RESEARCH ARTICLE

Annual migratory patterns of Long-billed Curlews in the American West

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ABSTRACT

Effective conservation of migratory species requires comprehensive knowledge of annual movement patterns. Such information is sparse for the Long-billed Curlew (*Numenius americanus*), a North American endemic shorebird of conservation concern. To test hypotheses about individual and area differences in migratory patterns across western North America, we tagged 29 curlews with satellite transmitters at breeding sites in Oregon, Nevada, and Montana. Transmissions from 28 birds for up to 4 years demonstrated that all wintered within the species' known winter range, including 9 from Oregon tracked to agricultural areas of California's Central Valley; 5 from Nevada tracked to the Central Valley, northern Gulf of California, or west coast of Baja California, Mexico; and 14 from Montana that wintered inland, from the Texas Panhandle south to the Mexican Plateau, or near the Gulf of Mexico. Montana breeders migrated east of the Rocky Mountains and traveled more than twice the distance of Oregon and Nevada breeders. Montana birds also stopped more often and longer during most passages. As a group, curlews arrived on their Oregon breeding grounds earlier than in Montana, while males preceded females in Montana and possibly Oregon. No consistent pattern emerged between sexes in departure from breeding areas, although within pairs males departed later than their mates. Individuals exhibited strong fidelity to breeding and wintering sites, and many birds showed a strong propensity for agricultural regions during winter. Our results underscore the importance of studying migration behavior across the breeding range to adequately capture variation in migratory patterns of a species.

Keywords: Long-billed Curlew, migration route, migration timing, satellite telemetry, sex differences, stopover, wintering area

Patrones de migración annual del Zarapito Americano en el oeste de los Estados Unidos

RESUMEN

La conservación eficaz de especies migratorias requiere un conocimiento amplio de sus patrones de movimientos anuales. Para el Zarapito Americano (*Numenius americanus*), un ave playera endémica norteamericana de interés para la conservación, esta información es escasa. Para probar hipótesis sobre diferencias individuales y de área en patrones migratorios a través del oeste norteamericano, marcamos 29 zarapitos con transmisores de satélite en sitios de reproducción en Oregon, Nevada, y Montana. Transmisiones de 28 individuos por un máximo de 4 años demostraron que todos invernaron dentro del área de invernada conocida para esa especie, incluyendo 9 individuos de Oregon los cuales fueron seguidos hasta áreas agrícolas en el Valle Central de California; 5 individuos de Nevada que fueron seguidos hasta el Valle Central, el norte del Golfo de California, o la costa oeste de Baja California; y 14 individuos de Montana que invernaron tierra adentro, desde el norte de Texas hacia el sur en la Meseta Mexicana, o cerca del Golfo de México. Individuos que se reprodujeron en Montana migraron hacia el este de las Montañas Rocosas y recorrieron más del doble de la distancia recorrida por individuos que se reprodujeron en Oregon y Nevada. Aves de Montana tambien pararon más frecuentemente y por más tiempo durante la mayoría de sus recorridos. Como grupo, los zarapitos llegaron a sus áreas de reproducción en Oregon más temprano que a Montana, mientras que los machos precedieron a las hembras en Montana y posiblemente en Oregon. No se observó un patrón consistente entre sexos en cuanto a su partida de las áreas de reproducción, pero dentro de parejas los machos partieron después de sus hembras. Individuos mostraron una marcada fidelidad a sitios de reproducción y de invernada, y muchas aves mostraron una propensidad por regiones agrícolas durante el invierno. Nuestros resultados resaltan la importancia de estudiar el comportamiento migratorio a través del área reproductiva para capturar adecuadamente la variación que existe en los patrones migratorios de una especie.

INTRODUCTION

The varied migration strategies of shorebirds have been the focus of considerable study and conservation interest (del Hoyo et al. 1996, Piersma 2007). One well-known strategy involves spectacular migrations across hemispheres by Arctic-breeding species that stop at only a few staging sites along their routes where they accumulate energy reserves to fuel their next long flights (Harrington 2001, Johnson et al. 2012, Battley et al. 2012). Less well-known, and sometimes more difficult to study, are the migrations of species that stop only briefly at stopover sites, disperse broadly across the landscape, and hop short distances between sites (Skagen 2006). These species pose conservation challenges because often little is known about their habitat requirements during migration or connectivity between breeding and wintering areas. Such is the case for the Long-billed Curlew (*Numenius americanus*), a short-distance, broadly dispersed migrant for which migration patterns of birds from different portions of the range are poorly understood (Dugger and Dugger 2002).

The Long-billed Curlew is a temperate-breeding, North American shorebird categorized as a species of high conservation concern in the United States, Mexico, and Canada (Donaldson et al. 2000, Brown et al. 2001, USSCP 2004). The basis for concern is loss of about 30% of its historical breeding range, its small population size, apparent declines over portions of its remaining breeding range, and ongoing anthropogenic threats to its breeding and nonbreeding habitats (Fellows and Jones 2009). Although recent surveys on the breeding grounds have resulted in a greatly increased overall population estimate of more than 100,000 individuals (Stanley and Skagen 2007, Andres et al. 2012), a comprehensive status assessment by the U.S. Fish and Wildlife Service (Fellows and Jones 2009) concluded that a high level of concern was still warranted for the species.

Long-billed Curlews currently breed in the Great Plains, Great Basin, and intermountain valleys of the western United States and southwest Canada (Dugger and Dugger 2002). Two subspecies are sometimes recognized (Bishop 1910, American Ornithologists' Union 1957): a smaller-bodied, more northerly race, *N. a. parvus*, and a larger-bodied, more southerly race, *N. a. americanus*. During the nonbreeding season, Long-billed Curlews primarily occur along the Pacific and Gulf of Mexico coasts of North America, in the Central Valley and Salton Sea basin of California, and throughout northern and central Mexico (Dugger and Dugger 2002).

Although Long-billed Curlews are the largest and one of the most charismatic shorebirds in North America, little is known about how individuals from different breeding areas distribute themselves during the nonbreeding season or if migration behavior differs among groups (Dugger and Dugger 2002). Based on proximity of their breeding and nonbreeding ranges, they have been classified as a short-distance migrant (Skagen and Knopf 1993). In the only migration study of satellite-tagged and color-banded individuals, curlews from the Ruby Valley, Nevada, breeding grounds traveled 700–1400 km to wintering areas including coastal wetlands from Humboldt Bay, California, to the west coast of Baja California, agricultural lands in California's Central Valley, and the northern Gulf of California (A. Hartman and L. Oring, personal communication). Additionally, a color-banded breeding curlew from Idaho has been reported in Long Beach, California, and another in Haiti (R. L. Redmond in Dugger and Dugger 2002).

Given its heightened conservation status and the many unknown factors that might be affecting its population size, we designed a satellite tracking study in 2007 to investigate the migration strategies and migratory connectivity among Long-billed Curlews from three widely separated breeding areas. Specifically, we compared the migratory routes and distances, winter destinations, and stopover behavior of curlews from these areas. Although the primary intent of the study was to collect observational information that would aid in the conservation of Long-billed Curlews nesting in these regions and provide the basis for future work, we posed several a priori questions based on current knowledge of the species' reproductive strategy. Because males acquire territories to display to mates (Allen 1980) and females abandon broods earlier than males (Allen 1980, Redmond 1984, Pampush and Anthony 1993), we hypothesized that the different breeding roles could affect migration timing such that males would arrive on the breeding grounds earlier and depart from the breeding grounds later than females. We also hypothesized that the timing of northward migration might be influenced by the climatic regimes of breeding areas, specifically that birds would arrive earlier at areas with milder spring temperatures.

METHODS

Study Area and Habitats
We selected three locations with breeding concentrations of Long-billed Curlews that would facilitate capture and differ markedly in longitude, land cover, and the type and

extent of agricultural practices. The Oregon study area (45°46′N, 119°41′W) at the Naval Weapons Systems Training Facility near Boardman, Oregon, is within the sagebrush steppe region of the Columbia Basin and is mostly grazed grassland that has experienced occasional burns within the past few years (Humple and Holmes 2006). Long-term averages (1981–2010) of mean monthly temperatures in spring are 7.7°C (March) and 11.5°C (April) (Western Regional Climate Center, http://www.wrcc.dri.edu, February 20, 2013). The Nevada study area (40°44′N, 115°11′W) in the Ruby Valley consisted of privately owned cattle ranches with flood-irrigated hay fields, open rangeland, and shrub–desert rangeland. Curlews were captured in lightly grazed hayfields; further information on the area is available in Hartman and Oring (2009). Mean March and April temperatures each average 5.4°C colder at Ruby Valley than at Boardman. The Montana study area (47°55′N, 108°19′W) near Zortman was on the northern mixed-grass prairie at The Nature Conservancy's Matador Ranch in Phillips County, where curlews were trapped in moderately to heavily grazed short-grass prairie. The Montana site had the coldest March and April temperatures of the three areas, averaging 7.8°C and 6.7°C, respectively, colder than at Boardman. The Nevada site was within the breeding range of *N. a. americanus* and the Oregon and Montana sites each within the range of *N. a. parvus*.

Capturing and Marking

We systematically searched for and captured incubating adults by gently dropping a 12 m long, 4-tier, 100 mm mesh mist net on them. Capture sites were all <10 km apart in each breeding area with the exception of one Montana site that was up to 34 km from the others. We banded all birds on the tarsus with a U.S. Geological Survey band and on the tibio–tarsus with a black alpha–numeric flag. We measured exposed culmen, diagonal tarsus, flattened wing, and body mass to assess sex and race, but also collected 70 μL of blood to confirm sex through molecular analysis.

We fitted each bird with an 18 g solar-powered satellite transmitter (PTT) (Microwave Telemetry, Columbia, MD) with a duty cycle of 10-hr-on and 24-hr-off, and a life expectancy of 3 years. PTTs were equipped with sensors that measured ambient temperature, bird activity (moving, not moving), and battery charge. We attached transmitters to the lower back with a leg loop harness (Mallory and Gilbert 2008) made of 4.7-mm-wide, brown Teflon tape, looped around the legs, fitted, and then crimp-locked with brass sleeves. The 4–5 g harness mass resulted in load ratios (PTT and harness mass $\times$ bird mass^{-1} $\times$ 100) of 3–4% for females ($n = 13$) and 4–5% for males ($n = 15$). Curlews were released within 45 min of capture.

Data Collection and Processing

We obtained locations of the PTTs and their sensor data from Collecte Localization Satellites (CLS, http://www.cls.fr), which uses the Argos data collection system and Doppler geolocation to calculate locations and assign them to accuracy classes of 3, 2, and 1 representing the most accurate standard classes, and 0, A, B, and Z representing less accurate auxiliary classes. We used the Douglas Argos-filter (DAF) algorithm (Douglas et al. 2012) to exclude implausible auxiliary locations based on the hybrid filtering method for which we prescribed a maximum movement rate threshold of 120 km hr^{-1} and a spatial redundancy threshold of 10 km. This resulted in 68,380 total locations (58% standard-class and 42% auxiliary), or between 157 and 4,675 locations per bird (median = 2,145). When an activity sensor stopped registering movement, we considered that the transmitter had failed or been shed or the bird had died, and we truncated its tracking dataset to the last active location.

We plotted locations in Google Earth (Plate Careé projection) to visualize movements, help pinpoint arrival and departure dates at sites, and evaluate which birds were wintering in agricultural areas, identified by concentrations of adjacent circles, rectangles, or quadrilaterals signifying the boundaries of fields. Movement patterns were further assessed by examining plots of location latitudes through time for each bird per year. To characterize stopover locations, we plotted their mean latitude and longitude in ArcGIS 9.3 (ESRI 2007) over the North American Environmental Atlas (edition 2006) available from Commission for Environmental Cooperation (http://www.cec.org/naatlas/), and extracted the corresponding Level II ecological region or broad land-scape class (e.g., North American Warm Deserts, West-Central Semiarid Prairies).

Statistical Analysis

We summarized each bird's annual migration by a track composed of points based on its last breeding area location (point where directional southbound movement began), all in-flight locations, first and last locations at all stopovers, first wintering area location (point where directional southward movement ceased), southernmost location by late October (see below), last wintering area location (point where directional northward movement began), and first breeding area location the following year (i.e. arrival within 5 km of capture site). We identified stopover locations by point clusters where a bird's rate of movement (and often change in direction) indicated it had interrupted its flight.

We calculated the cumulative length (km) of a bird's southbound migration track by summing the vectors formed by a point-by-point route connecting locations between the last breeding area location and the first

wintering area location. Similarly, the cumulative north-bound path was the comparable route between the last location at a wintering area and first location at the previous year's breeding area. We considered the southernmost location reached before or during the last duty cycle in October to represent a generalized "wintering area" for a bird because birds seldom moved farther south after they reached this point. All distances are great circle route distances (i.e. orthodromes), and we used mean values for individuals tracked for >1 yr in our calculations.

We defined duration of migration as the number of days between last breeding area location and first winter location for the southbound trip and the reverse for the northbound trip. The travel speed equaled the total kilometers traveled divided by days en route. Times spent at stopovers are number of hours between first and last stopover locations and are minimum estimates because the exact time a bird reached or departed an area was rarely tracked. Further, because PTTs were on a 10-hr-on, 24-hr-off cycle, some birds undoubtedly briefly interrupted and then resumed migration without the stopovers being identified.

For comparing departure timing we used the last dates on which individual curlews were recorded at their breeding or wintering areas, and for arrival timing we used the first dates they were recorded back at their wintering or breeding areas. Intervals between the last transmission on breeding or wintering areas and the first transmission during migration were usually ≤36 hr (95% of 98 migrations across locations and years); hence, most departures and arrivals occurred the day of or day after assigned dates. For individuals we used Julian dates to calculate mean arrival dates, departure dates, and migration durations.

We tested our hypotheses concerning differences in breeding ground arrival and departure dates of birds from the different areas and between the sexes by comparing these dates from our two sites with the largest sample sizes, Oregon and Montana. We used the Wilcoxon Rank Sum test (statistic W) to compare these dates between all females and all males at the two sites in spring and two sites in fall (four tests) and to compare the two sites by sex in spring (two tests). We also compared breeding ground departure dates between males and females within two Oregon and six Montana marked pairs during the first season they were identified as paired, using the Wilcoxon Signed-Rank Test (V). We were not able to determine mate fidelity for these pairs in subsequent years. We calculated the test statistics manually and used exact statistics whenever possible due to small sample sizes. For two of the tests we used a (continuity-corrected) normal approximation (test statistic z) that accounted for the changed null distribution due to ties (Lehmann 1975). To minimize ties we used mean rather than median dates for birds with

more than a single year of data for a season. We used the sequential Bonferroni procedure for multiple tests to maintain an overall $\alpha = 0.05$ over the seven tests (Holm 1979). While we acknowledge that statistical test results apply to the sample of birds studied, we believe our samples are comparable to ones randomly selected from the breeding populations in our study areas. We also recognize that the small sample sizes (although generous for a satellite tag study) limit our power to detect all but the clearest differences between curlews from different breeding areas or between sexes. Except for morphometric data (Table 1), values are reported as median (minimum–maximum).

RESULTS

We put PTTs on 29 curlews, including 10 in Oregon (May 3, 2007 and May 2–6, 2008), 5 in Nevada (May 16–17, 2007), and 14 in Montana (May 15–21, 2009, and May 16–21, 2010). About equal numbers of each sex were instrumented at each site (Table 1). We tracked 28 of the 29 curlews (one Oregon bird shed its transmitter or died before the first departure) during 54 southbound passages and 24 curlews during 43 northbound passages, thus documenting 43 complete journeys by 24 birds over the 4 years of the study. Included in this dataset are eight southbound passages by pairs of birds in the same year (two pairs from Oregon and six pairs from Montana).

While the mass and culmen of curlews tagged in Oregon and Montana overlapped those from Nevada of similar sex (Table 1), the measurements of the latter birds were all at the largest extreme of the measurement range, consistent with the contention that Nevada birds belonged to the larger *N. a. americanus* race and the smaller Oregon and Montana birds to the *N. a. parvus* race described by the American Ornithologists' Union (1957).

Migration Routes

Fall and spring migration routes of Oregon curlews were usually confined to a narrow eastern California–western Nevada corridor that crossed the Sierra Nevada Range (Figure 1), with occasional exceptions to this route across years; for example, in fall 2008 a curlew traveled markedly east of the other eight birds (Figure 1).

Fall passages of Nevada birds spanned a wide range of directions from a southwest route over central Nevada to the Central Valley of California to south–southwest tracks crossing eastern Nevada and southeast California to termini at the Colorado River Delta or the west coast of Baja California, Mexico (Figure 1). We detected deviations from these routes when in 2007 a bird flew southwest toward the Central Valley before turning south to the west coast of Baja California, and in 2009 when a bird headed south before turning southwest to its Central Valley

TABLE 1. Mean mass (g ± SD), diagonal tarsus (mm), flattened wing (mm), and straight culmen (mm) of female and male adult Long-billed Curlews from three breeding areas. Sample sizes for each parameter in parentheses.

	Oregon	Montana	Nevada
Female			
Mass	624 ± 14 (4)	617 ± 35 (6)	717 ± 67 (3)
Tarsus	84 ± 6 (4)	79 ± 2 (6)	99 ± 5 (3)
Wing	279 ± 1 (4)	282 ± 6 (6)	296 ± 6 (3)
Culmen	150 ± 9 (4)	161 ± 7 (7)	174 ± 8 (3)
Male			
Mass	541 ± 45 (6)	518 ± 29 (7)	620 ± 0 (2)
Tarsus	77 ± 1 (6)	77 ± 3 (7)	94 ± 2 (2)
Wing	269 ± 8 (6)	268 ± 6 (7)	272 ± 4 (2)
Culmen	119 ± 8 (6)	121 ±7 (7)	134 ± 4 (2)

wintering area (Figure 1). In spring, Nevada curlews followed fairly direct routes back to breeding areas.

The fall tracks of Montana curlews ran south–southeast in a fairly narrow band along the front range of the Rocky Mountains through Montana, Wyoming, and Colorado to the Texas Panhandle or northeast New Mexico (Figure 1). In 2010, the easternmost track arched through southwestern South Dakota, Nebraska, western Kansas, and northwestern Oklahoma to Texas. From Texas or northeast New Mexico, some birds continued directly south–southeast (or in one case in 2010 arched) to northeast Tamaulipas State, Mexico, while others veered southwest, or southwest and then southeast, to destinations on the Mexican Plateau. Spring tracks of Montana birds largely overlapped fall tracks but occupied a wider band (Figure 1).

The length of southbound migratory tracks differed among birds from the three groups with Montana curlews traveling more than twice the distance of those of Oregon and Nevada birds, which migrated similar distances (Table 2). The fall migratory tracks of all birds from Montana were longer than those of any birds from Oregon or Nevada. Within areas, spring tracks were of similar length to fall tracks, and male tracks of similar length to female tracks (Table 2).

Winter Locations

Wintering patterns of tagged curlews differed by breeding area (Figure 1). All 9 curlews from Oregon wintered relatively close to each other in agricultural regions of the Central Valley, California (Figure 1), between roughly 36–39°N (Figure 2) and 120–122°W. The 5 Nevada breeders wintered over an adjacent but broader range than those from Oregon (28–36°N, 114–119°W), with one Nevada bird wintering in the Central Valley and others traveling to coastal areas in either western Baja California (2 birds) or the northern Gulf of California (2 birds). One of the latter birds subsequently moved north about 90 km before the

end of October to spend the winter in an agricultural region of the Mexicali Valley, Mexico. Montana breeders wintered across the broadest range (22–34°N, 97–107°W) and did not overlap with birds from the other two areas. Two of the 14 wintered inland in agricultural regions of the southern High Plains of the Texas Panhandle; 5 wintered along the western margin of the Laguna Madre, Gulf of Mexico in areas of rangeland and wetland; and 7 went to agricultural areas of the Mexican Plateau. These overall patterns held across years as individuals tracked for ≥2 years exhibited strong fidelity to their wintering sites; 8 returned to the same wintering area in 2 consecutive years, 6 in 3 consecutive years, and 2 in 4 consecutive years. More detailed information on site fidelity and habitat use is the focus of a separate study on the home ranges of the curlews in the Central Valley of California (K. Sesser personal communication) and is not reported in more depth here. Pairs tended not to winter together; members of 2 Oregon pairs wintered about 250 km apart and those of 4 Montana pairs 300–1100 km apart; however, members of 2 pairs wintered within 100 km.

Movement Patterns

Most birds stayed close to the southernmost points they reached by the end of October, but three Oregon birds traveled 1–2° north from their southernmost destination by September 2008, and a Montana bird moved 6° farther south in late December 2010 (Figure 2). One Oregon female took an indirect route north in 2009. In late March, she traveled 300 km northeast from her Central Valley wintering area to near Pyramid Lake, Nevada (40°N), where she stayed for <48 hr before returning to her Central Valley wintering area. She resided there for only 5–6 days before commencing a direct flight back to her Oregon breeding area on April 5 or 6.

Stopover Behavior

The frequency and duration of detected stopovers varied among the curlews from the three breeding sites. Many migrations of Oregon birds in spring and fall and of Nevada birds in spring appeared to be nonstop, whereas all passages by Montana birds involved stopovers. Specifically, during fall, fewer migrations by curlews from Oregon included stopovers (43% of passages with stops, $n = 21$ passages) than migrations from Nevada (92%, $n = 13$) or Montana (100%, $n = 20$). During fall, individuals migrating from Oregon and Nevada made up to 3 stops and individuals from Montana up to 8 stops. These stopovers were <1 day for 73% of the 11 stops made by Oregon breeders, 71% of the 17 stops by Nevada breeders, and 49% of 73 stops by Montana breeders. Median (maximum) stopovers >1 day were 4.6 (5.9, $n = 3$) days for Oregon breeders, 12.7 (70.6, $n = 5$) for Nevada breeders, and 7.5 (108.3, $n = 37$) for Montana breeders.
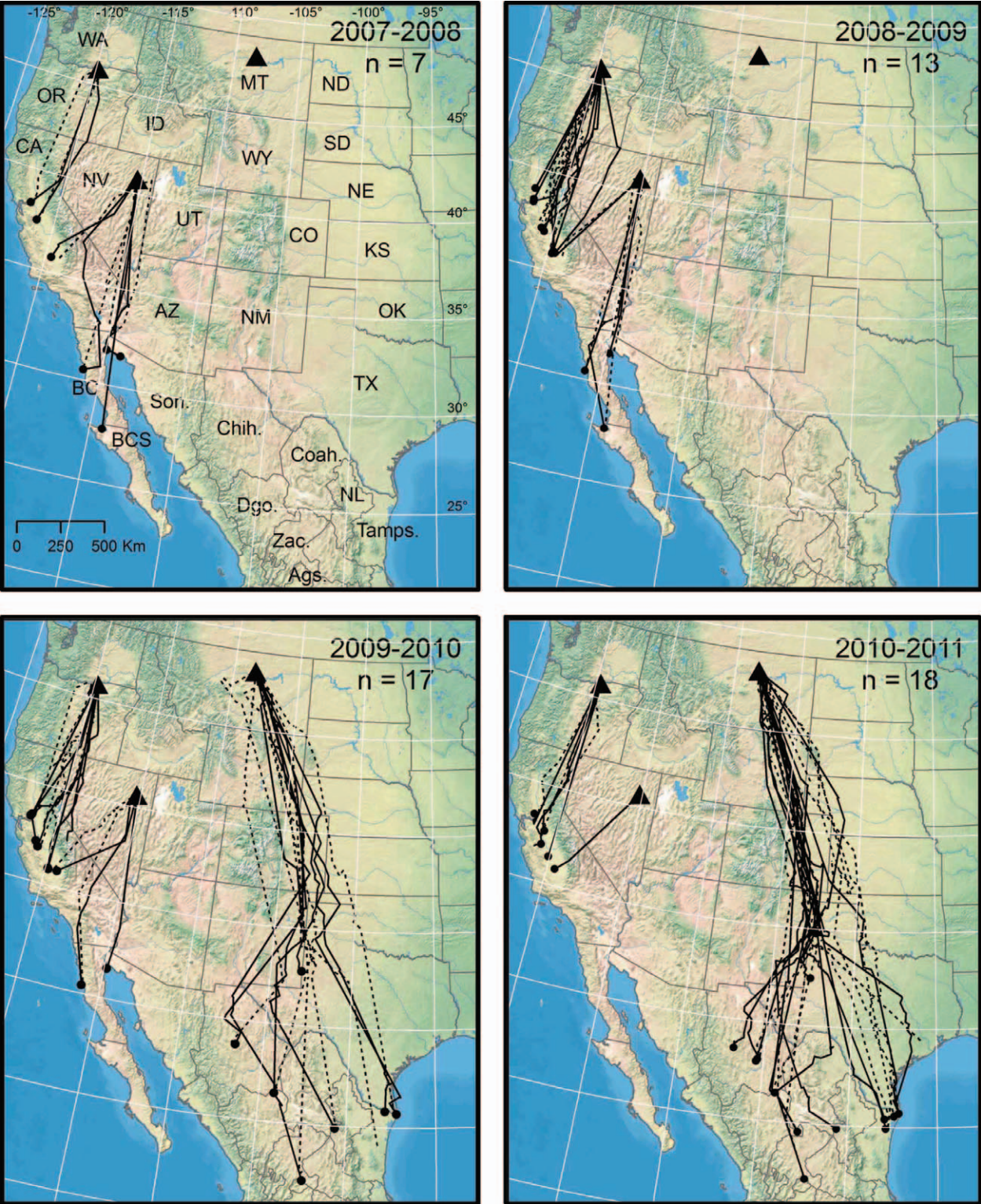
FIGURE 1. Migratory tracks and winter locations (circles) of satellite-tagged Long-billed Curlews from breeding areas (triangles) in Oregon, Nevada, and Montana, 2007–2011. Solid lines denote fall migration and dashed lines spring migration in the following year.

TABLE 2. Median (minimum–maximum) of the mean migration distances (km), durations (days), and travel speeds (km day^{-1}) of the migrations of individual male (M), female (F), and total (T) Long-billed Curlews from three breeding areas. Sample size (n) is the number of individuals.

		Southbound migration				Northbound migration		
	n	Distance	Duration	Speed	n	Distance	Duration	Speed
Oregon								
M	5	1018 (842–1116)	3 (1–5)	282 (218–842)	4	996 (875–1139)	2 (2–4)	479 (239–620)
F	4	1102 (856–1157)	3 (1–3)	474 (364–643)	3	1089 (980–1151)	3 (2–12)	384 (91–490)
T	9	1038 (842–1157)	3 (1–5)	370 (218–842)	7	1036 (875–1151)	2 (2–12)	389 (91–620)
Nevada								
M	2	1140 (1058–1223)	20 (5–35)	123 (35–212)	1	1182	3	358
F	3	1013 (676–1467)	5 (3–10)	225 (98–293)	3	910 (668–1679)	2 (2–4)	420 (334–607)
T	5	1058 (676–1467)	5 (3–35)	212 (35–293)	4	1046 (668–1679)	3 (2–4)	389 (334–607)
Montana								
M	7	2682 (1564–2875)	16 (4–119)	168 (21–683)	7	2747 (2355–2972)	25 (15–40)	102 (71–183)
F	7	2774 (1862–3098)	95 (4–115)	33 (19–694)	6	2431 (1716–3290)	30 (26–41)	84 (42–113)
T	14	2707 (1564–3098)	68 (4–119)	42 (19–694)	13	2551 (1716–3290)	29 (15–41)	87 (42–183)

In spring, relatively more passages occurred without evidence of stopovers by curlews returning to Oregon (38% of passages with stops, $n = 16$ passages) and Nevada (40%, $n = 10$) than by birds headed to Montana (100%, $n = 18$). Individuals returning to Oregon made up to 4 stops per migration, to Nevada up to 2, and to Montana up to 8 stops. Stopovers were <1 day for all 5 stops made by Nevada breeders, for 58% of 12 stops made by Oregon breeders, and for 46% of 68 stops made by Montana breeders. Median (maximum) stopover lengths >1 day were 5.5 (5.9, $n = 5$) days for Oregon breeders and 8.8 (39.8, $n = 37$) for Montana breeders.

Stopover areas of Oregon birds were concentrated in northeast California and southern Oregon (Figure 3) in landscape classes Mediterranean California ($n = 5$), Northwestern Forested Mountains, Western Cordillera ($n = 5$), and North American Cold Deserts ($n = 13$). Nevada curlews tended to stop along the Colorado River and in the Imperial or Mexicali valleys (Figure 3) in North American Cold ($n = 7$) and Warm ($n = 15$) deserts. Montana curlews stopped all along their routes, with the longest stops occurring in western Texas, eastern New Mexico, and northern Chihuahua State during southbound migration, and in western Texas and eastern New Mexico while northbound (Figure 3). The landscape at stops of Montana curlews was mostly South Central Semiarid Plains ($n = 89$) and North American Warm Deserts ($n = 22$), with fewer (2–14) in other plain, prairie, and desert classes.

Migration Timing and Duration

Timing of all fall departures from the three breeding areas spanned June 5–July 19 but varied in some aspects between sexes and areas. All females departed earlier than males in Oregon ($W = 10$, $P = 0.008$, Bonferroni α-level = 0.013; Table 3) but a pattern of female-before-male departure was not significant for Montana birds ($z =$ 1.28, $P = 0.10$, Bonferroni α-level = 0.05). Females of the two Oregon and six Montana pairs departed 1–22 days before their mates during the first year we documented them to be paired (median 6.5 day difference, $V = 0$, $P = 0.004$, Bonferroni α-level = 0.008). Fall arrival on the wintering grounds extended from June 12 to July 6 for Oregon birds, June 16 to September 25 for Nevada birds, and June 25 to October 28 for Montana birds.

The timing of all spring departures of tagged curlews from the wintering grounds extended from March 6 to April 11. Males arrived at their Montana breeding areas earlier than the females ($z = 2.53$, $P = 0.006$, Bonferroni α-level = 0.01; Table 3). Oregon males also arrived earlier (Table 3), but the difference was not statistically significant ($W = 10$, $P = 0.03$, Bonferroni α-level = 0.025, although this is the highest possible significance value with our sample of only four males and three females). Spring arrival of both male and female curlews was significantly earlier at the Oregon breeding area than the Montana area (males: $W = 10$, $P = 0.003$, Bonferroni α-level = 0.007, and females: $W = 6$, $P = 0.011$, Bonferroni α-level = 0.017; Table 3). Spring arrival on the breeding grounds varied from March 19 to April 16 for Oregon birds, April 3 to 14 for Nevada birds, and April 13 to 28 for Montana birds.

The durations of both migrations varied among groups primarily due to differences in time spent at stopovers. Birds from Oregon and Nevada migrated more quickly than those from Montana on both fall and spring migrations (Table 2).

DISCUSSION

The three samples of birds we studied exhibited differences in migrations routes, winter destinations, stopover behavior, and migration timing. Migration routes of
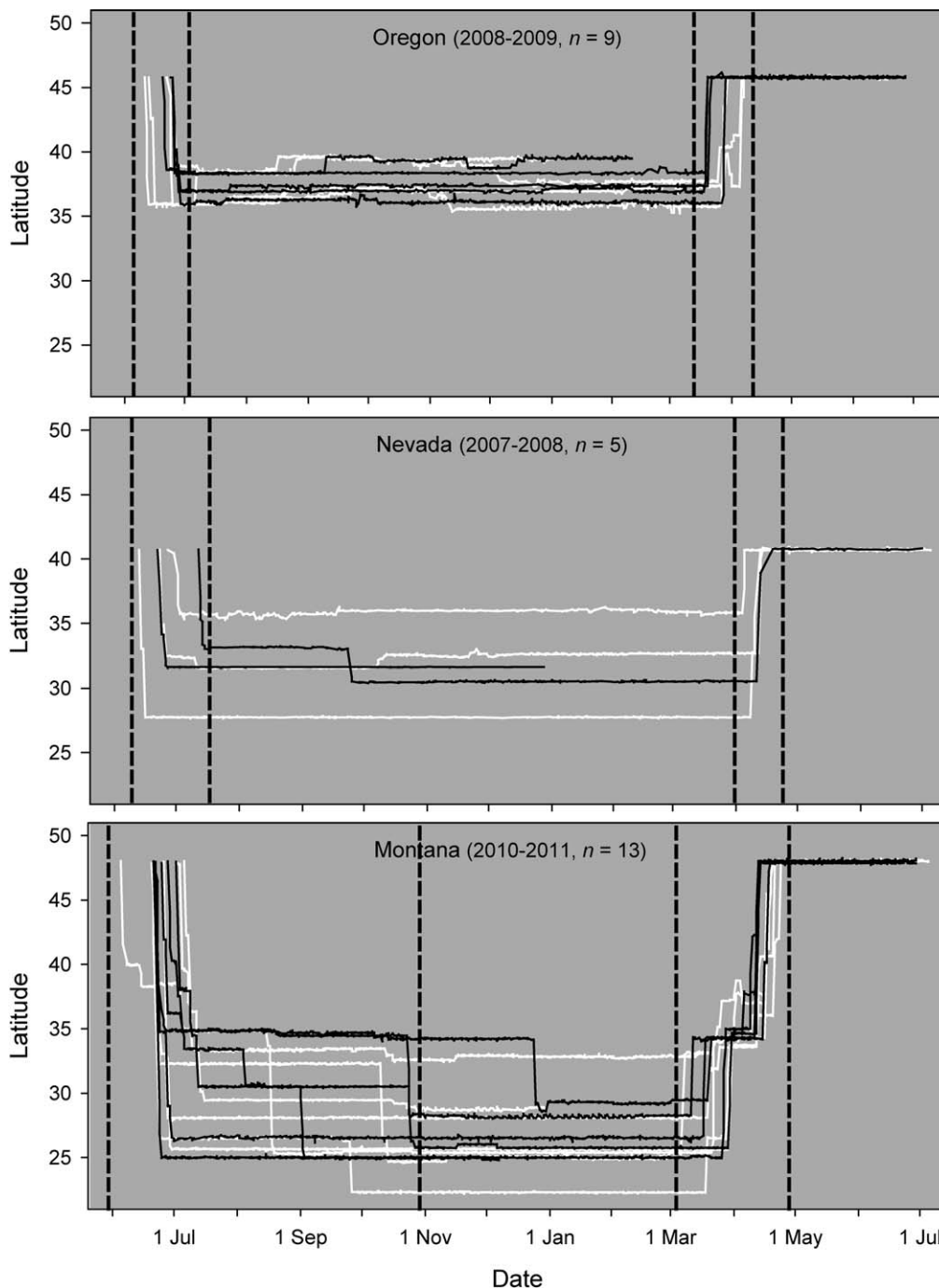
FIGURE 2. Seasonal movement by latitude of male (black lines) and female (white lines) satellite-tagged Long-billed Curlews from three breeding areas, 2007–2011. Periods of north–south movement of most birds during their summer–autumn and spring migrations are enclosed by dashed lines. The annual cycle with the largest sample of tagged birds is depicted for each breeding area.

shorebirds are shaped by internal navigation mechanisms (Grönroos et al. 2010), external forces such as wind patterns (Åkesson and Hedenström 2000, Liechti 2006), physical features such as coastlines (Warnock et al. 2004), and ecological conditions (Berthold 2001). The migrations of Nevada and Oregon curlews tended to be relatively short and direct, consistent with birds following constant compass courses (Alerstam 2006), while those of Montana curlews appeared to be shaped additionally by topography as they navigated roughly 1500 km along the eastern slope
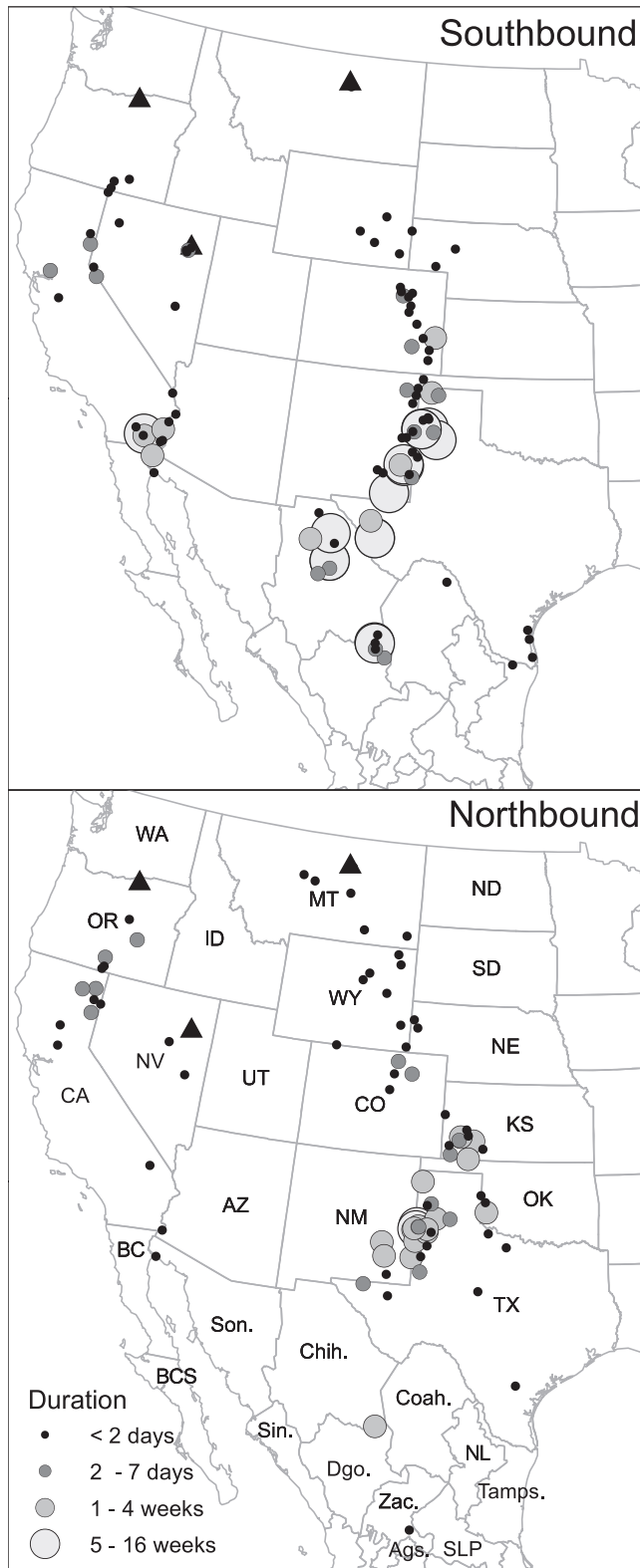
FIGURE 3. Locations and durations of stopovers of Long-billed Curlews during south- and north-bound migrations, 2007–2011. Triangles denote breeding areas; sizes of circles denote stopover durations. Stopovers shown for Oregon birds are based on 21

of the Rocky Mountains before veering in various directions. While the mountains may act as a barrier to migration, Montana birds were more likely responding to the availability of the grassland habitat of the high plains that provides potential foraging opportunities along most of their route.

Curlews we tagged from the three breeding areas differed in wintering areas. Those from Montana wintered much farther south and east and over a wider range than those from Oregon and Nevada. In turn, the range of birds from Nevada was broader and extended farther south than that of Oregon birds. The only region of winter sympatry occurred between the Nevada and Oregon birds in the Central Valley of California, a pattern also found in a previous study (A. Hartman and L. Oring personal communication) in which satellite-tagged or color-banded birds from Ruby Valley, Nevada, were found in winter along the Pacific coast from Humboldt Bay in northern California to Ojo de Liebre in Baja California Sur, and in the Central Valley. The migration tracks of some of these birds that traveled to the coast would theoretically have crossed those of our Oregon sample, suggesting more extensive overlap in migratory movements, and probably wintering areas, between Nevada and Oregon curlews than our relatively small sample suggests. In contrast, none of the Montana curlews migrated to the wintering areas of Oregon or Nevada birds, even though that course could have shortened their migration routes. Possibly the risk of crossing over the precipitous Rocky and Sierra mountain ranges is too high relative to longer passages over more benign terrain en route to the Mexican Plateau or Laguna Madre.

Of the three groups, the only potential overlap in winter distribution was between two presumably different subspecies represented by the Nevada and Oregon breeders. If *N. a. parvus* and *N. a. americanus* represent valid subspecies (and this has been questioned by Grinnell 1921), the marked size difference of these subspecies could suggest that selective forces acting on body size are potentially stronger for curlews on the breeding grounds than the wintering grounds; however, body size differences could have arisen historically in response to isolating mechanisms on both breeding and wintering areas that are now absent during winter. The migration data presented here, which suggest some level of population structure, serve as a hypothesis for a future phylogenetic assessment of Long-billed Curlews in western North America.

TABLE 3. Median (minimum–maximum) of mean departure (Dep.) and arrival (Arr.) dates at and from the breeding (BG) and wintering (WG) grounds of adult Long-billed Curlews from breeding areas in Oregon (OR), Nevada (NV), and Montana (MT). Sample sizes (n) are the number of individuals.

	Female	Male
Fall		
OR		
n	4	5
Dep. BG	Jun 17 (Jun 11–22)	Jun 23 (Jun 23–27)
Arr. WG	Jun 19 (Jun 13–24)	Jun 27 (Jun 25–30)
NV		
n	3	2
Dep. BG	Jun 24 (Jun 17–Jul 3)	Jun 28 (Jun 22–Jul 4)
Arr. WG	Jul 4 (Jun 23–Jul 6)	Jul 18 (Jun 27–Aug 8)
MT		
n	7	7
Dep. BG	Jun 23 (Jun 5–Jul 5)	Jun 28 (Jun 21–Jul 11)
Arr. WG	Sep 26 (Jun 28–Oct 26)	Jul 27 (Jun 25–Oct 25)
Spring		
OR		
n	3	4
Dep. WG	Mar 30 (Mar 27–Apr 5)	Mar 19 (Mar 18–25)
Arr. BG	Apr 7 (Mar 30–Apr 11)	Mar 23 (Mar 20–27)
NV		
n	3	1
Dep. WG	Apr 8 (Apr 4–9)	Apr 9
Arr. BG	Apr 10 (Apr 6–12)	Apr 12
MT		
n	6	7
Dep. WG	Mar 22 (Mar 17–29)	Mar 23 (Mar 9–31)
Arr. BG	Apr 20 (Apr 18–26)	Apr 16 (Apr 13–19)

Stopovers by migrating birds are usually associated with the opportunity to rest and refuel for further energetically demanding flights (Alerstam and Lindström 1990, Warnock 2010). Despite being relatively short-distance migrants, individuals from all three groups stopped for some length of time during north and south migrations. The function of these stops is unclear for the Oregon and Nevada birds because individuals from both areas were able to traverse these same routes with no apparent stops. Perhaps these birds are employing a more opportunistic strategy, especially during the less time-constrained fall migration, to take advantage of feeding opportunities along the route. In contrast, southbound Montana birds commonly traveled twice the distance on average compared with Oregon and Nevada birds, stopping for 1–3 months on the southern High Plains or northern Mexican Plateau, about two-thirds of the way into their southbound journeys. These layovers seemed much longer than necessary to accumulate reserves for subsequent flights of only 400–1100 km farther south and may instead have been made by birds undergoing prebasic molt (Pyle 2008), an energetically costly process; however, we lack information on the molt status or body condition of birds in this region in fall. Many Montana birds returned to stage on

the southern High Plains during northbound migration, perhaps to accumulate body reserves for breeding or to better gauge when conditions in Montana were conducive to breeding.

Among breeding areas, we found differences in the timing and duration of migration, especially between Montana and Oregon birds. While commencement of southbound migration of Montana birds was modestly different from Oregon birds, their arrival on the wintering grounds was up to 1 and 3 months (for males and females, respectively); their later arrival on wintering grounds was proximately influenced by their longer stopovers. Montana birds initiated their first northbound movements at the same time as Oregon birds, and the proximate cause that delayed their arrival on the breeding grounds relative to Oregon birds was differences in stops along the way. The later arrival of Montana curlews on the breeding grounds by 2–3 weeks in spring may be an adaptation to the lower average spring temperatures there, although this remains to be tested. Spring arrival schedules of shorebirds at breeding areas have a fitness component because earlier arriving birds have greater access to territories and mates than later arrivals (Colwell 2010). We detected this pattern in our Montana sample where male curlews arrived earlier than females; the pattern was similar in Oregon, but our sample size there was too small to obtain a significant result with multiple tests.

Fall departure schedules of monogamous shorebirds with bi-parental care, such as the curlew, usually involve females commencing migration before males (Colwell 2010). Within our Long-billed Curlew pairs, females commenced fall migration about a week earlier than males, also consistent with Colwell's (2006) finding that female Long-billed Curlews arrived earlier than males on their coastal California wintering grounds. The overall pattern of departures by sex did not show this pattern, however, likely due to early departures by failed breeders of both sexes. We found little evidence that pairs of curlews migrated or wintered together, an expected finding because females migrate earlier than males and because birds are site-faithful to wintering areas presumably established when they were juveniles (Townshend 1985).

Our finding that curlews from all three areas occur in agricultural landscapes during winter reinforces the growing recognition that agricultural areas are important to Long-billed Curlews (Shuford et al. 2009, Saalfeld et al. 2010, K. Sesser personal communication). Since 1982, the United States has lost approximately 12% of its croplands to development and other changes (U.S. Department of Agriculture 2009), and some of the largest losses have occurred in Texas (24%) and California (11%), key migration and wintering areas for the curlews we studied. The strong tendency of Long-billed Curlews and other godwit and curlew species to return to the same breeding

and nonbreeding areas year after year (Colwell and Oring 1989, Gill et al. 2002, this study) suggests an important fitness component to site fidelity. How habitat loss at traditional sites and the varied schedules of habitat manipulation inherent in agricultural landscapes affect different groups of Long-billed Curlews, and in turn the entire population, are unknown. Further studies into the potential effects of habitat loss and conversion on Long-billed Curlews would help guide conservation actions.

Satellite telemetry offers an opportunity to further examine the migratory connectivity of Long-billed Curlews. Tracking more individuals at additional sites in the Columbia Basin, Great Basin, and Prairie breeding areas would provide a more complete picture of the degree of separation of their nonbreeding distributions. In addition, the relatively new GPS/Argos satellite transmitters are now small enough to deploy on Long-billed Curlews. GPS data can be used to track fine-scale local movements so that conservation implications for Long-billed Curlews on a changing landscape can be directly studied. For example, fine-scale movements of birds could be tracked in relation to patterns of land use (e.g., seasonal rotation of crops, flooding/irrigation regimes, livestock grazing). More also could be learned about stopover behavior, including how different patterns originate, the degree of variation in stopover behavior within and among individuals, and the ecological function of stopovers. In particular, more could be learned about the effect of environmental variables on the migration behavior of Long-billed Curlews.

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