances into 50-m increments (Buckland 2001) and re-evaluating model parameters. We used Akaike's Information Criterion (AICc) framework adjusted for low sample size to rank competing models (Akaike 1981). We post-stratified density estimates from top-ranked models, so that we had unique values for year, subsite, and species (corvids only).

Variables that did not meet requirements for inclusion in density estimates via distance sampling (e.g., target shooters, badger sign) were still useful for informing our understanding of threats within each site, so we present and discuss qualitative descriptions of these disturbances (Appendix A.4).

Nest-site Habitat Selection Modeling

We used a conditional logistic regression to compare used nest-site to random site characteristics with the ‘survival’ package in R (Therneau 2015, R Core Development Team 2017). We included only nests with age estimates so that we could standardize vegetation measurements. If pairs of predictor variables were highly correlated (Pearson’s correlation; $|r| \geq 0.7$), we eliminated the variable of lesser biological significance based on available literature. We also eliminated variables for which occurrence was extremely rare prior to modeling. Because we were interested in whether nest placement adjacent to cowpies was non-random, we created a binomial category for the presence or absence of a cowpie within 50 cm based on measurements to nearest cowpie from the nest or random site. We explored all possible combinations of the remaining variables, which included presence of a cowpie within 50 cm, effective visible height, percent concealed, percent grass, percent forb, percent bare ground, and percent shrub.

Using Akaike’s Information Criterion framework adjusted for small sample size (AICc) and Akaike weight, we ranked and evaluated models (Burnham and Anderson 2002; Table 1.1.). If a model within 2 AICc was simply the nested top model plus one additional parameter, we considered the additional parameter redundant when removal of that parameter failed to change coefficient estimates of remaining parameters by more than 20% (Hosmer et al. 2013), and if the associated p-value of the parameter was greater than 0.15 (Arnold 2010).

Table 1.1 Model selection table of conditional logistic regression models which best described selection of nest-sites used by curlews compared to random sites within the same territory as the nest.

Parameters	k	logLik	ΔAICc	ω
Cowpie+Vis. Height+% Bare Ground+% Grass+% Shrub	5	-164.57	0.00	0.571
Cowpie+Vis. Height+% Bare Ground+% Grass	4	-167.05	2.92	0.133
Cowpie+Vis. Height+% Grass+% Shrub	4	-167.16	3.14	0.119
Cowpie+Vis. Height+% Shrub	3	-168.56	3.92	0.080
Cowpie+Vis. Height+% Bare Ground+% Shrub	4	-168.29	5.41	0.038
Cowpie+Vis. Height	2	-170.78	6.35	0.024
Cowpie+Vis. Height+% Grass	3	-169.99	6.79	0.019
Cowpie+Vis. Height+% Bare Ground	3	-170.18	7.17	0.016
Cowpie+% Bare Ground+% Grass+% Shrub	4	-178.76	26.35	0.000

Nest Success Modeling

We modeled nest survival using a generalized linear model with a logistic exposure link (Shaffer 2004) using the package 'lme4' in R (Bates et al. 2015, R Core Team 2017). Nest success was the binomial response variable and, as fixed effects, we used predictor variables within 5 categories for which we hypothesized influenced nesting success: 1) communal defense capacity, 2) nest initiation timing, 3) concealment/visibility, 4) predator density, and 5) disturbance/anthropogenic features (Table 1.2). Only nests with known age and fate were included in the analysis (N = 128). We used percent conspicuous object acquired from SamplePoint analyses for nest survival models instead of the presence of cowpie within 50 cm variable because we were interested in the effect of any conspicuous objects near the nest-site, and nests at some sites had conspicuous objects, but not cowpies due to absence of cattle. Nests with and without cowpies in a 50 cm radius had significantly different percent cover of conspicuous objects (Welch's $t = -5.39$, $df = 64.57$, $p < 0.0001$), and cowpie density was strongly correlated (Pearson's correlation; $r = 0.72$, $df = 125$, $p < 0.0001$) with percent cover of conspicuous objects, so we concluded % conspicuous object was an appropriate metric that accounted for cowpie presence/absence within 50 cm. We had complete information for all selected variables except perch distance, because at some nests or random sites observers neglected to collect perch data, so we excluded that variable from the main analysis and conducted a separate analysis on the subset of the data which had complete perch information (N = 100). Variable selection proceeded with the retention of the variable with greater biological significance from highly correlated pairs (Pearson's $|r| \geq 0.7$), or if both variables were equally important, creation of model sets which did not include correlated pairs. We then ran exploratory models for all possible combinations of remaining variables.

We ranked models using AICc and examined all models within two AICc of the top-ranked model (Burnham and Anderson 2002). When lower-ranked models were simply the top-ranked model plus one additional parameter, we again conservatively considered that parameter redundant if removal did not change any remaining parameter coefficient estimate by >20% (Hosmer et al. 2013), and the p-value for the removed parameter was greater than 0.15 (Arnold 2010).

We followed the same model selection process for both the full nest success analysis (N = 128), and the separate nest success analysis which included the distance to nearest perch (N = 100). For the full analysis, the final candidate set included 5 models, with the parameters non-raven corvid density and % conspicuous object occurring in all models (Table 1.3). We selected the most parsimonious of the equally suitable models. In the separate perch distance analysis, the final candidate set included 4 models, with non-raven corvid density again occurring in all models, as well as perch distance (Table 1.4). Two of the candidate models were equally parsimonious. However, because anthropogenic features such as roads have management implications and were central to our research question, we selected the parsimonious model in which distance to nearest road was included.

We did not include random effects in nest survival models because with the addition of a random effect, coefficient values remained consistent with comparable fixed effect models and the variance of the random effect was approximately zero. We tested site, subsite, and year/subsite as random effects, and each produced the described outcome, indicating that the variation was accounted for by the fixed effects, and inclusion of random effects was unnecessary.

For nest survival comparisons with previous work, we also calculated nest success using 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.

Table 1.2 Descriptions of parameters used in modeling Long-billed Curlew nest success.

Category	Parameter	Description
Communal Defense	Curlew Density	Density of curlews (km^{-2}) in focal nesting area, measured at season start, during the year the nest was active.
Initiation Timing	Initiation Date	Day of year nest was initiated (first egg laid).
	Relative Initiation Date	The number of days post site green-up date nest was initiated.
Concealment/ Visibility	% Concealed	Percent of "curlew dummy" squares >50% concealed when viewed from .75m high, 10m away.
	Effective Visible Height	Height (cm) at which a white board, viewed from 25 cm above nest and 10m away from a nest, was 90% obscured.
	% Conspicuous Object	Percent cover of cowpies and rocks ≥ softball-diameter in approx. 2m radius of nest.
Predator Density	Raptor Density	Density (km^{-2}) of diurnal raptors at a subsite, during the year the nest was active.
	Non-raven Corvid Density	Combined density (km^{-2}) of American Crows and Black-billed Magpies at a subsite, during the year the nest was active.
	Raven Density	Density (km^{-2}) of Common Ravens at a subsite, during the year the nest was active.
Disturbance/ Anthropogenic Features	Road Distance	Distance (m) from nest to nearest road.
	Perch Distance*	Distance (m) from nest to nearest perch.
	Site/subsite	The nesting area site or subsite.

*We conducted a separate analysis for perch distance.

Table 1.3 **Candidate models for Long-billed Curlew nest success using generalized linear models and logistic exposure links. Models within two AICc of the top model are shown, and weights are based on this candidate set of five models.**

Parameters	**df**	**ΔAICc**	**ω**
Curlew/km^2+NRcorvid/km^2+%ConspicObj	4	0.00	0.334
Curlew/km^2+NRcorvid/km^2+%ConspicObj+RoadDist	5	0.74	0.231
Curlew/km^2+NRcorvid/km^2+%ConspicObj+%Conc	5	1.50	0.158
NRcorvid/km^2+%ConspicObj+RoadDist+%Conc	5	1.73	0.141
NRcorvid/km^2+%ConspicObj+RoadDist+%Conc+Raptor/km^2	6	1.78	0.137

Table 1.4 **Candidate models for Long-billed Curlew nest success using generalized linear models and logistic exposure links. Models within two AICc of the top model are shown, and weights are based on this candidate set of four models.**

Parameters	**df**	**ΔAICc**	**ω**
Curlew/km^2+NRcorvid/km^2+PerchDist+Raven/km^2	5	0.00	0.388
Curlew/km^2+NRcorvid/km^2+PerchDist	4	0.97	0.239
NRcorvid/km^2+PerchDist+RoadDist	4	1.24	0.209
Curlew/km^2+NRcorvid/km^2+PerchDist+RoadDist	5	1.72	0.164

Results

Overall Nesting Success and Causes of Failure

Overall curlew nesting success at our sites in the Intermountain West during 2015 and 2016 was 27.1% (N = 128), calculated for historical comparison purposes using the Mayfield Method (Mayfield 1961, 1975) to account for exposure time (Table 1.5) with a 33-day nesting period. 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 two sites in 2015: the revisited historical site in the Upper Green River Basin, Wyoming (40.0%; N = 25) and the Pahsimeroi Valley (39.1%; N = 17). At the second revisited historical site, the ACEC in southwest Idaho, Mayfield nest success for 2015 and 2016 combined was 18.8% (N = 46). Nest initiation dates varied by latitude and elevation, with initiation dates generally later at more eastern latitudes and higher elevations (Appendix A.2).

Table 1.5 Long-billed Curlew nest success estimates for Idaho and Wyoming sites in 2015 and 2016. Nests with unknown fate or unknown age are not included.

Year	Site	N	Apparent Hatch Rate (%)[1]	Mayfield DSR[2]	Mayfield Estimate (%)[3]
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 & 2016	128	41.41	0.961	27.08

[1] Percent of nests hatched out of the total number of nests.

[2] Mayfield daily survival rate (DSR).

[3] Mayfield nest success estimate, using an estimated 33 days of nesting (~4.5 days laying, 28-29 days incubating).

Of 74 unsuccessful nests, the majority (52 nests; 70%) failed due to nest depredation, and nine (12%) failed either from unknown causes or we were unable to distinguish whether abandonment or depredation occurred first. Of the remaining 13 failures (18%), two nests flooded and the intact eggs were subsequently abandoned, three nests flooded and the nest cups were empty so we suspected flooding followed by depredation, two nests were abandoned well after projected hatch date suggesting infertile eggs, two nests appeared to have failed due to cattle trampling, two nests showed signs of both cattle trampling and flooding, and two nests with intact eggs were abandoned for unknown reasons. Of 52 depredated nests, we suspected avian predators of the *Corvidae* family at 12 nests, mammalian predators (badger and coyote primarily, and rarely skunk) at 21 nests, and we were unable to identify the predator category 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. A small proportion of curlews in our study were marked with alpha flags, and we confirmed re-nesting attempts by 2 marked individuals following nest failure, and suspected re-nesting for unmarked birds in other territories.

Nest-site Selection

Nest-site selection by curlews was best approximated by the model which included presence of ≥1 cowpie within 50 cm, effective visible height, % bare ground, % grass, and % shrub (Table 1.1). Nest-sites were six times more likely to have a cowpie within 50 cm than random sites (85% CI = 4.125 – 8.581; Table 1.6). Relative to random sites within a nesting area, nest-sites had greater visibility of surroundings by incubating birds. 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 (85% CI = 0.971 – 0.941; Table 1.6). Nest-site vegetation composition also varied from random sites in that 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 1.6). A moderate, but statistically significant negative correlation (Pearson's correlation; $r = -0.54$, $df = 126$, $p < 0.0001$) between grass and forb cover suggested that forb cover replaced decreasing grass cover at our study sites. Bare ground at our study sites occurred at dirt roads, in slickspots, within native sagebrush habitats, interspersed among bunchgrass, and at badger mounds from excavated burrows.

Table 1.6 Parameter estimates (β), standard errors, and 85% confidence intervals from top-ranked conditional logistic regression model of nest-site selection by Long-billed Curlews.

Parameter	β	SE	85% CI	Wald χ^2	p-value
Cowpie within 50cm	5.95	0.25	4.125 to 8.581	53.9469	<0.0001
Effective Visible Height	-0.96	0.01	0.971 to 0.941	28.0085	<0.0001
% Bare Ground	-0.96	0.02	0.936 to 0.986	1.19480	0.027
% Grass	-0.98	0.01	0.965 to 0.989	6.27240	<0.05
% Shrub	-0.52	0.65	0.203 to 1.306	4.95300	<0.05

Correlates of Nest Success

Probability of nesting success was positively associated with curlew density in focal nesting areas (Table 1.7; Fig. 1.2A; Appendix A.3 for focal area density estimates). 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 per square kilometer (Table 1.7; Fig. 1.2B). Percent cover of conspicuous objects also had a positive association with nest success. The odds of nest success increased by 15.8% for each additional 1% of cover of cowpies and large rocks (Table 1.7; Fig. 1.2C). We also found a weak, but statistically significant, positive correlation between percent cover of conspicuous objects at the nest, and the density of all corvids (Common Raven, American Crow, and Black-billed Magpie) by year at the subsite level (Pearson's correlation; $r = 0.23$, $df = 126$, $p < 0.01$).

Table 1.7 Generalized linear model parameter estimates from binomial survival of Long-billed Curlew nests (N = 128) modeled using a logistic exposure link. Log-odd coefficients (β) are exponentiated as odds ratios (OR) and 85% confidence intervals (CI) are associated with the OR for interpretation.

Parameter	Units	β	OR	85% CI	p-value
Curlew Density	birds/km^2	0.0727	1.0754	1.0356 to 1.1186	<0.05*
Non-Raven Corvids	birds/km^2	0.1063	1.1122	1.0557 to 1.1830	<0.05*
% Conspicuous Object	% cover	0.1463	1.1576	1.0535 to 1.2979	0.0541

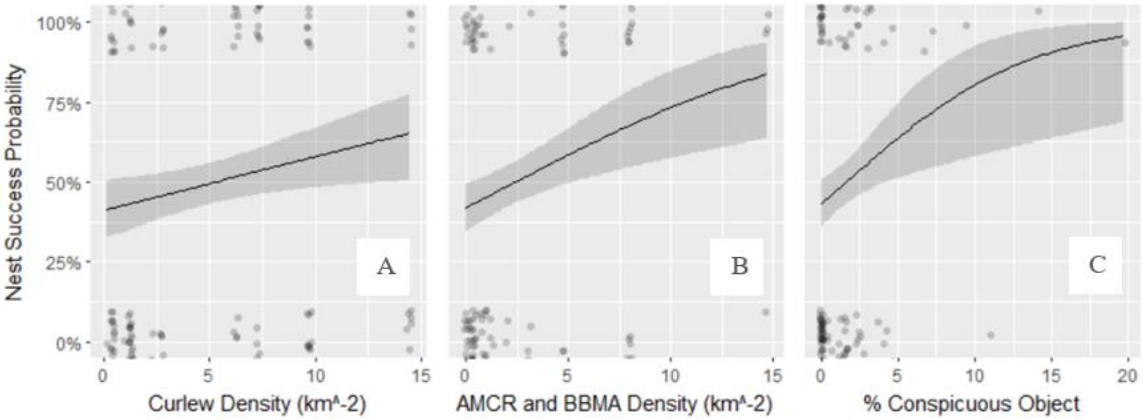

Figure 1.2 Predicted probability of nest survival for parameters in selected model, shown with 85% confidence intervals. Probability of nesting success varied with A) curlew density in the nesting area, B) density of non-raven corvids including American row (AMCR) and Black-billed Magpie (BBMA) at the subsite, and C) percent cover of conspicuous objects in immediate nest vicinity.

To further explore how anthropogenic features on the landscape might interact with predators and influence nest success, we conducted a second analysis on the subset of nests which had complete perch data (N = 100). Because anthropogenic features such as roads have management implications and were central to our research question, we selected the most parsimonious model in which distance to nearest road was included from among a candidate set of 4 equally suitable models. This model included three 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 1.8; Figs.

1.3A−C). The distance from the nest to the nearest perch had a positive relationship with nest survival. Nests were 3.9% more likely to survive for every 10 m distance away from a perch (Table 1.8; Fig. 1.3A). The 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. As in the full model, nest success was positively associated with density of non-raven corvids at the subsite (Table 1.8; Fig. 1.3B).

Table 1.8 Parameter estimates for correlates of Long-billed Curlew nesting success from a subset of nests which included perch distance data (N = 100). We used a generalized linear model with a logistic exposure link. Log-odd coefficients (β) are exponentiated as odds ratios (OR) and 85% confidence intervals (CI) are associated with the OR for interpretation.

Parameter	Units	β	OR	85% CI	p-value
Non-Raven Corvids	birds/ km^2	0.1112	1.1176	1.0534 to 1.1959	<0.05*
Perch Distance	meters	0.0038	1.0039	1.0020 to 1.0059	<0.01*
Road Distance	meters	0.0017	1.0017	1.0007 to 1.0028	<0.05*

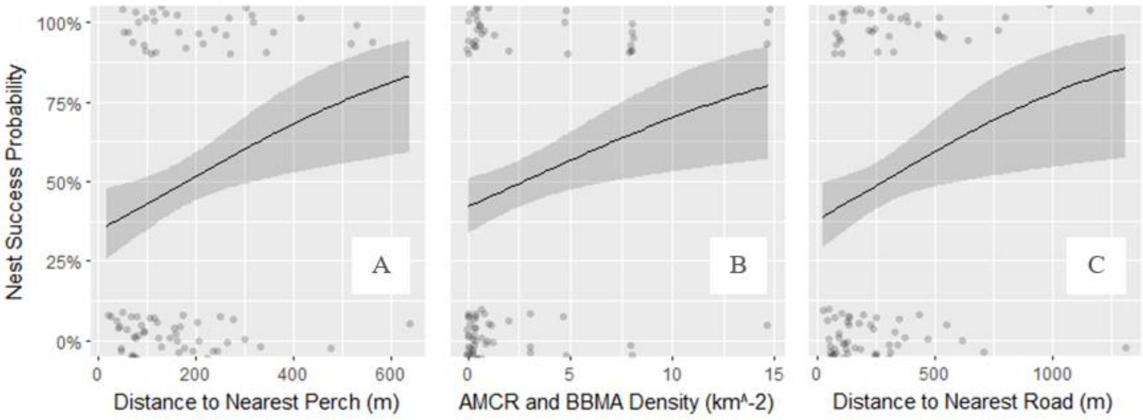

Figure 1.3 Predicted probability of Long-billed Curlew nest success modeled with a nest data set with complete perch information (N = 100) and shown with 85% confidence intervals. The model parameters included A) distance to from the nest to the nearest perch, B) density of non-raven corvids at the subsite, and C) distance to the nearest road.

Predators and Disturbances

Anthropogenic disturbance information gathered from transects provides additional understanding of site-specific threats to nesting curlews (see Appendix A.4 for qualitative summary). At the ACEC in southwest Idaho we documented at least one active target shooting event (audible shots) during 47.4% of the 116 transects completed during 2015 and 2016. We did not have enough live mammal sightings to fit detection curves and estimate mammalian density, however each site hosted specific predators as evidenced by sign and sightings recorded both within and outside of designated transects. We noted fresh badger sign along nearly every transect at the ACEC – an area known locally for very high badger numbers. We observed wolves only in Jackson, documented skunks only in the Upper Green River Basin area, and observed coyotes at every site. Finally, we noted more off-road travel (i.e., crushed vegetation caused by OHV or vehicle not on an established trail or road) at the ACEC than at other sites.

Discussion

Our results indicate habitat selection occurs within territories, suggest at least one habitat component is directly associated with nesting success, and identify correlates of nesting success which are relevant to management. We also found varied nest success among study sites, with one site showing concerning low success in comparison to historical research. We attributed most nest failures to mammalian or avian predators, and found raven density was not associated with nesting success in our study, and that crows and magpies were positively associated with nest success. Our prediction that structural vegetation features (e.g., vegetation height and concealment) would reduce depredation risk was not supported. Instead, a combination of broad scale site characteristics, as well as potentially density-mediated communal defense, appear to be influencing nesting success.

We found curlew nest success at Intermountain West sites in 2015 and 2016 generally fell within the range of nest success measured in other studies, but was lower than this range at two sites. In other areas with multiple years of study and high sample sizes, nest success ranges from 31% (N = 215 in Nevada hay fields; Hartman and Oring 2009), to 69% (N = 40 in annual grasslands in North-central Oregon; Pampush and Anthony 1993), while we measured nest success to be 12 - 40% in our study. Based on continuous territory monitoring, it appeared that re-nesting attempts occurred after failures which occurred earlier in the breeding season at all sites in our study, but more frequently at sites with earlier arrival dates and longer breeding seasons. We confirmed two re-nesting attempts by marked curlews in southwest Idaho during our study and these curlews began egg-laying for re-nesting attempts approximately 7 to 10 days after failure. Evidence of re-nesting contrasts with the findings of Redmond and Jenni (1986) in the same area and Paton and Dalton (1994) at the Great Salt Lake in Utah, but supports the findings of Hartman and Oring (2009) in northeastern Nevada. At the site with lowest nesting success (12%), small sample size and only one season of data prevented us from drawing in-depth inferences, but we suspect a period of heavy storms was detrimental to nesting. Additionally, continued work in 2017 showed substantially higher apparent hatch rate at this site than in 2016. The low success at the other site, in southwest Idaho, does not appear to be an anomaly (Pollock et al. 2014).

Comparisons from two of our study sites with historical research in the same areas provides useful information about long-term trends. The Upper Green River Basin had similar but slightly higher nest success compared to historical estimates; 33.6% in 1982 (N = 21; Cochran and Anderson 1987) compared to 40.0% in 2015 (N = 25). Alarmingly, at the ACEC in southwest Idaho, we found nest success fell from 40.0% in 1977 through 1979 (N = 119, Redmond and Jenni 1986) to 18.8% overall in 2015 and 2016 (N = 50). Nest monitoring at the ACEC from 2008 through 2014 and in 2017 measured similarly low apparent hatch rates, averaging 25.0% and ranging from 15%−38.5% in each year (Pollock et al. 2014, Carlisle et al. 2017), an indication that 2015−16 are not isolated seasons of low productivity. Further evidence of a concerning trajectory are point-count survey comparisons between the 1977−79 and 2008−17 time periods that indicate a population decrease of more than 95%, and concentrated declines in areas with high levels of human recreational use (Redmond and Jenni 1986, Pollock et al. 2014).

Nest-site Selection

Habitat at nest-sites differed significantly from random sites. For vegetation structure, we hypothesized that curlews balance a trade-off between visibility from the nest and concealment when incubating. This was partially supported as nest-sites did afford better visibility of the surrounding habitat, which could increase the chances of an adult detecting and escaping predation, or diverting a predator from the nest (Götmark et al. 1995). Additionally, we found lower percentage of shrub cover around nests than random sites, which also relates to visibility of surroundings. However, our measure of concealment was not significantly different between nests and random sites, and in nesting success models neither visibility from the nest (i.e., vegetation height) nor concealment were important predictors of nest success. In continued nesting research during 2017, we recorded curlew nest initiations in newly planted agricultural fields with zero vegetative cover which suggests visual obstruction provided by natural vegetation and topography may be relatively unimportant given the already cryptic coloration of curlews. Camp et al. (2012) found that visibility and concealment interact to shape the perception of risk by pygmy rabbits, which in turn influence predator avoidance behaviors. Increased visibility of surroundings and increased concealment lowered perceived predation risk as measured by flush initiation distance (Camp et al. 2012). For other grassland bird species, increased visibility via shorter vegetation reduced predation risk, at the cost of decreased food availability (Whittingham and Evans 2004). Our results suggest that some habitat attributes selected by curlews do not reduce predation risk during incubation, but nonetheless could still influence predation risk during other stages of breeding such as chick-rearing.

Correlates of Nest Success

We found curlew density to be an important predictor of nest success. Specifically, higher curlew density in nesting areas was associated with higher probability of nesting success. Because males establish territory boundaries early, and maintain territories throughout the season, early-season curlew density should approximate relative later-season densities, and by proxy, nesting density. Although our data does not in itself prove this as a causal factor, in a review of shorebird studies, MacDonald and Bolton (2008) found that nesting density was a consistently identified correlate of nest success. Pampush and Anthony (1993) also found highest curlew nesting success in a habitat with highest curlew nest density. Effective communal defense may be dependent on nesting density and to a degree, synchronized nesting phenology

(Hernández-Matías et al. 2003). At high-density breeding sites, curlews commonly recruit six or more conspecifics to fend off predators (Pampush 1980). Asynchronous nesting could become apparent when females with failed nests leave to forage in agricultural fields or at other gathering places, while males remain on territories. For sites with low curlew density and less synchronized nesting phenology, antipredator behavior may be less effective because fewer curlews are available to recruit from nearby nesting territories, contributing to an Allee effect where low density perpetuates low nesting success (Berec et al. 2007). Furthermore, negative impacts of low-density breeding may be exacerbated by weather conditions for nests initiated during temporal extremes of the breeding season. In southwest Idaho for example, the climate is arid and temperatures frequently exceeded 100°F in late June. Necropsies of chicks that died shortly after hatching in two different nests revealed incomplete yolk-sac retention, which was similarly observed at this site by Redmond and Jenni (1986), and attributed to heat and insufficient humidity. In Wyoming study sites, snow storms early in the breeding season may increase propensity for nest flooding through snow-melt. Though communal defense capacity is a reasonable mechanism through which curlew density may affect nest success, further research is needed as, alternatively, high density may be a consequence of high nest success, characteristic natal philopatry, or habitat conditions which promote smaller, more tightly clustered territories and indirectly increase probability of nest success.

We found a positive relationship between nesting success and non-raven corvid density. This surprising result is likely explained by surrounding conditions at two subsites, New Fork in the Upper Green River Basin of WY, and Goldburg in the

Pahsimeroi Valley, ID. At Goldburg, there was a known crow roost and nesting area in some nearby willows at one corner of the meadow, and at New Fork magpies nested in abundant large shrubs along the edges of nesting meadows, leading to high crow and magpie densities, respectively. These areas also had high nesting success, but we do not believe there is a direct relationship between non-raven corvid density and nesting success. Of five nest failures at these two subsites and the specific years with high non-raven corvid density, we did not suspect failure caused by avian depredation at any nests; four were suspected mammalian depredations, and one was flooded and subsequently abandoned. 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 which we did not measure.

Nest placement next to conspicuous objects was not random, and interestingly, we found conspicuous objects were associated with increased probability of nest success. Some avian species 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). For curlews nesting in areas with higher densities of avian predators, an adaptive strategy could include selecting nest-sites near conspicuous objects for aerial camouflage. Our research is the first known statistical confirmation that curlews selectively place nests adjacent to conspicuous objects such as cowpies at a territory scale, and that this strategy results in greater nest success. Because we found a positive correlation between corvid density in an area and percent cover of conspicuous objects at nests, this could suggest adaptive plasticity for curlew nest placement, and warrants further exploration. However, our attempt at estimating density of all predators was unsuccessful, and without concurrent knowledge of nesting success and predator communities, interwoven scenarios such as these may obscure interpretations of habitat selection and nest survival.

Mammalian depredation was the main proximate cause of nest failure at our study sites, but we were unsuccessful at calculating mammalian predator density using a diurnal line transect approach. 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. In experimental manipulations, Howlett and Stutchbury (1996) found evidence of incidental depredation when they physically altered nest concealment to create either highly visible or concealed nests in the same area, and it did not affect depredation rates. Similarly, Cortés-Avizanda et al. (2009) found increased incidental nest predation by scavengers in plots where prey items (fish carcasses) were experimentally supplemented. Mammalian depredation of curlew nests across breeding sites is also likely incidental, as curlew eggs are not a primary prey item for the generalist mammals that are present, especially in southwest Idaho where there is a high density of ground squirrels (Pollock et al. 2014). In nesting areas where ground squirrel shooting leaves an abundance of easily-scavenged carrion, a spillover effect could apply to curlews if mammalian and avian predators are attracted to the area for either live ground squirrels or carrion, and then incidentally encounter curlew nests. Mammalian predator density is clearly a complex, but important, metric for predicting nest success. Considering the challenges associated with density estimates of primarily nocturnal predators in grassland habitats, we propose future studies seeking predator estimates use an index of abundance or, with more substantial funding, camera traps on grids to better estimate mammalian predator density.

We found that distance to the nearest perch was an important predictor of curlew nest success. This potentially offers an example of an anthropogenic variable mediating the effects of predation on curlew nesting success. This is not a surprise as interactive effects of predators and anthropogenic features alters predation-risk across a number of landscapes (*reviewed in* Evans 2004). In contrast, research with other *Charadrii* waders has also shown avoidance of tall structures (suitable perches for raptors or corvids) for nest placement, but found no effect of perch distance on nest success (Wallander et al. 2006). There are many ways in which perches could affect nesting curlews. Along with potential avian predators locating nests or adults via a perch vantage point, perched avian predators near a nest may decrease nest attendance by stimulating defensive mobbing, thereby increasing opportunity to depredate an unguarded nest (Strang 1980, Schmidt and Whelan 2005) or increasing the frequency at which a curlew may reveal nest location when they return to incubate. Inattendance and more conspicuous behavior heightens vulnerability to both avian and mammalian depredation (Smith et al. 2012).

Other anthropogenic features such as roads and related edge effects are also of interest, as they may serve as corridors for some predators, coincide with perches for avian predators (i.e., fences and utility poles), or function as ecological traps (Fahrig and Rytwinski 2009). In our selected nest success model, we found curlew nest success was positively associated with increasing distance to the nearest road. Roads may directly and indirectly affect all portions of the annual cycle. For example, we discovered most shot adults adjacent to roads (this study and in Jenni et al. 1981), we documented one potential vehicular impact mortality of a tagged adult during our study, and roads pose threats to less-mobile chicks through dust asphyxiation and direct vehicular impact (Jenni et al. 1981). Examining nest success in relation to perches and roads is pertinent because modifying or removing anthropogenic features may provide a more sustainable, discernable, and cost-effective conservation solution than predator removal (Evans 2004).

It must be noted that 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 one or more 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 a rigorous estimate of predator densities. However, other disturbance factors at specific sites within our study may be having a large impact. Specifically, six of 17 birds with PTT units attached in southwestern Idaho between 2013 and 2017 have been illegally shot and killed (Carlisle 2017). We also found several unmarked adult birds shot and killed on the ACEC during the breeding seasons of 2015 and 2016 and shooting mortalities occurred in historic studies of this area as well; Jenni et al. (1981) found a total of 9 dead and suspected shot near roads in 1977 (N = 1) and 1979 (N = 8). These mortality events have the capacity to directly lead to a nest failure, but also pose localized threats in other important ways. Curlews may live to more than 30 years of age (e.g., longevity record for Eurasian Curlew, *Numenius arquata*, is at least 31 years; Kuhk

1956) and at most raise one successful clutch per year, a life history strategy that emphasizes adult survival to enable many years of breeding attempts. Loss of one or more parents not only reduces the chance of juveniles surviving to independence by making them more vulnerable to climatic extremes and predation, but also the loss of long-lived, conservatively-breeding adults is extremely detrimental to curlew population stability (Jenni et al. 1981, Redmond and Jenni 1986). Though we did not monitor juvenile survival, we did document adult curlew mortalities on the ACEC that were caused by shooting and coincided with early season chick-rearing. No other study site had this shooting component, and our estimate of shooting events and mortalities is likely underestimated because we avoided conducting some transects due to safety concerns for researchers presented by shooters, and thus came across mortalities by coincidence. In total, population declines in southwest Idaho greatly contrast with regional BBS trends of apparently stable or slightly increasing curlew populations (Sauer et al. 2017), and require immediate attention.

Conclusions and Management Implications

Nest success at our Intermountain West field sites suggest curlew nesting is compatible with some working lands, including flood-irrigated pastures, but modifications are necessary to improve nesting success and stem population declines in southwest Idaho. Specifically, persistent, elevated adult mortality via illegal shooting is a major threat to the southwest Idaho population, and has been since it was first studied in the 1970s. Tangible effects of a detrimental occurrence may take years to precipitate in populations of long-lived species, and this could be what is happening in southwest Idaho. Broadly, reducing nest depredation, the main cause of nest failure across all sites, may bolster populations. Our results suggest some management actions may improve nest success, and we provide guidance for necessary future research.

Based on modeled nest success, we found it may be possible to mediate nest depredation risk by shaping habitat conditions and potentially by adjusting anthropogenic features, including perches, within nesting areas. We observed a positive association between nest success and increased distances to the nearest perch. Because curlews will return to the same or nearby territories to breed year-after-year, possible management options could be removal of unnecessary perches, or refraining from constructing new perches in known curlew breeding areas. These options require further experimental research, as our study did not control for other variables often associated with perches such as roads (e.g., parallel fences and utility lines). Direct control of predators through lethal control programs is often used with the intention of improving nesting success, but efficacy varies (*reviewed in* Côté and Sutherland 1997). When lethal control of predators is effective it is perhaps due to more direct predator-avian trophic relationships (e.g., experimental removal of foxes, crows, and magpies significantly increased productivity of grey partridge; Tapper et al. 1996), but lethal control may be detrimental to nesting success if there is subsequent mesopredator release (Mezquida et al. 2006). For example, lethal control of an apex predators (coyotes) in western Texas resulted in an increase of several mesopredators, including badgers (Henke and Bryant 1999). At the site in southwest Idaho, mammals at all levels of the trophic cascade are already affected by legal shooting by varmint hunters and indiscriminate shooting, so it is unclear how further control would affect curlew productivity.

Threats to nesting curlews are also specific to a particular breeding season, and require dynamic land management, between years, for optimal conditions. For example, few nests were affected by flood irrigation in the years of our study, but in years for which early season storms or snowfall delay onset of incubation, postponing irrigation may increase nesting success. Low-intensity grazing did not severely impact curlew nesting success in 2015 and 2016, and may have created more desirable habitat conditions (Bicak et al. 1982). Zero nests failed due to trampling at sites where grazing was intentionally timed to avoid the nesting season. However, we caution that our study did not measure grazing intensity, nor did it include the chick-rearing stage of the breeding season. Clarke (2006) found higher grazing intensity associated with lower nest success in western South Dakota and tentatively suggested reducing grazing densities to 33 cattle/km^2 or 220 bison/km^2 or less during the breeding season and further reducing densities during years following drought or fire. Curlew chicks require habitat mosaics and may benefit from patches of shrubs or agriculture that provide cover from predators (Blake 2013). Landscapes managed for curlews could use grazing before the breeding season to create preferred nesting habitat, reduce or remove grazing pressure during the breeding season, and consider habitat alterations such as planting small patches of low shrubs or other cover vegetation in areas of homogenous annual grasses to develop valuable habitat mosaics.

A challenge for conservation is recognizing and addressing extinction lag, the time delay between detrimental habitat degradation or loss and drastic population response (Kuussaari et al. 2009). Extinction lag is longer with long-lived species, and can act at the population or ecosystem level (Kuussaari et al. 2009). We lack information in two areas which would inform management decisions in regard to possible extinction lag occurring with curlews. First, on the breeding grounds there is a paucity of age structure data. Understanding the age structure of a population may aid in pinpointing the timing of past habitat degradation, and determining if a specific curlew population is experiencing extinction debt (i.e., moving toward local extirpation because of historical perturbance). Second, for many populations, we do not have sufficient knowledge of migratory connectivity to understand how declines we see on the breeding grounds may be linked to the wintering ground threats. For example, wintering in poorer quality habitat may lead to reduced body condition for spring migrants which could negatively impact breeding success in the subsequent season, and act on individuals or populations (Norris 2005). Further, we lack information on body condition of curlews arriving to the breeding grounds, and this may be factor in nesting success if curlews in better condition have an advantage in initiating early nests or defending their nests from predators.

Breeding seasons are inextricably linked to other portions of the annual cycle. For Long-billed Curlews in the Intermountain West, our data suggest at least some populations may be limited in the breeding grounds by low nesting success, adult mortality, or both. The positive association between nest success and curlew density calls for targeted management in remaining high-density areas to maintain potential source populations. Reduced reproductive success may also be precipitated by low success or poor habitat quality in in the non-breeding season (Norris 2005, Norris and Taylor 2006, Harrison et al. 2011), and elucidation of such carry-over effects are important for future conservation. Based on our data and information from earlier studies, we consider breeding curlews in some Intermountain West areas to be under greater threat than previously expected, and urge careful planning and management practices for ensuring the viability of these critical populations.

CHAPTER TWO: SPATIAL DISTRIBUTION AND SITE FIDELITY OF LONG-BILLED CURLEWS WINTERING IN CALIFORNIA AND MEXICO

Abstract

Migratory birds face threats throughout the annual cycle, and cumulative effects from linkages between the breeding and non-breeding grounds may impact species at the population level. Mapping connectivity and spatial distribution within varied habitats pinpoints conservation issues, yet for many species we lack this fundamental knowledge. Long-billed Curlews (*Numenius americanus*) are a migratory shorebird of conservation concern that show population declines at some regional and local scales. Little information is available regarding their spatial distribution on the wintering grounds, particularly for Mexico. We used satellite transmitters to track 21 curlews that bred in the Intermountain West and wintered in California and Mexico, and studied home range size and inter-annual site fidelity with dynamic Brownian Bridge Movement Models. We documented four main wintering areas: Central Valley of California, the adjoining Imperial and Mexicali Valleys of California and Mexico, the Chihuahuan Desert of inland Mexico, and coastal areas of western Mexico and the Baja Peninsula. Curlews wintering in coastal areas had significantly smaller home ranges and fewer core use areas than those wintering in inland areas. Home ranges in the Central Valley were larger than other inland areas, and Central Valley females had larger home ranges than Central Valley males. We measured site fidelity with a Utilization Distribution Overlap Index and found that inter-annual fidelity for wintering curlews was high, regardless of habitat

type or sex. These findings provide valuable information for full annual cycle conservation and will be particularly constructive for conservation planning once range-wide migratory connectivity is mapped.

Introduction

Connecting distant portions of the annual cycle of migratory birds is a long-standing conservation target (Webster et al. 2002). The continuing advancement of genoscape mapping and tracking technologies have revealed insights into migratory connectivity, which has significant implications for development of holistic conservation strategies (Webster et al. 2002, Ruegg et al. 2014). However, for many migratory bird species foundational information such as the location of key wintering areas, spatial use and distribution in those areas, and links between segments of the annual cycle, remains unknown. A better understanding of the complete annual cycle of many migratory species is essential for identifying causal factors of declining populations. For example, habitat quality and fine-scale conditions experienced by wildlife in one stage of the annual cycle may induce carry-over effects, where fitness consequences emerge in subsequent portions of the annual cycle (Norris and Taylor 2006, Norris and Marra 2007, Harrison et al. 2011), and if threats are localized, different segments of a wide-ranging population will be disproportionately affected. Delineating the spatial distribution of a species is a fundamental step towards the conservation of declining migratory birds as it provides a framework for identifying habitat requirements as well as pinpoints threats to a population.

A migratory bird group of particular concern include the wading shorebirds of the *Numeniini* tribe, which are recognized as imperiled and in need of collaborative conservation action. Of 13 species, seven are critically endangered, endangered, or near threatened (Pearce-Higgins et al. 2017). *Numeniini* share life history traits which cumulatively increase susceptibility to extinction, including long-distance migrations (Sanderson et al. 2006), late age of reproductive maturity, and low fecundity (Piersma and Baker 2000). Within the *Numeniini* tribe, Long-billed Curlews (*Numenius americanus*) are a North American wading shorebird that is recognized as a Species of Conservation Concern by US Fish and Wildlife Service and a Sensitive Species by the Bureau of Land Management. Recent research has suggested that population numbers of the Long-billed Curlew across its range may be greater than previously thought (Stanley and Skagen 2007, Fellows and Jones 2009), however, severe localized declines continue to be observed (Pollock et al. 2014, Sauer et al. 2017) and State Wildlife Action Plans in 16 states continue to list curlews as a Species of Greatest Conservation Need (USGS SWAP 2017).

The decline of Long-billed Curlew numbers has generally been attributed to habitat loss, degradation, and fragmentation of the curlew’s breeding grounds across the grasslands of North America (Dugger and Dugger 2002). However, curlews spend approximately 75% of the year on their wintering grounds, where they may experience diverse threats. The non-breeding range encompasses a broad range of coastal and inland areas of California, Texas, and Mexico, inland areas of Arizona and New Mexico, and a small portion of the southeastern coast of the US (Dugger and Dugger 2002). The non-breeding range has not been immune to habitat loss and degradation, with one key curlew wintering area, the Central Valley of California, losing more than 30% percent of its crucial wetlands between 1939 and the mid-1980’s (Frayer et al. 1989). Relative to studies that have focused on the breeding grounds, wintering ground research for curlews is sparse. The proportion of the annual cycle that is spent on the wintering grounds, and the notable habitat degradation that has also occurred in this region, highlights the importance of focusing on the complete annual cycle for the curlew, including identifying threats in some wintering regions that may drive noted population declines.

The complete annual cycle of many migratory bird species has previously been studied through genoscape mapping and chemical isotopes, but at present, curlews are not a suitable species for either technique due to sample collection challenges; they are neither captured at banding stations, nor are their nests easily located. As such, non-breeding season research to date has incorporated the use of satellite transmitters to track curlews (Sesser 2013, Page et al. 2014, Kerstupp et al. 2015), on-the-ground monitoring of abundance and distribution (Colwell and Landrum 1993, Colwell 2000, Mathis et al. 2006, Shuford et al. 2013), or close-range observation for diet studies (Leeman et al. 2001, Saalfeld et al. 2010). Despite recent major advances in the knowledge of migratory connectivity of curlews from Page et. al (2014), connectivity for much of the Intermountain West remains unmapped and we lack knowledge about the home range and site fidelity of curlews on their wintering grounds.

Home range characteristics can be influenced by such factors as population density, access to mates, or habitat quality (Wolff 1985). For example, Imre et al. (2004) observed that home range size varied relative to resource availability and competitive pressure. For wading birds, home range patterns may be correlated with foraging opportunities, where habitat with reliably high-density prey is associated with territoriality and sparse or patchy foraging habitat is associated with flocking (Bryant

1979). Curlews are known to exhibit a dichotomous foraging behavior in different habitats on the wintering grounds: territoriality versus flocking (Colwell 2000, Colwell and Mathis 2001, Leeman et al. 2001, Mathis et al. 2006), and ultimately these behavioral patterns may shape wintering home ranges of the curlew. However, opportunities to examine this contrast in multiple wintering areas, and the extent to which individual curlews may switch between strategies, have been rare.

Although curlews are more of a generalist species in comparison to other *Numeniini*, past studies indicate individuals have high site fidelity to breeding areas (Redmond and Jenni 1982), which may limit plasticity for home range shifts following habitat degradation or loss. Non-breeding site fidelity research is limited but so far suggests variation at different spatial scales, with curlews showing high fidelity to winter home ranges and lower fidelity to small-scale foraging patches (Sesser 2013). It could be the case that despite varying resource availability and territoriality on wintering grounds, spatial distribution of curlews is strongly dictated by site fidelity because familiarity with a site is crucial for survival; potentially facilitating foraging, hastening access to refugia, and decreasing energy expended on predator avoidance (Piper 2011). Because of the significant challenges associated with measuring site fidelity, however, including the need for multiple years of location data, knowledge gaps exist for many species, including curlews. Sesser (2013) quantified wintering area fidelity for eight curlews in the Central Valley of California, but bigger sample sizes are needed and we lack fidelity information for other key wintering areas as well as insight into variability based on foraging strategy.

Our research builds upon past studies to fill existing knowledge gaps in winter spatial distribution and site fidelity for curlews breeding in the Intermountain West and wintering in coastal and inland areas of California and Mexico. Notably, we examine winter utilization distributions of 21 curlews captured on the breeding grounds and compare a series of spatial distribution characteristics to better understand and manage this stage of the curlew's annual cycle.

Methods

Study Area

We attached transmitters to curlews in three different states, at 11 different locations (FIGURE 2.1). In Idaho, transmitter deployment areas included two sites in southwest Idaho, two nearby sites in the Pahsimeroi Valley in the central part of the state, and a site at the Nature Conservancy's Flat Ranch in eastern Idaho. In Wyoming, we attached transmitters to birds at the National Elk Refuge near Jackson, at two sites near Pinedale in the Upper Green River Basin region of the state, and to birds at two sites near Cody, in northwest Wyoming. Lastly, in western Montana, we attached transmitters at MPG Ranch near Florence, and in the Ruby Valley east of Dillon.

Tracked curlews migrated to four main wintering areas in California and Mexico:

Central Valley, CA− Historically grasslands and wetlands, the Central Valley is now predominantly irrigated agriculture, and one of the most productive agricultural regions in the world. It encompasses more than 18,000 square miles (47,000 km^2) and, at approximately 50 miles wide and 400 miles long, stretches through most of the length of California (USGS 2017). The Coast Ranges and Sierra Nevada mountain ranges bound the western and eastern edges, respectively. The climate is Mediterranean, drier in the southern parts of the valley, and with a rainy season that begins in mid-autumn and ends in mid-spring. Several of the most common agricultural crops associated with wintering curlew include rice, winter wheat, alfalfa, and hay (Sesser 2013). Other common crops are walnuts, grapes, pistachios, almonds, corn, and tomatoes (MangoMap, 2017).

Imperial Valley, CA and Mexicali Valley, MX− Located in southeastern California, the Imperial Valley includes a 50-mile-long area circling from the Salton Sea in California nearly to the Gulf of California (Sea of Cortez) in Mexico that is dominated by agriculture in a hot, dry climate that requires substantial irrigation. In Mexico the adjacent Mexicali Valley is part of the same agricultural complex, and we refer to the area as the Imperial/Mexicali Valley. We considered coastal mudflats along the Gulf of California in Mexico separate from inland agricultural areas of the Imperial/Mexicali Valley. Alfalfa is a major crop type, but other crops include carrots, citrus, hay, wheat, lettuce, asparagus, and temporarily fallow fields as the climate allows year-round crop rotation (USDA Cropland 2013). In the winter, sheep grazers bring lambs to some alfalfa crops where they rotate amongst fields until spring (Bell and Guerrero 1997).

Inland Mexico− Curlews wintering in central Mexico used areas that broadly are part of the North American Desert and Semi-Arid Highland ecoregions, and more specifically occurred within Mexican High Plateau in the south, Western Sierra Madre Piedmont to the east, and Warm Desert areas of those ecoregions (CEC 2017). Within the North American Desert ecoregion, The Chihuahuan Desert spans the Mexican states of Durango, Coahuila, and Zacatecas, parts of Nuevo Leon and San Luis Potosi, and reaches north into the U.S. states of New Mexico and Texas. Most curlews wintering in inland Mexico in our study spent at least part of the winter in the Chihuahuan Desert. It is known as one of the most biologically diverse arid ecoregions of the world and between the Sierra Madre Occidental and Sierra Madre Oriental mountain ranges, the vegetation is composed of grasslands, shrubs, cacti, and other xeric plants (Dinerstein et al. 2000). Agriculture is interspersed throughout the region, and was used by all individuals wintering in this area in our study for at least part of the wintering season.

Coastal Mexico/Baja− We grouped all coastal areas of the Baja Peninsula and western coast of Mexico into this category. Common habitats along the coastline include tidal mudflats, river deltas and estuaries, lagoons, and beaches. The Colorado River drains an area of more than 246,000 square miles (637,000 km^2) of the U.S. and Mexico into the northern Gulf of California. Except for La Niña flood years, agricultural and municipal water demands throughout the region all but eliminate flow at the mouth of the Colorado River. Reduced freshwater has increased salinity, particularly in northern waters and coastal areas of the Gulf of California, which may alter availability of coastal invertebrates from historical states (Arias et al. 2003).

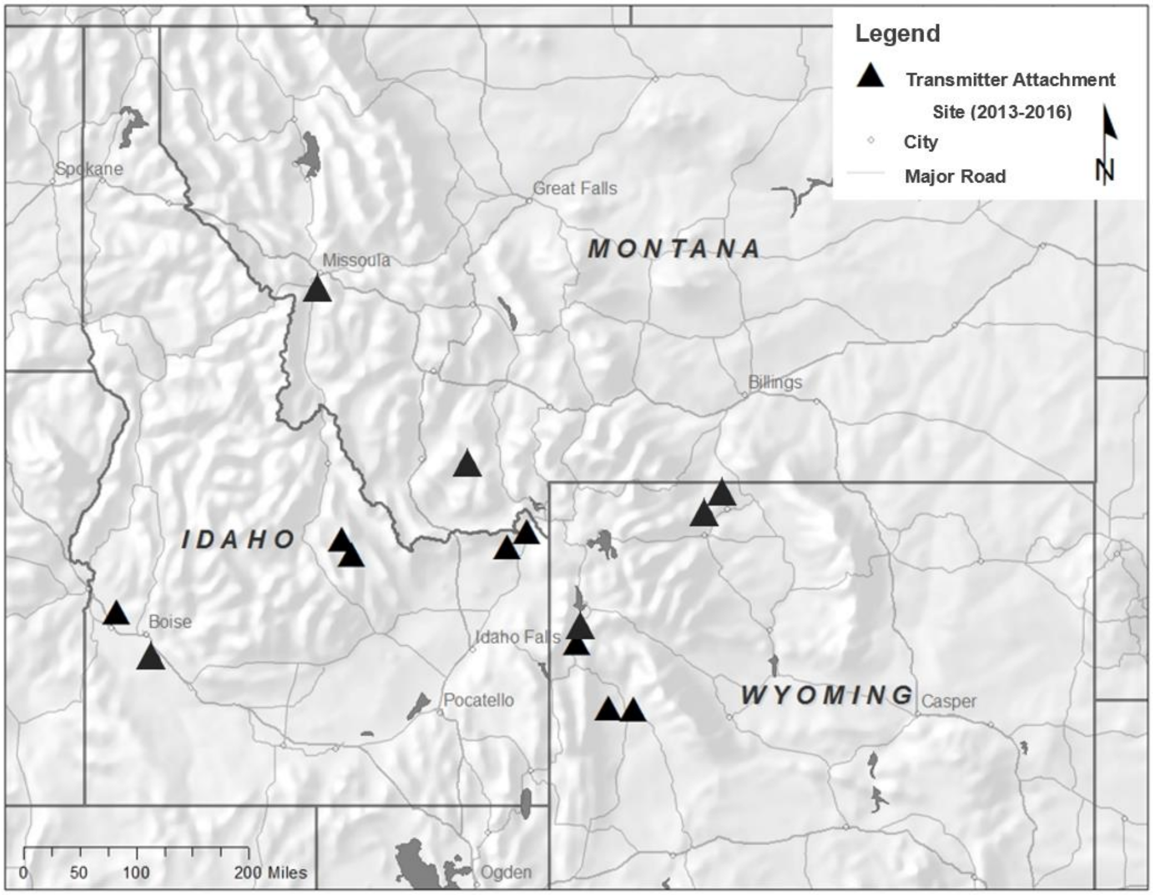

Figure 2.1 Transmitter attachment sites for Long-billed Curlews during 2013 through 2016 breeding seasons.

Satellite Transmitter Attachment

We captured incubating curlews by carrying an 18m mist net horizontally between two people, and then lowering the net onto a targeted nest. We attached Microwave Telemetry 9.5g solar-charged PTT units with a leg loop harness to adult curlews. Transmitters were scheduled for a 24-hour off-period during which the battery charged, followed by a 5-hour on-period and, in most cases, this resulted in at least a few high-quality locations for each bird every 29 hours. Four ARGOS doppler-shift location signals for each on-period were typical, but transmitters could log up to 10 locations. Location quality is categorized automatically by an estimated error radius associated with the number of satellites and the signal strength. Each bird received an aluminum USGS band on their lower leg, and a green/white alpha flag for visual identification on the opposite tibiotarsus. We used bill length and body mass to determine sex of each curlew before release. We followed IACUC protocols authorized under federal permit number 22929, Idaho permit number 990121, Montana permit numbers 2015-034 and 2016-034, and Wyoming permit number GRTE-2016-SCI-0019.

Statistical Analyses

We used ARGOS satellite location data collected from the non-breeding seasons of 2013-14 through 2016-17 to spatially model curlew distribution and intensity of use, via utilization distributions (UDs), on the wintering grounds for individual curlews. We used ArcMap (ESRI 2017) to compute home range size for all individuals and Utilization Distribution Overlap Indices (UDOI) for curlews with multiple seasons of data. All other statistical analyses were completed in R (R Core Team 2017).

To create UDs, we used dynamic Brownian Bridge Movement Models (dBBMM) with the R package ‘move’ (Kranstauber et al. 2017). Unlike traditional kernel density estimators, a BBMM assumes temporal autocorrelation, whereby modeling probability of occurrence based on sequential, random movement paths between points, given the travel time of an animal (Horne et al. 2007). BBMMs can also handle large volumes of irregularly sampled data (Horne et al. 2007, Kranstauber et al. 2012), as occurred with the transmitter duty cycle we used for tagged curlews in our study. A *dynamic* BBMM (dBBMM) further accounts for behavioral changes by incorporating variance in Brownian Motion, ‘behavioral change points’, thus providing a more realistic and accurate depiction of animal movement (Kranstauber et al. 2012, Byrne et al. 2014). This is applicable to the curlew non-breeding season because individuals may change foraging resources, habitats, or even strategy depending on seasonal habitat conditions (Leeman and Colwell 2005, Sesser 2013).

We ran models for every individual curlew in each case where location data spanned the entire winter season (approximately July through March but sometimes including June and April), amounting to 21 individual curlews. We considered the first and last location in the non-breeding area the start and end of the winter season, respectively. When tracking data included stopover sites or in-flight locations, we excluded those data. Most curlews in our study traveled directly to non-breeding season areas with no extended staging, however, several individuals made extended stops upon reaching the wintering grounds, but then moved to a ‘final’ wintering area within approximately two weeks. Our analyses used the final wintering areas for these individuals. We discuss both final, and full season measurements in our results.

We preprocessed data with the Douglas Argos-Filter Algorithm in Movebank to remove duplicates and location errors (Douglas et al. 2012). We filtered location data to retain only locations with an estimated error radius less than 500m, resulting in an average of 552 locations (± 71m SD; range 427 – 745m) per individual, per season. Conservatively, we used the average estimated error radius for filtered points (226 ± 8m SD; range 207 − 238m) in models because we did not have *in situ* estimates. Prior studies have indicated that BBMM home range size estimates are robust to variable GPS location error values (Fischer et al. 2013; who found home range size estimates differed by less than 1.5% when they changed estimated error from 15m to 30m to 50m), and dBBMMs have previously been used to analyze migration from less accurate ARGOS-derived locations (Palm et al. 2015). Based on the transmitter schedule and *a priori* behavioral assumptions suggested by Kranstauber et al. (2012), we selected a window size for dBBMMs spanning approximately 10 days, and window margins approximately one-quarter to one-third of the window size. We parameterized models to produce UDs with spatial resolutions of 300m^2.

We calculated home range size by delineating 95% isopleth contours based on UDs again using the ‘move’ package in R (Kranstauber et al. 2017). In the same manner, we delineated the 50% isopleth, defining this contour as the ‘core use’ area. The 95% and 50% contours refer to the percentage of the total volume of the utilization distribution (i.e., 95% of the time, the animal can be expected to be located within the delineated range), and are commonly used to define home- and core ranges (Anderson 1982, Kie et al. 2010). In ArcMap, we calculated the area within home range and core use contours for each curlew (ESRI 2017).

We quantified inter-annual site fidelity for curlews with two or more complete winter seasons with a Utilization Distribution Overlap Index (UDOI), an assessment of the degree of similarity of space use between two UDs. An index score of 0 indicates no overlap, a value of 1 indicates high overlap and uniform distributions, and values greater than 1 indicate high overlap and non-uniform distributions (Fieberg et al. 2005). We carried out intermediate steps with QGIS and ArcMap, and followed procedures to calculate UDOI based on Fieberg et al. (2005). For statistical analyses of UDOI and home range size, we compared values among wintering areas, habitat type (i.e., coastal or inland, inland consisting almost entirely of agricultural lands but a few individuals also used grasslands), and sex. For individuals with more than one season of data, we used average of all seasons to calculate home range size, and the average of consecutive-year pairs to calculate UDOI. With the 50% isopleth, we compared the number of distinct core use areas by habitat type as an assessment of dispersion on the wintering grounds.

We tested for normality with Sharpiro-Wilk's Test, and used Levene's Test to examine homogeneity of variance. When data were not normally distributed, and variance was homogenous we used the non-parametric Wilcoxan-Mann-Whitney test. When data were normally distributed, but variance and sample sizes were unequal, we used Welch's t test because of better performance under these circumstances than Wilcoxan-Mann-Whitney tests (Fagerland and Sandvik 2009). In cases where sample size was inadequate for statistical tests, we present means and standard error.

Results

Wintering Home Range and Core Use

We tracked 21 unique individuals, which included 12 females and 9 males. Mean non-breeding season duration was 269 (± 11 SD) days and ranged from 249 to 288 days. Long-billed Curlews tracked from Intermountain West breeding areas migrated to dispersed coastal areas along the Gulf of California and the Baja Peninsula of Mexico (n=5); condensed, but distal regions of inland Central Mexico (n=2); and two key agricultural areas the Central Valley in California (n=7) and the neighboring Imperial/Mexicali Valley in California and Mexico (n=5; FIGURE 2.2). Three males split the winter season between agricultural areas in the Imperial/Mexicali Valley and coastal areas in the Gulf of California. One did not follow the same cross-habitat pattern for the two winters he was tracked; his second winter is included in the Imperial/Mexicali Valley sample. Home ranges were dominated by agriculture in all three inland wintering areas.

Coastal wintering areas included beaches, coastal lagoons, and tidal mudflats on the west coast of Mexico and the Baja Peninsula.

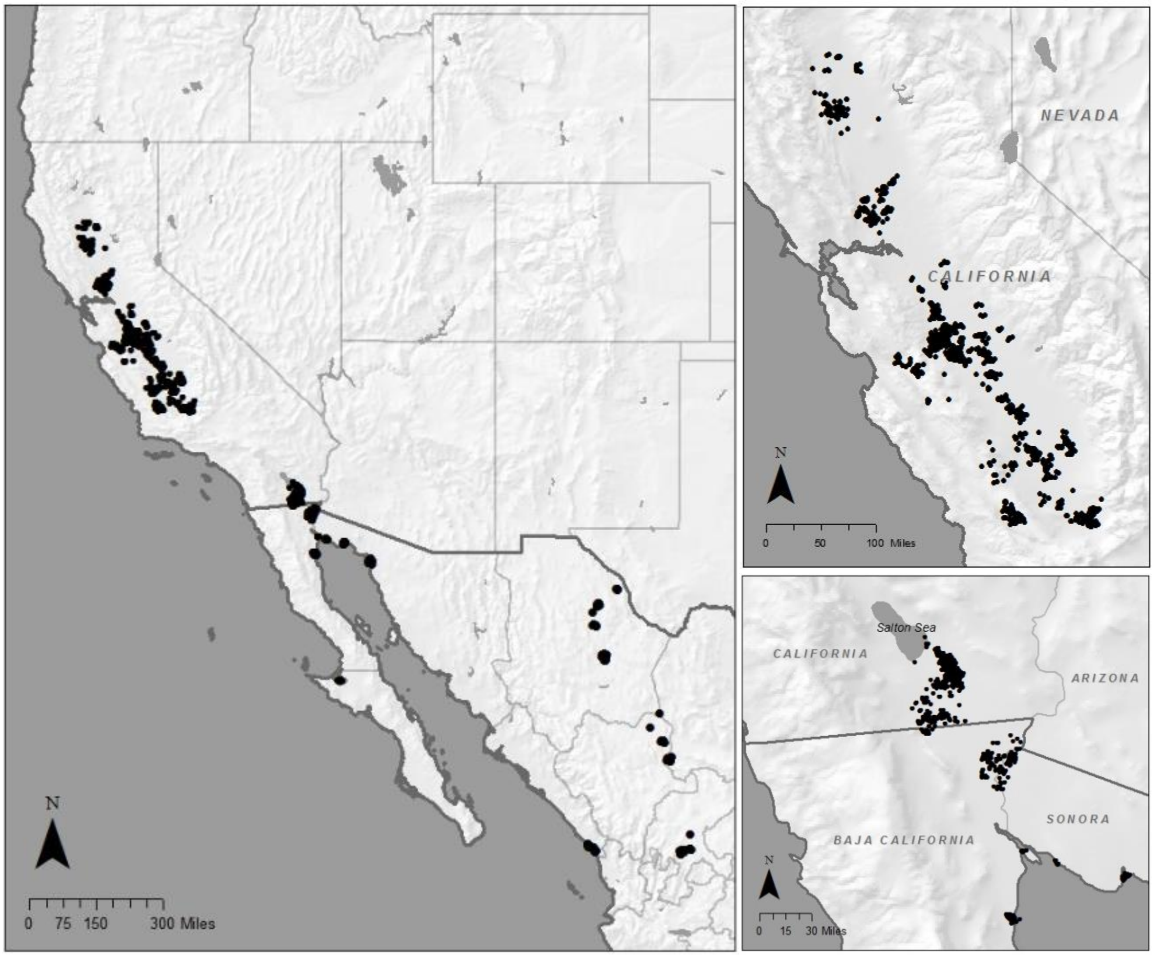

Figure 2.2 High-quality location points (error radius <500m) for wintering Long-billed Curlews tracked from Intermountain West breeding sites.

Home range size ($\bar{x}$ ± SE) ranged from 157.9 ± 50.7 km^2 in coastal Mexico and Baja to 6042.3 ± 1337.1 km^2 in the Central Valley of California. Home range sizes in the Imperial/Mexicali Valley and Inland Mexico were intermediate, at 1421.0 ± 172.9 km^2 and 1943.8 ± 810.9 km^2, respectively. Core use areas comprised approximately 6% of total home range area and varied in size from 7.5 ± 1.4 km^2 in coastal Mexico and Baja Peninsula, to 351.0 ± 81.7 km^2 in the Central Valley, with the Imperial/Mexicali Valley

(110.8 ± 8.9 km^2) and inland Mexico (89.9 ± 14.8 km^2) also intermediate in this measure (FIGURE 2.3).

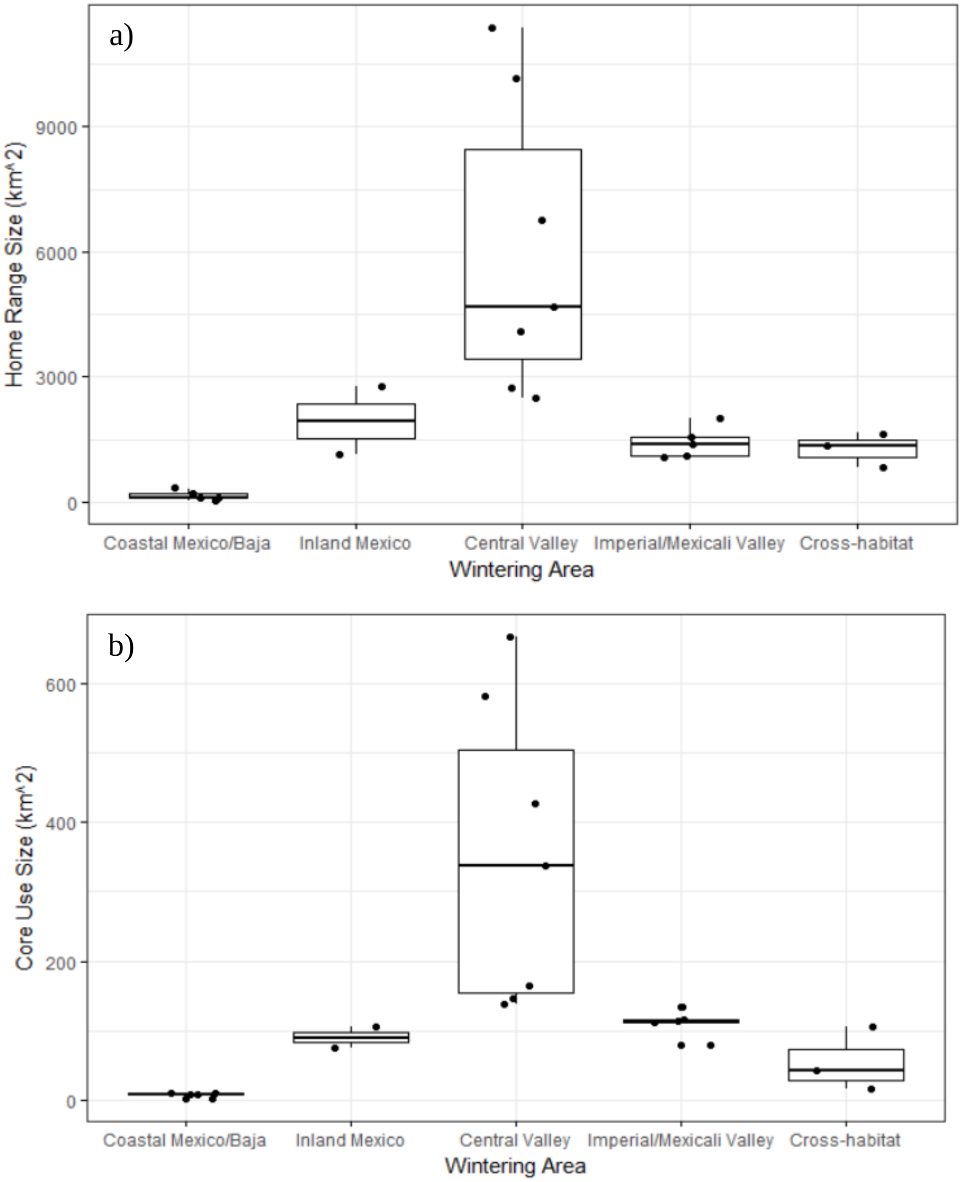

Figure 2.3 Non-breeding season a) 95% isopleth home range and b) 50% isopleth core use size for Long-billed Curlews in the wintering California and Mexico.

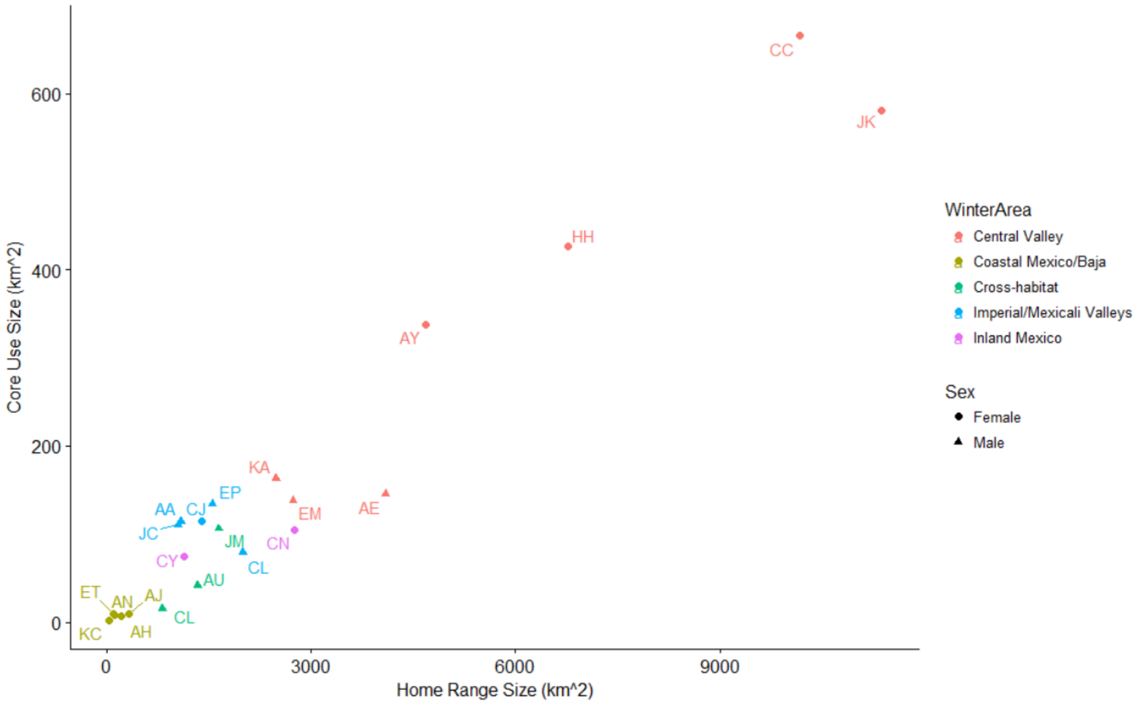

Figure 2.4 Home range and core use area comparisons for Long-billed Curlews in different non-breeding season areas; two-letter codes indicate letters on alpha flags for each bird.

Home range size was associated with habitat type and sex. Curlews wintering in coastal areas in the Gulf of California and along the Baja Peninsula had significantly smaller home ranges than curlews wintering in inland, predominantly agricultural, areas (coastal $\bar{x}$ = 158 km^2, inland $\bar{x}$ = 3806 km^2; Wilcoxon W = 0, $p < 0.001$; FIGURE 2.5). The number of distinct core use areas within a home range during a season was also significantly less for coastal birds than for inland birds (coastal $\bar{x}$ = 1.1, inland $\bar{x}$ = 5.1; Wilcoxon W = 0, $p < 0.01$; FIGURE 2.6). In the Central Valley, where we had adequate sample size for each sex (four females and three males), we found that females had significantly larger home ranges than males (Central Valley female $\bar{x}$ = 8244 km^2, Central Valley male $\bar{x}$ = 3106 km^2; Welch's t = 3.18, df = 3.60, $p < 0.05$).

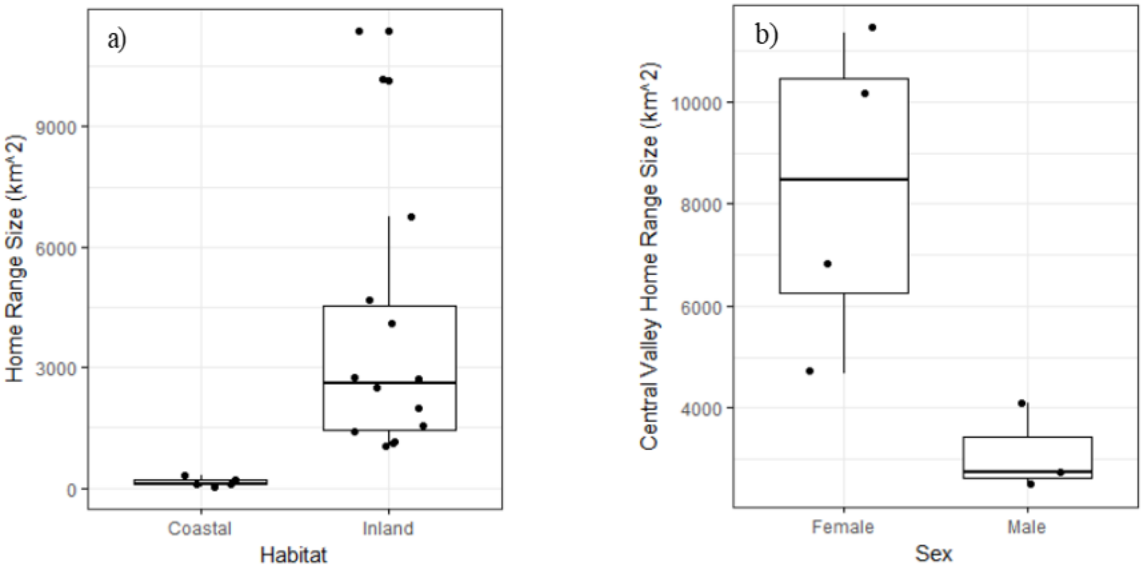

Figure 2.5 **Size of 95% isopleth home range for Long-billed Curlews a) wintering in coastal versus inland areas and b) comparing home range size of Central Valley females to Central Valley males. Home range size was significantly greater for curlews wintering inland and for Central Valley females, than for coastally wintering birds and Central Valley males.**

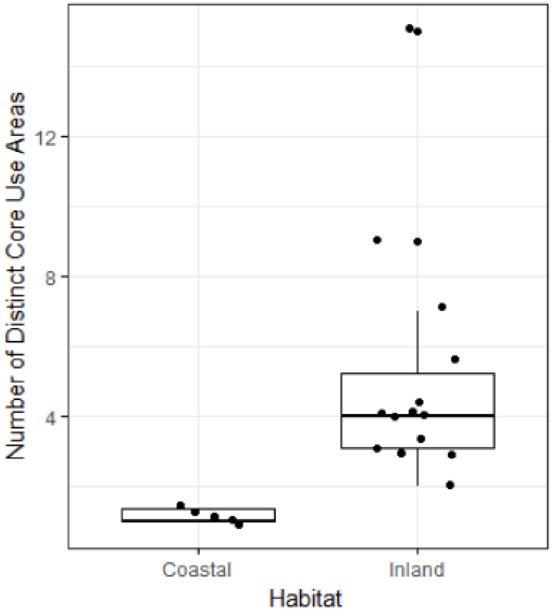

Figure 2.6 **Number of distinct core use areas for Long-billed Curlews wintering in coastal and inland habitats.**

Males with cross-habitat winter patterns (n = 3) consistently made only one move between the Gulf of California and the Imperial/Mexicali Valley, and their spatial distribution within these areas tracked expected patterns based on other coastal or Imperial/Mexicali-wintering birds. Alpha flag individuals AU and CL spent July to November and July to December in restricted coastal areas before moving north to cover broad areas of agricultural habitat for the remainder of winter and departing the wintering grounds in April. Alpha flag individual JM moved within the Imperial Valley from July to February, and then shifted south to a small coastal area until spring migration in April. Average home range size for the separate coastal and inland portions of the cross-habitat winter were similar to full-season averages found in the same winter areas. In the coastal portion of the season, average home range size was 57 km^2 (full-season $\overline{x}$ = 158 km^2) and 1253 km^2 for the Imperial/Mexicali Valley portion (full-season $\overline{x}$ = 1421 km^2).

Site Fidelity: Utilization Distribution Overlap Index

Curlews had high degrees of inter-annual UD overlap in all wintering areas (Appendix B.1 for all inter-annual UDOI values). For curlews tracked at least two winter seasons, the mean inter-annual UDOI was 4.96 (n = 14; SD = ± 3.53). Mean UDOI was highest for curlews wintering in coastal areas of Mexico (n = 5, 7.69 ± 3.66), lowest for curlews in the Imperial Valley (n = 3, 2.06 ± 1.67) and inland Mexico (n = 2; 2.83 ± 1.50), and intermediate UDOI values in the Central Valley UDOI averaged 4.80 ± 3.09 (n = 4; FIGURE 2.7). UDOI values were not significantly different between sexes (Welch's t = 1.25, df = 9.23, p-value = 0.24; FIGURE 2.8), habitat type (Welch's t = 2.31, df = 6.15 p-value = 0.06; FIGURE 2.8), or amongst sexes grouped by habitat (ANOVA, $F_{2,11}$ = 3.06, p = 0.09; FIGURE 2.9). Most UDOI values were greater than one, indicating high overlap and non-uniform distribution (Fieberg et al. 2005). The single UDOI value below one was the overlap of 'CL', who split the winter between in the Imperial/Mexicali

Valley and the Gulf of California one year, and spent the entire winter in the Imperial/Mexicali Valley during the following year.

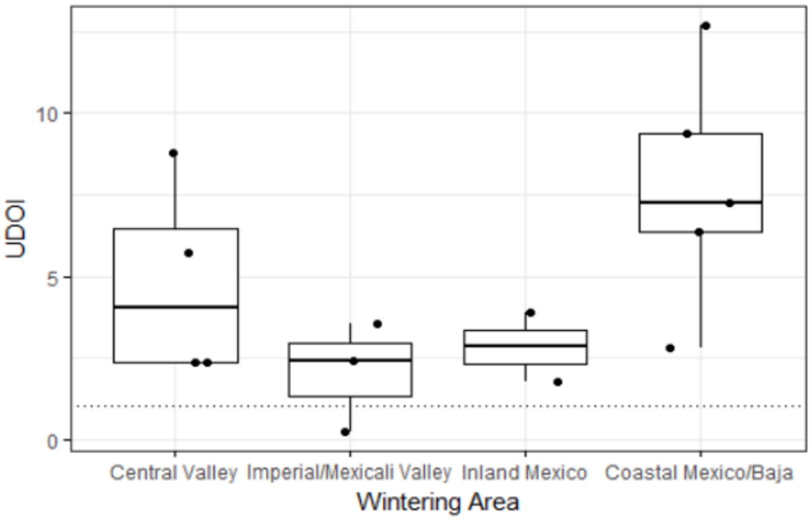

Figure 2.7 Inter-annual UDOI for Long-billed Curlews in California and Mexico wintering areas. For individuals tracked three seasons, we used the average of consecutive seasons for analyses.

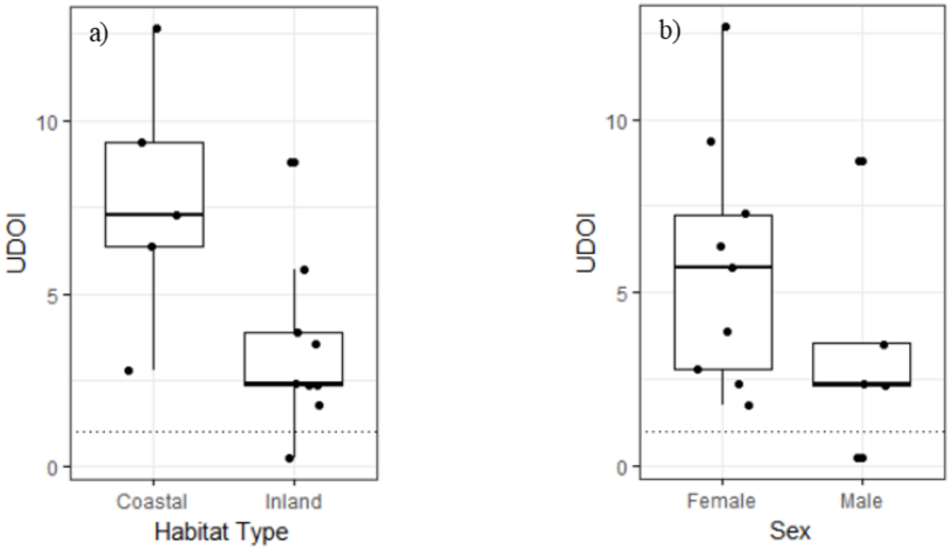

Figure 2.8 Average inter-annual UDOI scores for a) coastal and inland habitats and b) female and male Long-billed Curlews. For individuals tracked three years, we used the average of UDOIs from consecutive years. All UDOI values were greater than one (dotted line), indicating a high degree of home range overlap between years.

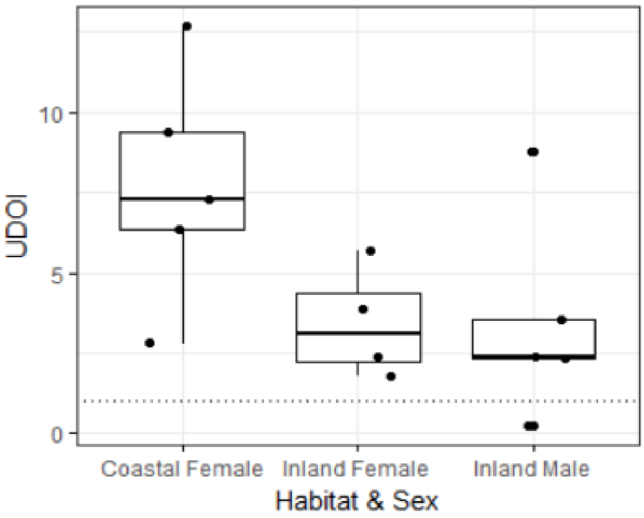

Figure 2.9 Inter-annual UDOI for Long-billed Curlews grouped by sex and habitat type. For individuals tracked three years, we used the average of consecutive years. No male curlews were tracked for more than one year in coastal areas.

Discussion

The curlews we studied from the Intermountain West wintered in a number of geographically distinct locations. These included dispersed coastal areas along the Gulf of California and the Baja Peninsula of Mexico; condensed, but distal regions of inland Central Mexico; and two key wintering areas in California: the Central Valley and Imperial/Mexicali Valley. We found key differences in spatial distribution in coastal areas compared to inland areas. Specifically, curlews in coastal areas had smaller home ranges and used fewer core use areas than curlews in inland wintering grounds. Though we did not find statistically significant differences in site fidelity, UDOI values were higher on average for coastal birds. Our research fills a migratory connectivity knowledge gap for curlews breeding in the Intermountain West. To create a holistic picture of curlew life history and management concerns, we will couple these findings with a discussion on spatial distribution across wintering grounds as a way to set the stage for future mapping of range-wide migratory connectivity for curlews.

Home Range and Core Use Size

Upon arrival at their non-breeding grounds, we found that curlews exhibited a significant difference in home range size depending on where they were wintering. Home ranges varied in size between 158 km^2 in coastal areas and 6042 km^2 further inland. While winter home range values for inland curlews have been documented (Sesser 2013, Kerstupp et al. 2015) and fall approximately within the range that we report here, this study is the first to report home range size for coastal, non-breeding curlews. Curlews wintering in inland areas utilized much larger home ranges and showed more movement throughout the non-breeding season, presumably tracking patchy resources on agricultural lands, whereas coastal-wintering birds were apparently able to meet energetic requirements in relatively small home ranges.

Inland areas have been modified from historical habitats, but irrigated agricultural fields may provide a functional equivalent for lost wetland habitats (Elphick 2000), and a wealth of research indicates these substitute habitats play an important role for wintering curlews (Dugger and Dugger 2002, Shuford et al. 2013, Sesser 2013, Kerstupp et al. 2015). For example, in the southeastern Chihauhuan desert, Kerstupp et al. (2015) found tagged curlews in agriculture and fallow fields 50% of the time, and in the Central Valley, curlews were highly associated with irrigated alfalfa and irrigated pasture (Shuford et al. 2013, Sesser 2013).

The difference in home range size between coastal and inland curlews is likely associated with a dichotomous behavioral system, where individuals in coastal areas (smaller home range) display much greater territoriality (Colwell and Mathis 2001) than individuals observed inland (larger home range) who tend to demonstrate flocking behavior (Shuford et al. 2013, Kerstupp et al. 2015), presumably in search of patchy food resources. In many species, territoriality and home range size can be related to food abundance and the size of a home range is generally predicted to decline as food abundance increases (Imre et al. 2004). This may be the case with curlews given that mudflats in coastal regions of California and Mexico likely have consistently productive invertebrate communities whereas food abundance at inland sites can be temporally fleeting depending on crop rotation and irrigation schedules (Shuford et al. 2002, Arias et al. 2003, Shuford et al. 2013).

Although food abundance can be a primary explanatory factor in territoriality, this is likely mediated by a suite of interacting variables that function at multiple scales. For example, at the territory scale, use of estuary and tidal mudflats by shorebirds is correlated with body size as well as prey abundance and distribution, which in turn is highly dependent on habitat at a fine scale (Bryant 1979, Mathis et al. 2006). Territoriality is also more common in some taxa of *Charadriformes* shorebirds than others, and it has been suggested that this may be the result of visual versus tactile detection of prey (Colwell 2000). Morphological differences should also be considered as Townshend (1981) observed that male Eurasian Curlews with shorter bills moved to nearby fields to forage while longer-billed females remained in estuaries when prey availability decreased, and burrows of primary prey deepened in intertidal areas. Finally, juvenile Long-billed Curlews appear to be non-territorial, suggesting age may be an additional factor in spatial distribution patterns (Colwell and Mathis 2001, Mathis et al. 2006).

In contrast to strong territoriality, flocking curlews exhibit similar patterns of distribution across agricultural areas as documented for some marine organisms; high site fidelity, but opportunistic foraging in patches of prey abundance within those home ranges (Arthur et al. 2015, Wakefield et al. 2015). Habitat-driven prey abundance, age, and, to some extent, sexual dimorphism of bill length or body size may determine foraging strategy. At a large scale, we suspected patchy concentration and ephemeral abundance of prey in inland agricultural fields would play a larger role than age or sex, following behavioral threshold theories based on resource abundance and energy economics (Gill and Wolf 1975, Carpenter and MacMillen 1976, Frost and Frost 1980). In support of a resource-driven spatial distribution, we found three curlews during our study that split the winters between a strategy of territoriality in the Colorado River delta, and a foraging flock in the Imperial/Mexicali Valley. At a finer scale, sexual dimorphism in curlews and foraging opportunities in mudflats compared to intertidal coastal areas may influence individual strategies. Based on diet studies, larger-bodied female curlews wintering in inland areas would need to spend the greatest proportion of the day foraging; approximately 15.2 hours per day, compared to intertidal coastal areas where females would require approximately 12.2 hours per day of foraging and smaller-bodied males would meet energetic demands in approximately 10.5 hours per day (Dugger and Dugger 2002, Leeman et al. 2001, Leeman 2000). It would be valuable to quantify spatial and temporal aspects of food availability in coastal versus inland areas to verify hypotheses about what drives the territoriality versus flocking strategies employed by curlews in each habitat type.

Except for three curlews tracked by Kerstupp et al. (2015), our research is the first known transmitter-based home range analysis for curlews outside of California's Central Valley and, importantly, the only transmitter-based analysis in coastal areas to date. It is also the first to use dynamic Brownian Bridge Movement Models (dBBMMs) with Long-billed Curlews. Despite different approaches to creating UDs, our 50% core use area estimates for curlews wintering in the Central Valley are comparable to Sesser (2013) who calculated Kernel Density Estimates (KDE) divided into 'wet' and 'dry' seasons for 90% home ranges (as opposed to the 95% isopleths we used) and 50% core use areas. We loosely compared our 50% core use area results to Sesser (2013) by summing reported wet and dry season areas. Total core use area in Sesser (2013) ranged from $53 - 895$ km^2 (n = 10), compared to a similar range of $90 - 773$ km^2 for Central Valley birds (n = 7) in our study. Estimates we derived from Sesser (2013) may overestimate core use area size in relation to our results because we did not account for overlap between dry and wet seasons when we summed seasonal home range values from the study. However, in general, utilization distributions calculated from dBBMMs rather than KDEs may increase home range area estimates due to bridged connections between areas of high use created by dBBMMs that are not represented similarly by KDE's (Horne et al. 2007). Regardless, the use of newly available dBBMMs rather than KDE's is a step toward maximizing the usefulness of high volume transmitter data and creating more biologically accurate depictions of animal movement patterns (Horne et al. 2007, Kranstauber et al. 2012, Fischer et al. 2013).

Site Fidelity

We found very high inter-annual wintering site fidelity for individual curlews, with coastally wintering birds returning to the same, and relatively small, home ranges year after year. Curlews wintering in inland areas also returned to similar home ranges year after year, and core use areas within home ranges frequently overlapped. Our results that curlews have high wintering site fidelity regardless of habitat type is surprising, particularly for expansive and dynamic agricultural areas. While a utilization distribution overlap index is a more informative method than other methods of overlap which overlook intensity of use or have less discriminatory power (Fieberg et al. 2005), the technique is relatively new, and thus it is a challenge to make equivalent comparisons within the limited existing literature on the topic. Other studies have observed moderate or high inter-annual overlap for curlews. Sesser (2013) found a mean inter-annual VI (Volume of Intersection; scale of 0-1) of 0.48 for diurnal observations in the Central Valley, and Kerstupp et al. (2015) tracked a single male in the southeastern Chihuahuan desert who returned to the same foraging and roosting areas for three seasons.

High site fidelity in coastal territories compared to inland areas would fit with patterns of high fidelity to breeding ground territories, but we found no statistically significant differences between non-breeding habitat types. However, our sample size may yet be too small to discern differences, and comparisons between estimates with a high degree of UD overlap such as we found in our study may be irrelevant, as many UDOIs were greater than one (with one being complete overlap and uniform distribution, and values greater than one indicating high overlap and non-uniform distribution). As such, the difference in degree of overlap between two UDOI values which are both greater than one may not be biologically meaningful. Male curlews with high territory fidelity on the breeding grounds (Redmond and Jenni 1982) appear to remain faithful to territories despite habitat degradation (e.g., anthropogenic disturbance in breeding areas; Redmond and Jenni 1986, Pollock et al. 2014). This suggests curlews have strong site fidelity throughout the annual cycle, which is concerning if curlews stay in degraded habitat instead of seeking higher quality habitat. In response to habitat quality changes, wading bird species with high site fidelity may show changes in local abundance before contractions or expansions in range (Méndez et al. 2017). Thus, long-term monitoring of abundance and habitat quality in identified key wintering areas is particularly valuable for curlew conservation.

Conclusions

Given the complexity and spatial extent of the non-breeding season, and the necessity of linking the complete annual cycle, model simulations will be crucial for rapid development of effective management solutions in the face of realized or new threats. Individual-based models have been used to predict population-level response of shorebirds in response to loss of habitat (Durell et al. 2005), rising sea levels associated with climate change (Sutherland 1996, Goss-Custard and Stillman 2008), and anthropogenic disturbance (Stillman et al. 2007, West et al. 2007). Furthermore, being able to examine outcomes under different modeled scenarios facilitates the development of management strategies with the potential to mutually benefit wildlife and industry (e.g., Oystercatchers and shellfish industry; Caldow et al. 2004). As such, future research directions should fill in remaining gaps needed to model population dynamics under different circumstances (Stillman and Goss-Custard 2010, Hostetler et al. 2015).

For curlews, many diet and habitat association studies have shed light on wintering ecology (e.g., Stenzel et al. 1976; Leeman et al. 2001; Shuford et al. 2002, 2013; Mathis et al. 2006) but notable gaps include broad-scale migratory connectivity, prey availability and nutritional content, as well as disturbances, and density-dependent relationships in other parts of the winter range, particularly Mexico. However, one concern with making inferences based on satellite transmitter data is that sample sizes are commonly low because of the associated equipment costs and technical complexities of field work. Despite our study having the largest sample size of any study on tracked Long-billed Curlews, we still suggest caution when extrapolating from our results. Nevertheless, we believe our findings are generalizable for curlews in similar habitat types, as observations concurrent with tracking indicate agricultural-foraging birds occur in flocks. For example, Kerstupp et al. (2015) re-located wintering curlews with satellite transmitters and found them in flocks of 100-200, and, similarly, territorial behavior of curlews on tidal mudflats suggests that individuals defend smaller feeding territories in California (Colwell 2000, Colwell and Mathis 2001, Leeman et al. 2001, Mathis et al. 2006) and Mexico (Carlisle, pers. obs., E. Palacios and E. Soto, pers. comm.).

Describing key components of a species’ life history is fundamental for conservation efforts. Curlews that we tracked spent approximately 75% of their annual cycle on the non-breeding grounds. Duration on the wintering ground alone does not convey the importance of wintering ground research as the context of a species of conservation concern experiencing population decline in many parts of their range is reason for urgency. Moreover, regional or local population declines could be influenced by carry-over effects, necessitating an examination of linkages within broader temporal scales (Norris and Marra 2007, Harrison et al. 2011). Our research facilitates insights into declines by identifying spatial extent of home ranges and quantifying site fidelity, adding to a growing body of work on curlew wintering ecology and a clearer picture of the entire life history. Our results also highlight the importance of varied crop rotation schedules and spatial diversity of high-quality foraging areas for inland wintering sites, and the conservation of high-quality habitat in coastal wintering areas. Collaborative efforts to characterize further details for prey distribution, energetic constraints, and wintering ground threats will allow for predictive modeling and ultimately shape management strategy and conservation outcomes.

COMMENTS ON INDIVIDUALITY AND ANOMALIES

Long-billed Curlews are often described as ‘charismatic’ and while generalized trends and patterns have the capacity to dull this description, we also observed a wide range of noteworthy occurrences and individuality among curlews. On breeding grounds, hours of observations in vastly different habitats allowed detailed accounts of these behavioral, physical, and potentially physiological differences. The very nature of tracking via satellite transmitters unavoidably provided insight into individual behavior and there were several instances where curlews deviated from the ‘norm’. We recognize with further research, many of these apparent anomalies may turn out to be common. Here, we detail some of the outliers which were not discussed in either data chapter.

We noted distinct temporal variations among nesting pairs. Behaviorally-based nest searching led us to focus on incubation switches, a reliable twice-daily occurrence for nesting curlews (Dugger and Dugger 2002). These switches generally occur soon after dawn and before dusk (Allen 1980), but the more specific patterns of incubation switch timing seemed dependent on the tendencies of curlews in the area, and varied by pair. When not on incubation duty, usually during the night, females in our study often left their nesting territories and foraged in agricultural areas or near water. Close to sunrise, the females tended to depart from these foraging places at nearly the same time, meaning incubation switch timing was somewhat synchronized for areas with one central foraging location. Evenings had more spread in incubation switch timing, but we noticed the timing was often consistent for a pair, supporting the observations of Allen (1980).

When eggs hatched, they sometimes were synchronized and all hatched the same day, but other times the eggs hatched one at a time, one egg per day. With asynchronous hatching, one adult usually continued incubation while the other tended to the chicks nearby. Asynchronous hatching occurred at sites farther east, especially in Wyoming, and may have been affected by the onset of incubation occurring earlier in the laying stage or incubation temperature (Hepp and Kennamer 2018).

More frequently observed physical variations in nesting included the extent of nest-building and differences in egg coloration or shape. In southwest Idaho, nest cups were generally sparse and thinly lined with dry grass and sometimes ground squirrel feces. We sometimes saw more nesting material, usually senesced grasses, in nest cups farther east. Curlews conduct nest-building by tossing materials into the nest cup from a standing position either within the nest cup or from a short distance away (Allen 1980). We never observed curlews tossing nest materials from more than approximately one meter away, and it is possible that the discrepancy in nest-building extent was a result of availability of loose materials close to the nest cup. Egg coloration and shape is varied (Allen 1980). Curlew eggs are speckled and we saw base colorations ranging from bluish-green, green-brown, tan, to pink-brown (one occurrence), all with varied degrees of darker brown maculation (Pictures 1–5). Brown pigmentation is associated with protoporphyrin, a compound thought to enhance structural strength of eggshells and derived from calcium availability in the environment, while blue-green pigmentation is associated with biliverdin pigment and positively correlated with female condition (Cherry and Gosler 2010). Eastern bluebirds lay blue-green, white, or pink eggs and Siefferman et al. (2006) suggested pink and white coloration could be the effect of genetic mutations which inhibit the production or deposition of biliverdin. Eggs within clutches are usually similar in shape relative to inter-clutch variation (Redmond 1986), but the exception would often be a single, more spherical egg. Curlews organized their clutch with their bills using a stirring motion, and eggs tended to be arranged in a star shape, narrower pyriform-end inward. As a means of determining the status of a nest which we suspected may have been abandoned, we rearranged eggs opposite this preferred pattern and checked if curlews had made adjustments in subsequent visits.

Picture 1. **Blue-green curlew egg coloration with larger dappled maculation. Flat Ranch, Island Park, ID. May 2015. Photo credit: Hattie Inman.**

Picture 2. **Blue-green curlew egg coloration with uneven maculation. ACEC, southwest ID. May 2015. Photo credit: Stephanie Coates.**

Picture 3. **Brownish-green curlew egg coloration with fine, evenly distributed flecks. Big Creek, Pahsimeroi Valley, ID. May 2017. Photo credit: Ben Wright.**

Picture 4. Tan curlew egg coloration, with one egg pipping. ACEC, southwest, ID. June 2016. Photo credit: Stephanie Coates.

Picture 5. Curlew egg coloration with pink hues. National Elk Refuge, Jackson, WY. May 2016. Photo credit: Erica Gaeta.

We encountered several abnormal nesting cases. For example, in one three-egg clutch, we noticed a small piece of woody debris, roughly half the volume of an egg, which seemed to be serving as a spacer. The eggs were arranged in the pattern of a more typical four-egg clutch (Picture 6) and the woody debris remained in the nest cup for at least a week. We saw something similar in one other instance (Picture 7), though the debris did not appear to be keeping the eggs in a specific arrangement and may have been incidental. Rarely, we documented five-egg clutches, thus far only at the Flat Ranch in eastern ID, and in the Upper Green River Basin in western WY. In another infrequent case, a male curlew died during the incubation stage (necropsy suggested small mammal depredation), and the female subsequently abandoned the nest, and re-nested with a neighboring male. The female and deceased male were both recognizable by alpha flag leg-markings. This occurred at a site which, based on numerous unpaired males displaying throughout the season, had an unbalanced sex-ratio. Alternatively, at the same breeding area when a female with a transmitter died of unknown causes, her mate with a transmitter, failed to nest that season. At five different nests in southwest Idaho during 2016, we noticed dented eggs. The dents were shallow and dime-sized or smaller in circumference (Picture 8). Dented eggs in other years or at other sites may have been overlooked because we were not aware to look for dents, and because often we inspected the eggs and visited the nest only once, usually shortly after the eggs had been laid. Blus et al. (1985) detected DDE, an organochlorine pesticide implicated in eggshell-thinning, in all seven tested eggs, but determined the level insufficient to affect hatching success.

Picture 6. **Three-egg clutch of a curlew with a wood debris 'spacer'. ACEC, southwest ID. May 2015. Photo credit: Stephanie Coates.**

Picture 7. **Three-egg clutch of a curlew with a cow dung debris 'spacer'. Big Creek, Pahsimeroi Valley, ID. May 2017. Photo credit: Ben Wright.**

Picture 8. Dent in a Long-billed Curlew egg. ACEC, southwest ID. May 2016. Photo credit: Stephanie Coates.

Our research did not focus on the chick-rearing stage, but we did notice interesting behaviors by chicks and adults with chicks. When a threat is perceived, chicks typically remain motionless (Forsythe 1973), and tall, dense vegetation is important for concealing chicks (King 1978, Allen 1980, Jenni et al. 1981). We observed an adult apparently herd its chicks into taller vegetation (*Sysimbrium altissimum*) by charging at them. On a hot day in early July, we noticed a juvenile temporarily enter a badger burrow, perhaps for shelter from the heat or from our presence (Picture 9). The juvenile made repeated “peep-beep” calls prior to entering the burrow, but no adults were in the area and we found a similarly-aged depredated juvenile nearby. Based on Forsythe (1970) and context, we presume the calls were contact calls.

Picture 9. **Badger burrow which a juvenile curlew entered and remained for approximately 15 minutes. ACEC, southwest ID. July 2016. Photo credit: Stephanie Coates.**

Satellite transmitter data highlighted differences in individual migration strategies, and movement patterns that bent breeding site fidelity ‘rules’. In general, curlews breeding in Idaho completed a non-stop migration or made a brief stopover, less than a day in length. Curlews breeding in Montana and Wyoming, however, sometimes had extended stops of several days to approximately two weeks on the journey south, matching patterns described by Page et al. (2014) for curlews breeding in Montana, Nevada, and Oregon. We documented 5 mortalities during migration, and through transmitter recovery efforts, attributed at least two of the deaths to Peregrine Falcon depredation. One curlew possibly lent insight to navigation mechanisms of curlews when she wintered on the Pacific coast of the Baja Peninsula in 2015-16, and then the following winter appeared to follow the western coast of mainland Mexico south to the same latitude. She remained at the mainland Mexico location for approximately two weeks before flying due west to the same wintering location of 2015−16. This pattern suggests the ability to detect latitude as well as some means of determining longitude. Another female made an extended stop during migration in Montana, approximately 100 miles from the breeding area where she nested and was captured. The following breeding season she returned to her original breeding area for only a few days before flying to the location where she had made the extended stop. Ultimately, she nested in the new location. Page et al. (2014) also described several instances of deviations from general migration patterns and undoubtedly, future transmitter work will reveal further atypical events.

Recognizing individuality and describing what may appear to be atypical patterns is important for curlew conservation in several ways. First, for some understudied areas of curlew research (e.g., migration), we are still in the process of assessing what is typical. Second, should some of these documented cases turn out to be widespread, they could point to problematic conservation issues. For example, dented eggs could suggest cumulative or acute pesticide exposure if dents are a result of thinned eggshells. Third, fine details added to behavioral descriptions could aid future research, either in terms of field methodology, or research directions. We acknowledge that our capacity to find nests was enhanced through accounts of incubation switches and nesting behavior. Finally, public outreach and education is a critical component of curlew conservation, and in our experience, it is specific stories, examples, and oddities, which resonate with people. Research approaches which retain naturalist styles of anecdotal accounts may help keep sight of some of the reasons which make curlews so compelling and distinctive.

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APPENDIX A

Breeding Supplemental Information

A.1 Location, ownership, vegetation, and land use characteristics of Long-billed Curlew study areas in 2015 and 2016.

Site Name	Subsite or Focal Area	Nearest Town, State Lat, Long Elevation (m/ft)	Land Ownership	Dominant Vegetation	General Habitat and Land Use During Nesting Season:
Long-billed Curlew Habitat Area of Critical Environmental Concern (ACEC)	Emmett A Focal	Emmett, ID 43.8N,-116.6W 820m/2700'	Bureau of Land Management (BLM)	*Bromus tectorum, Poa secunda, Taeniatherum caput-medusae, Elymus elymoides, Sisymbrium altissimum, Amsinckia sp., Vulpia myuros*	Arid annual grassland with dispersed cattle grazing, some OHV recreation, frequent target and ground squirrel shooting.
Long-billed Curlew Habitat Area of Critical Environmental Concern (ACEC)	Emmett B Focal	Emmett, ID 43.7N,-116.6W 810m/2700'	Bureau of Land Management (BLM)	*Bromus tectorum, Poa secunda, Elymus elymoides, Sisymbrium altissimum, Amsinckia sp., Vulpia myuros*	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 1780m/5800'	Private	*Medicago sativa, Triticum sp., Taraxacum officinale, Bromus tectorum, Poaceae, Brassicaceae*	Center-pivot agriculture adjacent to sagebrush steppe and cattle pastures.
Pahsimeroi Valley	Goldburg	May, ID 44.4N, -113.6 1900m/6200'	Private	*Carex spp., Juncus spp., Poaceae, Trifolium spp., Taraxacum officinale, Polygonum bistortoides, Salix sp.*	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 1950m/6300'	Private, State, and BLM	*Poa pratensis, Artemisia tridentata, Wyethia sp., Potentilla cracilis, Achillea millefolium, Aster spp., Taraxacum officinale, Lupinus sp.,*	Sagebrush steppe with pockets of irrigated wet meadows. Occasional access by landowners via OHV, and some grazing.

A.1 Continued.

Site Name	Subsite or Focal Area	Nearest Town, State Lat, Long Elevation (m/ft)	Land Ownership	Dominant Vegetation	General Habitat and Land Use During Nesting Season:
Island Park	Flat Ranch	Island Park, ID 44.6N, -111.3W 1960m/6400'	The Nature Conservancy (TNC)	*Phleum pratense, Alopecurus pratensis, Poa pratensis, Taraxacum officincale, Potentilla gracilis, Achillea millefolium, Wyethia helianthoides, Trifolium spp., Sysyrinchium montanum, Carex 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 (NER)	Jackson, WY 43.5N, -110.7W 1940m/6400'	Federal	*Bromus inermus* Leyss., *Stipa comata, Agropyron cristatum* (L.) Gaertn., *Alyssum alyssoides, Taraxacum sp., Elymus trachycaulus, Festuca idahoensis, Poaceae, Hesperostipa comata, Medicago sativa, Tragopogon dubius, Phlox hoodii, Chrysothamnus vicidoflorus*	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 2300m/7500'	Private	*Phleum pratense, Agrostis palustris, Poa pratensis, Carex spp., Juncus spp., Taraxacum officinale, Potentilla sp., Trifolium spp.*	Flood-irrigated hay pasture, bullpens, cattle grazing
Upper Green River Basin	New Fork	Pinedale, WY 42.9N, -109.9W 2200m/7200'	Private	*Phleum pratense, Agrostis palustris, Poa pratensis, Carex spp., Juncus spp., Taraxacum officinale, Trifolium spp.*	Flood-irrigated hay pasture, bullpens, cattle grazing

A.2 Initiation date summary in 2015 and 2016 for Long-billed Curlew nests.

			Initiation Date		
Year	**Site**	**N**	**Mean**	**Median**	**Range**
2015	ACEC, ID	26	1-May	25-Apr	11 Apr to 27 May
	Upper Green River Basin, WY	25	10-May	7-May	27 Apr to 03 Jun
	Island Park, ID	13	6-May	4-May	25 Apr to 16 May
	Pahsimeroi Valley, ID	17	2-May	28-Apr	20 Apr to 27 May
2016	ACEC, ID	24	1-May	29-Apr	14 Apr to 22 May
	National Elk Refuge, WY	6	14-May	21-May	28 Apr to 27 May
	Pahsimeroi Valley, ID	17	5-May	30-Apr	19 Apr to 01 Jun

A.3 Long-billed Curlew density per square km in focal nesting areas during 2015 and 2016.

		Long-billed Curlews per km^2 (SE)	
Site	**Focal Nesting Area**	**2015**	**2016**
ACEC, ID	Emmett A Focal*	1.23 (0.32)	0.39 (0.20)
ACEC, ID	Emmett B Focal*	0.91 (0.35)	0.14 (0.10)
Pahsimeroi Valley, ID	Big Creek	2.74 (1.08)	2.30 (0.94)
Pahsimeroi Valley, ID	Goldburg	7.29 (2.62)	6.22 (2.61)
Island Park, ID	Flat Ranch	14.43 (2.26)	–
Island Park, ID	Shotgun Valley Focal*	2.70 (0.93)	–
Jackson, WY	NER	–	1.27 (0.62)
Upper Green River, WY	Horse Creek	9.69 (1.75)	–
Upper Green River, WY	New Fork	2.72 (0.74)	–

*Smaller parcel within subsite delineated as a focal nesting area.

A.4 Qualitative assessment of mammalian predators and anthropogenic disturbance within each subsite focal area. Some incidental sightings, especially for of mammalian predators, are presumed to be underestimates as we suspect sightings were under-reported, and crew presence varied.

Site: Subsite or Focal Area	Crew Size and Effort	Mammalian Predators: Approx. Frequency of Incidental Sightings	Anthropogenic Disturbance: Approx. Frequency of Incidental Sightings	Roads/Trails: Vehicular Impact and Access
ACEC: Emmett A Focal	2-3 people 7 days/week	Badger: 1/day Coyote: 1/week Dog: 1/season Long-tailed weasel: 2/season	Off-road travel: 2/month On-road OHV: 1/week Shooters: 3/week	» Public and rancher access via several unimproved dirt roads ~2 miles from paved road and through multiple barbed wire cattle pasture gates
ACEC: Emmett B Focal		Badger: 1/week Coyote: 1/month	Off-road travel: 3/month On-road OHV: 3/week Shooters: 1/day Trash dump sites: >10 in site	» Public access via paved road with traffic flow of ~1 vehicle/min » Many frequently-used OHV trail networks
Pahsimeroi Valley: Big Creek	1 person 5 days/week	Coyote: 2/month	Off-road travel: 1/season	» 2-lane paved road through area with traffic flow of ~2 vehicles/hour
Pahsimeroi Valley: Goldburg		Badger: 1/season Coyote: 1/week	On-road OHV: 1/month Off-road travel: 1/season	» 2-lane paved road through area with traffic flow of ~2 vehicles/hour
Island Park: Shotgun Valley	1-2 people 5 days/week	Coyote: 1/month Fox: 1/season	On-road OHV: 1/month Off-road travel 1/month	» 2-lane dirt road with traffic flow <1 vehicle per hour » Several 2-track roads through site
Island Park: Flat Ranch		Badger: 1/season Coyote: 1/month Dog: 1/season	Off-road travel: 1/month (workers) On-foot ranch visitors: 2/month	» 2-lane highway to West Yellowstone adjacent to site with traffic flow of ~600 vehicles/hour » Several 2-track roads through site

A.4 Continued.

Site: Subsite or Focal Area	Crew Size and Effort	Mammalian Predators: Approx. Frequency of Incidental Sightings	Anthropogenic Disturbance: Approx. Frequency of Incidental Sightings	Roads/Trails: Vehicular Impact and Access
Jackson: National Elk Refuge (NER)	1-2 people 5 days/week	Coyote: 4/week Wolf: 3/month	Off-road travel: 1/week (workers) On-road bicycle: 15/day On-road runners/walkers: 15/day	» 2-lane highway adjacent to part of site with traffic flow of ~150 vehicles/hour » 2-lane packed gravel road through refuge with traffic flow of ~40 vehicles/hour
Upper Green River Basin: Horse Creek	2 people 5 days/week	Coyote: 6/month Dog: 3/month Skunk: 2/month	Ranch equipment use: 2/month	» 2-lane paved highway through site with traffic flow of ~5 vehicles/hour » 2-lane dirt road through site with traffic flow of <1 vehicle/hour
Upper Green River Basin: New Fork		Coyote: 1/month Dog: 3/month Skunk: 2/month	Ranch equipment use: 2/month	» 1-lane paved highway adjacent to site with traffic flow of ~290 vehicles/hour » 1-lane gravel road through site with traffic flow of ~5 vehicles/hour

APPENDIX B

Wintering Supplemental Information

B.1 Inter-annual Utilization Distribution Overlap Index (UDOI) for Long-billed Curlews wintering in the Central Valley of California, the Imperial/Mexicali Valley of California and Mexico, coastal Mexico/Baja, and inland Mexico.

			Winter Season		
Winter Area	Winter Season	ID	2014-2015	2015-2016	2016-2017
Central Valley	2013-2014	AE	0.3070		
	2014-2015			4.3728	
	2015-2016	AY			5.7138
	2014-2015	CC		0.3160	
	2015-2016				4.4159
	2015-2016	EM			8.7773
Coastal Mexico/Baja	2014-2015	AH		9.2561	
	2015-2016				16.0855
	2014-2015	AJ		15.6933	
	2015-2016				3.0837
	2014-2015	AN		5.8802	
	2015-2016				8.6424
	2015-2016	ET			2.7977
	2015-2016	KC			6.3420
Imperial/Mexicali Valley	2014-2015	AA		2.6057	
	2015-2016				2.1751
	2015-2016*	CL			0.2473
	2015-2016	EP			3.5397
Inland Mexico	2015-2016	CN			3.8941
	2015-2016	CY			1.7738

*Cross-habitat winter compared to a single habitat winter in the 2016−2017 winter season.