Research Article

Molt Migration and Migratory Connectivity of the Long-Billed Dowitcher

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ABSTRACT Effective conservation of migratory shorebirds requires information on their stopover ecology and migratory connectivity in areas such as the Great Basin and interior California, USA, where freshwater is highly managed and maintenance of wetland networks requires planning across multiple regions. We captured long-billed dowitchers (Limnodromus scolopaceus; hereafter dowitchers) to study their molt patterns and length of stay in the Klamath Basin during fall migration and their migratory connectivity and overwinter space use in California’s Central Valley. Most dowitchers were in active primary molt when captured (83%, n = 116), and molt stage increased during August and September. Radio-tagged dowitchers had an average length of stay after capture of 31.9 days (n = 54). After departing the Klamath Basin, we located 57% of 81 radio-tagged dowitchers in the Central Valley from December to February; most of the 228 detections occurred in the Sacramento Valley (39%) or Grasslands Ecological Area in the San Joaquin Basin (47%). Space use by radio-tagged dowitchers differed among the Sacramento Valley, San Joaquin Basin, and Sacramento–San Joaquin Delta sub-regions, which demonstrated the influence of varying amounts and distributions of habitat. We recommend that managers in the Klamath Basin provide shallow-water wetlands to support migrant dowitchers for ≥30 days beginning around 1 August, but ideally wetlands should be maintained until 30 September if freshwater supplies are available. We also recommend coordinated management of shallow-water wetlands within and between the Klamath Basin and Central Valley to optimize the use of freshwater, a limited and unreliable resource. © 2015 The Wildlife Society.

KEY WORDS connectivity, Limnodromus scolopaceus, molt, shorebird, space use, staging area, stopover, telemetry, wetland management.

Information on stopover ecology and migratory connectivity are essential for conservation strategies that consider the full life cycle of migratory species (Martin et al. 2007). Migratory shorebirds (sub-orders: Charadrii and Scolopaci) use a network of wetlands for different purposes and amounts of time each year. During migration, migratory shorebirds use short-term stopover sites for a few hours or days to rest and refuel and long-term staging areas for several weeks to refuel for long-distance flights or sometimes to molt (Skagen 1997, Warnock 2010). Shorebirds that use interior migration routes will thereby establish a functional connection along a network of otherwise isolated wetlands (Haig et al. 1998), in part, because most undertake a series of short or medium distance flights between stopover or staging areas and wintering areas (Warnock 2010). Management actions can directly affect the resources available at a given site, thus influencing the time spent there and elsewhere in the network. This necessitates coordinated management within the network to ensure resources are available at geographic bottlenecks (Martin et al. 2007), which occur at staging areas where a significant portion of the population along an entire migration corridor can be affected by local environmental conditions (Myers 1983).

Migration and molt strategies are interdependent. After breeding, adult shorebirds undergo a complete prebasic molt in which nearly all body and flight feathers are replaced (Pyle 2008). The molting of flight feathers, or primary molt, is particularly challenging because the temporary loss of flight feathers can impede flight performance, thus increasing predation danger and the cost of long-distance flights (Hendenström 2003). Molt migration, in which primary molt occurs after a postbreeding movement to a staging area, has been documented in many waterfowl (Salomonsen 1968) and some passerines (Leu and Thompson 2002), but it is considered rare in shorebirds (Holmgren and Hendenström 1995, Putnam 2005, Colwell 2010).

Staging areas used for molt migration are uniquely important for conservation and management because birds concentrate in these areas for extended periods and they can...
become geographic bottlenecks (Myers 1983, Jehl 1990, Leu and Thompson 2002). Identifying these areas is challenging because it requires data on timing of molt, length of stay, and sometimes rate of fat deposition. The only well-known example of molt migration for a Nearctic-breeding shorebird is the Wilson’s phalarope (Phalaropus tricolor; Jehl 1987), which stages during prebasic molt at hypersaline lakes of the Great Basin in western North America. Long-billed dowitchers (Limnodromus scolopaceus; hereafter dowitchers) have been documented with missing primaries at numerous fall stopover sites throughout North America (Jehl 1963, Paulson 1993, Alexander and Gratto-Trevor 1997, Putnam 2005), and it has been suggested that some dowitchers molt entirely at stopover sites (Putnam 2005). However, whether dowitchers use molt migration staging areas to undertake active primary molt over lengthy stays is not known.

The Klamath Basin (on the Oregon-California border) and Central Valley of California are nearby regions and both are important to migratory waterbirds of the North American Pacific Flyway. Their water systems are highly managed and freshwater allocations are required to maintain most wetlands and flooded agricultural land. The amount of freshwater available for wetland maintenance in these regions is often limited because of drought and human use (Haig et al. 1998, Central Valley Joint Venture 2006), thus requiring conservation strategies that maximize the return on investment of management decisions (Lyons et al. 2008). Little is known about dowitcher molt in the Klamath Basin, but the region is a molt migration staging area for waterfowl (Miller et al. 1992, Fleskes et al. 2010), which have also been documented moving between the Klamath Basin and Central Valley (Miller et al. 2005, Fleskes et al. 2010). Comparable data on shorebird migratory connectivity will provide wetland managers with further rationale to collaborate across the Klamath Basin-Central Valley network of wetlands when developing management plans (Heglund and Skagen 2005).

Once migratory waterbirds arrive in the Central Valley, most are attracted to specific areas within 3 ecological sub-regions (Shuford et al. 1998, Central Valley Joint Venture 2006). From December to February in the Sacramento Valley sub-region, waterbird habitat consists of widespread, patchily flooded wetland complexes and rice fields, whereas the San Joaquin Basin sub-region is characterized by a single, nearly contiguous wetland complex (Central Valley Joint Venture 2006). These 2 sub-regions are conjoined by the Sacramento-San Joaquin Delta sub-region where patchily flooded wetland complexes and agricultural lands are confined to the western portion of the sub-region where the Sacramento and San Joaquin rivers meet saltwater. The differing amounts and distributions of potential habitat in these sub-regions may influence use by dowitchers and other migratory waterbirds, and demonstrate the effects of landscape-scale conservation efforts in the Central Valley.

In 2012, we began a 2-year study of fall migrant dowitchers to better understand their stopover ecology in the Klamath Basin and subsequent migratory connectivity and space use in the Central Valley. Dowitchers are important indicators of healthy freshwater wetlands, and along with other interior migrant shorebirds, they are among the most vulnerable to population decline (Brown et al. 2001, Galbraith et al. 2014). Here, we use the term migratory connectivity to describe the Klamath Basin-Central Valley network of stopover or staging wetlands and subsequent wintering areas used by non-breeding dowitchers. Our primary objectives were to determine 1) whether the Klamath Basin is a stopover site or a molt migration staging area for dowitchers, 2) the probability that a dowitcher migrating through the Klamath Basin will be located in the Central Valley during winter, and 3) whether space use by dowitchers differs within each of the 3 sub-regions of the Central Valley.

**STUDY AREA**

We conducted fieldwork at 2 wetland-agricultural complexes in western North America: the upper portion of the Klamath River basin along the Oregon-California border, and the Central Valley of California, USA (Fig. 1). The Klamath Basin is a mountainous region with several large watersheds converging into a relatively flat, high elevation valley (approx. 1,250 m) that is characterized by several freshwater lakes and managed wetland complexes. Even though most of the once expansive wetlands have been modified or converted to agricultural lands, during migration the Klamath Basin still attracts up to 80% of waterfowl in the Pacific Flyway (Gilmer et al. 2004) and >40 species of other waterbirds (Shuford et al. 2004). The Klamath Basin is a potentially important stopover or staging site for dowitchers; they are the most abundant shorebird in the Klamath Basin during August and September (Shuford et al. 2002, 2004) and a large portion of the world population of dowitchers migrates through the Klamath Basin and other Great Basin wetlands (Neel and Henry 1996, Warnock et al. 1998). The Klamath Basin has a continental climate with frequent drought that can lead to water shortages for agricultural lands and wetlands that are managed by multiple entities including, including the United States Fish and Wildlife Service (USFWS), United States Bureau of Land Management (BLM), Oregon Department of Fish and Wildlife (ODFW), The Nature Conservancy, and private landowners; our study coincided with a severe to extreme drought in the Klamath Basin and northern California (http://droughtmonitor.unl.edu/, Accessed 10 Nov 2014).

The Central Valley is a low-elevation region (<75 m) that attracts millions of migratory waterbirds during migration and winter because of its temperate climate and mosaic of flooded agriculture and managed wetlands. More than 95% of the historical wetlands in the Central Valley have been destroyed or modified (Central Valley Joint Venture 2006) and major wetland complexes are currently managed by the USFWS, California Department of Fish and Wildlife (CDFW), local water districts (e.g., Grassland Water District), non-governmental organizations (e.g., The Nature Conservancy, Ducks Unlimited), and private landowners. Our Central Valley study area was divided into 3 sub-regions: the Sacramento Valley, the Sacramento-San Joaquin River Delta and Suisun Marsh (Delta), and the San Joaquin
Basin, which included the Grassland Ecological Area (GEA) and Mendota area wetlands. The GEA was defined as the Grasslands Wildlife Management Area, Volta Wildlife Area (WA), Los Banos WA, San Luis National Wildlife Refuge (NWR), Merced NWR, and adjacent privately owned lands.

METHODS

Capture and Molt Status
We captured adult dowitchers using mist nets, leg-noose mats, and an air-powered net gun from 15 August to 17 September 2012 (n = 31) and 5 August to 15 September 2013 (n = 86). We used plumage characteristics to confirm species and age (Pyle 2008), and categorized each dowitcher into 1 of 8 primary molt stages that were based on wing molt observations of 303 museum specimens of dowitchers collected from July to October throughout North America (Putnam 2005; Fig. 2). Each molt stage was intended to represent an equal interval of the primary molt duration (Putnam 2005); thus, we considered the molt stages as a proxy for the percentage of primary mass grown (Summers et al. 1983). Lastly, we attached radio-tags with an expected lifespan of 153 days (1–1.5-g coded nano-tags; Model NTQB-4-2, Lotek Wireless, Newmarket, Ontario, Canada) to a subsample of dowitchers (n = 27 in 2012; n = 54 in 2013). We radio-tagged ≤5 dowitchers/day to obtain a representative sample across the peak migration of post-breeding adult dowitchers, which occurs during August and September (Takekawa and Warnock 2000). Captures

Figure 1. Study area for radio-telemetry surveys of fall migrant long-billed dowitchers (left). Klamath Basin study area (right) includes major managed wetland complexes and locations of radio-tagged long-billed dowitchers recorded during aerial surveys from August to October 2013. NWR = National Wildlife Refuge.

Figure 2. Primary molt stages of long-billed dowitchers developed by Putnam (2005). Molt stage 0 indicates all old and molt stage 7 all new flight feathers. © C. G. Putman.
included 35 dowitchers at Wood River Wetland, 12 at Williamson River Delta Preserve, 19 at Lower Klamath NWR, 38 at Tule Lake NWR, and 13 in a flooded agriculture field adjacent to Tule Lake NWR (Fig. 1). Our capture efforts followed guidelines approved by the North American Banding Council for safe and ethical treatment of shorebirds (Gratto-Trevor 2004); capture and marking were covered under United States Geological Survey Bird Banding Laboratory permit #09316.

To determine whether molt stage was advancing during migration, we used an ordered logistic regression with molt stage as the response and capture date as the predictor variable (Agresti 2013). We anticipated that most dowitchers would have a similar molt phenology and molt stage would have a positive relationship with capture date if active molt was occurring during migration. We considered the effect of capture date to be significant if the 95% confidence interval of its coefficient value did not overlap 0. We then calculated the average primary molt duration (in days) using the coefficient value for capture date (predictor), which was equivalent to the increase in molt stage (response) per 1-unit increase in capture date (Pimm 1976).

Length of Stay After Capture
We determined whether the Klamath Basin was being used as a stopover site or staging area (Ma et al. 2013) by tracking radio-tagged dowitchers via air and ground surveys from 14 August to 1 November 2013 and estimating their average length of stay after capture. Some aerial surveys were designed to detect all dowitchers present in the Klamath Basin study region (probability of detection near 1; Goymann et al. 2010). These region-wide surveys covered all potential shorebird habitat from roughly 400–800 m above ground every 14–20 days (n = 5). No dowitcher undetected during a region-wide aerial survey was detected during any subsequent air or ground survey; thus, we assumed that a dowitcher was no longer present in the Klamath Basin if it was not detected during a region-wide aerial survey.

We also conducted supplemental air and ground surveys that did not cover the entire region (probability of detection <1) to increase the accuracy of length of stay estimates. These data gave us more frequent detections and allowed us to use the latest detection for each dowitcher when calculating average length of stay after capture. Supplemental aerial surveys occurred along routes used for USFWS waterbird monitoring. They covered large lakes and wetland complexes in the Klamath Basin (Fig. 1) and occurred at low altitudes (approx. 100–200 m), using 0.8-km wide transects over lakes and large wetland areas, every 8–15 days from 4 September to 24 October 2013 (n = 5). We conducted ground surveys using handheld telemetry antennas from accessible roads from 14 August to 26 September 2013. Ground surveys covered potential shorebird habitat within or close to Lower Klamath NWR, Tule Lake NWR, Lake Ewauna in Klamath Falls, Williamson River Delta Preserve, Wood River Wetland, and several nearby privately-owned wetlands and flooded agricultural fields.

We defined length of stay after capture as the time period between the capture date and last detection of each dowitcher, plus the duration between its last detection and estimated departure date. To calculate length of stay after capture, we used a maximum likelihood estimate of daily survival rate (DSR) from the nest success model in Program MARK (White and Burnham 1999). First, we formatted our tracking data to generate an encounter history for each dowitcher by defining our survey season as the first capture date (day 1; 5 August 2013) to the last region-wide aerial survey (day 89; 1 November 2013). We then compiled encounter histories to include 5 pieces of information: 1) capture date, 2) date of the last detection, 3) date of subsequent region-wide aerial survey after last detection, 4) final fate of the bird (always 1 because all dowitchers departed the region by the end of the study period), and 5) the number of tagged birds with the same history. We considered the fitted DSR to be the daily probability that a radio-tagged dowitcher remained in the Klamath Basin. Finally, we calculated average length of stay after capture (S) using the fitted DSR (φ) and the life expectancy formula \[ E = \frac{1}{1 - \phi} \] as suggested by Efford (2005). We calculated the 95% confidence interval of \( S \) using the 95% confidence interval of the fitted DSR (φ).

Migratory Connectivity
We estimated the probability that a dowitcher migrating through the Klamath Basin would occur in the Central Valley by relocating radio-tagged dowitchers using aerial surveys during fall (Oct–Nov; \( n = 2 \) in 2012, \( n = 4 \) in 2013) and winter (Dec–Feb; \( n = 6 \) in 2012–2013 and 2013–2014). To ensure that we detected all radio-tagged dowitchers in the Central Valley during each survey (i.e., probability of detection near 1), we completed a test flight with radio-tags placed in known locations on the ground to determine optimal transect spacing (4.8 km) and altitude (approx. 1,000 m) prior to establishing survey routes (Point Blue Conservation Science, unpublished data). We did not survey when visibility was reduced by fog or low clouds.

We used detections of radio-tagged dowitchers in the Central Valley and logistic regression models to calculate 1) the probability of occurrence after 1 December (winter) anywhere in the Central Valley study area, and 2) the probability of occurrence between October and February in each Central Valley sub-region. We compared probability of occurrence models separately by year and sub-region; individual dowitchers detected in ≥1 sub-region contributed to the probability of occurrence for each sub-region of detection. We considered differences in probability of occurrence to be significant if their 95% confidence intervals did not overlap. Next, to provide context for migratory connectivity between stopover or staging areas in the Klamath Basin and wintering areas Central Valley, we calculated the Euclidean distance between the capture site and detection location, or the geometric center of multiple detection locations, in the Central Valley for each dowitcher detected after 1 December each year.

Finally, to quantify space use in the Central Valley, we used a fixed kernel density estimator to calculate a utilization
distribution (UD) for dowitchers in each sub-region (Seaman and Powell 1996); we pooled all detections during fall and winter by sub-region prior to analysis because the number of detections/individual was low (range = 1–9). We calculated the area of the 95% UD for each of the 3 sub-regions and the proportion of each sub-region that the 95% UD encompassed . We also used the 50% portion of the UD to identify important wintering areas within each sub-region.

RESULTS

Molt Status and Length of Stay After Capture

We observed active primary molt (molt stages 1–6) in 83% of 116 dowitchers captured in the Klamath Basin (Fig. 3). Although 14% of dowitchers had no old primaries remaining when captured (molt stage 6), none had completed growth of primaries 9 and 10 (molt stage 7). Between 4 and 6 primaries were growing on 24% of 116 dowitchers that we captured (molt stages 1 and 2), but all birds were capable of flight before and after capture. Average molt stage increased significantly with capture date (95% CI: 0.10–0.17; Fig. 3). The average primary molt duration for dowitchers in the Klamath Basin was 53.6 days (95% CI: 42.4–72.7 days).

We detected 80% of 54 dowitchers radio-tagged during 2013 at least once in the Klamath Basin, and estimated their average length of stay after capture to be 31.9 days (95% CI: 24.3–41.9 days). We detected fewer dowitchers during each successive aerial survey in the Klamath Basin until none were detected during our last survey on 1 November. Detections occurred primarily in wetlands associated with Upper Klamath Lake or Tule Lake NWR (Fig. 1), but some were also recorded at Lake Ewuana in Klamath Falls, a flooded agricultural field north of Lower Klamath NWR, and several smaller private wetlands. Three detections occurred in Lower Klamath NWR in October after flooding of semi-permanent wetlands began. No detections occurred near or within Klamath Marsh NWR or Clear Lake NWR.

Space use by radio-tagged dowitchers varied between sub-regions in the Central Valley (Fig. 4). In the Sacramento Valley, the 95% UD of dowitcher detections comprised 53% of the land area (9,595 km²); the 50% UD encompassed the Sacramento-Delevan-Colusa NWR complex and nearby rice fields, as well as complexes of privately owned managed wetlands and rice fields around 20 km southeast of Colusa NWR at 15 km southeast of Sutter NWR. In contrast, the 95% UD of dowitcher detections comprised 4% of the land area in the San Joaquin Basin (13,249 km²), primarily because 98% of 109 detections were within the GEA; the 50% UD occurred primarily in privately owned managed wetlands within the northwest and southern portions of the GEA. In the Delta, 47% of 32 detections occurred in wetlands or rice fields near Yolo Bypass WA and the 95% UD comprised 45% of the land area (8,445 km²); the 50% UD encompassed the Yolo bypass, Liberty Island WA, a portion of Suisun Marsh, and privately owned agriculture lands and wetlands on Staten, Bouldin, and Twitchell islands.

DISCUSSION

Our data indicate that most dowitchers undergo primary molt during fall migration and they use the Klamath Basin as a molt migration staging area from August to October. We observed advancing stages of primary molt in the Klamath Basin along with stays that lasted over a month on average. We established migratory connectivity to the Central Valley; more than half of radio-tagged dowitchers were located in the Central Valley after 1 December. We also found that space use by dowitchers differed between sub-regions of the Central Valley. When combined, our data highlight the need for conservation measures that protect the molt migration staging areas used by dowitchers in the Klamath Basin and wintering areas in the Central Valley and consider the effects of differing compositions and spatial distributions of habitat for dowitchers within 3 sub-regions of the Central Valley.

Molt Migration in Long-Billed Dowitchers

Shallow-water wetlands and flooded agricultural lands in the Klamath Basin are important molt migration staging habitat for dowitchers. Most adult dowitchers in the region molted primaries from late July until October and they required an
average of 54 days to complete primary molt; Putnam (2005) estimated average molt duration to be 66 days. Combining our estimates of molt duration and average length of stay (>32 days) suggests that most dowitchers undergo a substantial portion of their primary molt before departing the Klamath Basin. During August, many dowitchers likely had reduced flight performance (molt stages 1 and 2) making them more vulnerable to predation and less likely to begin a long distance flight because of increased energetic costs (Hendenström 2003). Maintaining adequate water levels in wetlands during August and September may be particularly important for the high proportion of adult

Table 1. Probability that a long-billed dowitcher radio-tagged in the Klamath Basin (along the Oregon-California border, USA) was located in the Central Valley of California and in 3 of its sub-regions. Individuals detected in ≥1 sub-region were included in probability of occurrence estimates for each sub-region (n = 5 in 2012 and n = 6 in 2013). The 95% confidence intervals are located below each estimate of probability.

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>Detected during winter</th>
<th>Sacramento Valley</th>
<th>Sacramento-San Joaquin Delta</th>
<th>San Joaquin Basin</th>
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<tr>
<td></td>
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<td></td>
</tr>
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<td>0.06–0.21</td>
<td>0.23–0.43</td>
</tr>
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</table>

*a* Fall or winter was October–February.  
*b* Winter was December–February.

Figure 4. Detection locations (black dots) in the Central Valley of California (n = 228) from October to February 2012–2013 and 2013–2014 for long-billed dowitchers radio-tagged in the Klamath Basin (n = 51; range = 1–9 detections/individual). We calculated 95% and 50% utilization distributions (UDs) using a fixed kernel density estimator. Water distribution depicts the average distribution of open water (<25% vegetated) from November to January 2000–2010 (Reiter and Liu 2011). National Wildlife Refuges (NWR) and State of California Wildlife Areas (WA) that contain managed wetlands are identified in maps of sub-regions.
dowitchers that use the Klamath Basin as a molt migration staging area.

Dowitcher molt migration also likely occurs elsewhere in North America. There are accounts of molting dowitchers during fall in New Jersey, USA (Jehl 1963), Washington, USA (Paulson 1993), and Saskatchewan, Canada (Alexander and Gratto-Trevor 1997). More notably, Putnam (2005) documented dowitchers with missing primaries on museum specimens collected between July and October at widespread locations, including 19 sites throughout the United States (3 sites in the Central Valley), 3 in southern Canada, and 3 in central Mexico. Taken together with our data, we suggest that a high abundance of dowitchers at an inland site during August and September may be indicative of a molt migration staging area; most hatch-year dowitchers do not migrate southward until October (Takekawa and Warnock 2000). For example, Shuford et al. (2002) recorded >2,000 dowitchers during August or September at 8 wetland complexes in the Great Basin, including the Klamath Basin and the Lahontan Valley, the latter a region consisting of several wetland complexes in western Nevada where >100,000 dowitchers were counted during migration (Neel and Henry 1996). Studies of dowitcher molt migration at these and other potential staging areas would increase our understanding of any significant intra-specific variation in molt strategies that may exist and provide specific management recommendations for those areas.

Our understanding of molt migration in shorebirds is limited, in part, because most exhibit considerable inter- and intra-species variation and flexibility in molt strategies (Remisiewicz 2011). Molt migration has now been documented for 3 interior migrant shorebirds, which often have flexible strategies because of the unpredictability of freshwater wetland resources (Piersma 2003, 2007). For example, the primary molt of wood sandpipers (Tringa glareola) that breed in Scandinavia has been documented during their stopovers in the Camargue region of southern France (100% of captured birds; Hoffmann 1957), but only up to 6% of those that breed in Siberia undergo primary molt at stopover sites in eastern Europe (Pinchuk et al. 2008). In North America, most female Wilson’s phalaropes staging at Mono Lake, California, molt ≤5 primaries prior to trans-equatorial flights to non-breeding areas in South America; most males, which migrate later than females, molt ≤3 primaries at Mono Lake prior to departure (Jehl 1987). In our study, the high proportion of dowitchers molting at capture (83%) combined with an increasing trend in molt stage suggests that individual variability in molt strategy and phenology may be limited in the Klamath Basin. Details on the numbers of primaries molted by dowitchers while in the Klamath Basin remains uncertain because we did not recapture any or know where they molted primaries prior to capture. It is possible that some dowitchers began primary molt farther north or that some with short stopover times molted primarily at wintering areas. However, we provide strong evidence that most dowitchers were molting during migration and advise that some variation in molt phenology is characteristic of molt migrants and other molting shorebirds.

**Drought and Migrant Long-Billed Dowitchers**

Drought can influence wetland availability and the stopover ecology of fall migrant shorebirds. Shorter stopover durations were recorded for fall migrant pectoral sandpipers (Calidris melanotos) during a year with low water availability along their interior migration route in the Mississippi Alluvial Valley in central North America (Lehnen and Krementz 2005), and a similar effect may have occurred because of reduced water availability to flood wetlands and agricultural lands in the Klamath Basin during our study. No water was available to flood wetlands at Lower Klamath NWR from March to late-September 2013, in part, because of an ongoing severe to extreme drought in central Oregon and northern California (http://droughtmonitor.unl.edu/, accessed 10 Nov 2014). Lower Klamath NWR is where Shuford et al. (2004) recorded the highest abundance of dowitchers in the Klamath Basin during August surveys, but the refuge currently relies on water diversions from the Klamath River or funding to import water from elsewhere (Mayer and Thomasson 2004). The paucity of water resulted in the drying of all wetlands in Lower Klamath NWR by August 2013 (e.g., Unit 12C; B. A. Barbaree, Point Blue Conservation Science, personal observation) and we did not locate a radio-tagged dowitcher within Lower Klamath NWR until 2 October 2013. Similar curtailments occurred during winter 2013–2014 in the Central Valley when water deliveries to most rice fields ceased after 1 December 2013. These observations underscore that shorebirds using interior migratory routes are relying on wetlands with highly variable (because of water policy and management) and often ephemeral availability (because of climatic variation), thus their stopover strategies must be flexible (Skagen and Knopf 1994, Warnock et al. 1998).

During drought years when water supplies are most limited and ephemeral wetlands are rare, interior migrant shorebirds must depend on the more consistent habitat provided by relatively large wetland ecosystems (Mettke-Hofman and Greenberg 2005). This can result in increased shorebird abundance at some interior staging areas (Robinson and Warnock 1997). If more migrant shorebirds use large wetland complexes during drought, identifying these areas and ensuring that shallow-water habitat is available, even when water is limited, will likely have a population-level value. When additional water is available, increasing wetland connectivity by flooding small, temporary wetlands along migration routes can provide functional stopover habitat for interior migrants (Haig et al. 1998).

**Klamath Basin and Central Valley Connectivity**

Our data indicate migratory connectivity between 2 regions of importance to migratory shorebirds in the Pacific Flyway. More than half of dowitchers migrating southward through the Klamath Basin were located in the Central Valley after 1 December, establishing connectivity between these regions for migratory shorebirds similar to waterfowl (Miller et al. 1992, 2005). Radio-tagged dowitchers likely arrived in the
Central Valley from August to October, a time period when water shortages can affect both regions. Increased coordination among wetland managers during this period would help maximize the value of limited freshwater to flood wetlands and agricultural lands for migratory shorebirds and waternfowl. Coordinated management during fall may be critical for dowitchers, and other interior migrant shorebirds, because they are among the most vulnerable to population declines in North America owing to limited inland water resources, the growing impacts of drought, wetland loss or degradation, and rapid environmental change (Galbraith et al. 2014).

Locations of radio-tagged dowitchers in the Central Valley highlighted the importance of the shallowly flooded habitat in the Sacramento Valley and the GEA in the San Joaquin Basin (Fig. 4). Dowitchers were more likely to be located in the Sacramento Valley or San Joaquin Basin than in the Delta, even though the Delta contains these regions. Our results support findings by Shuford et al. (1998) who recorded fewer dowitchers in the Delta region than in the Sacramento Valley or San Joaquin Basin. This information can be used to identify and prioritize locations where establishing wetland connectivity may be beneficial, such as southern portions of the Delta and northern portions of the San Joaquin Basin. Moreover, movements by dowitchers between Central Valley sub-regions in our study, and between the Central Valley and San Francisco Bay (Takekawa et al. 2002), suggest that dowitchers will move across large landscapes during the non-breeding season in California. Whether these movements are in response to predators, limited food or habitat, or other factors is not known.

Space Use in the Central Valley

Our study also indicates that dowitcher space use is different within sub-regions of the Central Valley from December to February. Dowitcher locations were widespread in the Sacramento Valley but were clumped almost entirely within the GEA in the San Joaquin Basin. This difference is mostly explained by the widespread but patchy distribution of wetlands and flooded rice fields in the Sacramento Valley compared to a nearly contiguous, but comparatively small area of managed wetlands in the GEA (Central Valley Joint Venture 2006; Fig. 4). Less use of the Delta by radio-tagged dowitchers suggests that most dowitchers prefer areas with more extensive or more contiguous habitat. The contrasting amounts and distributions of potential habitats in 3 sub-regions of the Central Valley are the result of landscape-scale conservation efforts that created wintering habitat for wetland-dependent birds (Central Valley Joint Venture 2006).

Landscape-scale conservation efforts over the past 25 years have resulted in differing amounts and distributions of potential dowitcher habitat in the Central Valley sub-regions. In 1990, the Central Valley Habitat Joint Venture Implementation Plan established conservation objectives within Central Valley sub-regions that included wetland protection, wetland restoration, and winter flooding of agricultural land (Central Valley Joint Venture 2006). As a result, between 1990 and 2003, >225 km² of wetlands were protected and >235 km² of wetlands were restored (>48 and >110 km² in Sacramento Valley, >18 and >35 km² in Delta, and >162 and >92 km² in San Joaquin Basin, respectively; Central Valley Joint Venture 2006). Also by 2003, there were >1,400 km² of rice fields regularly flooded during winter in the Sacramento Valley and >150 km² of winter-flooded rice and corn in the Delta; widespread flooding of agricultural lands does not occur in the San Joaquin Basin (Central Valley Joint Venture 2006). Results from our study demonstrate that the amount and distribution of habitat will influence the likelihood that dowitchers use an area, while also affecting their space use after arrival. Whether conservation efforts and the resulting variation in space use between sub-regions affects the fitness or survival of non-breeding dowitchers is not known. Ensuring that freshwater is available to flood wetlands and agricultural lands in the Central Valley is imperative to sustain non-breeding dowitchers and other wetland-dependent birds.

MANAGEMENT IMPLICATIONS

Our results suggest 3 actions that would improve the conservation and management of dowitchers and other interior wetland–dependent birds. First, we recommend that when water supplies are sufficient, shallow-water habitat should be maintained from 1 August to 30 September in the Klamath Basin and other potential dowitcher staging areas. When water is limited, shallow-water habitat should be maintained for a minimum of 30 days from approximately 1 August to 1 September, which is the period when reduced flight performance because of primary molt was most prevalent in dowitchers during our study (molt stages 1 and 2). Second, because of strong migratory connectivity between the Klamath Basin and Central Valley, inter and intra-regional management teams should be created to develop a structured decision-making process (Gregory et al. 2012) that strategically floods wetlands and agricultural lands to meet management objectives for waterbirds based on various water availability scenarios. This approach should prioritize locations that efficiently use limited water supplies and categorize locations as potential staging areas, wintering areas, or both. Lastly, we recommend long-term solutions such as the restoration or reclamation of once natural wetlands or marsh habitat (e.g., the Williamson River Delta Preserve near Upper Klamath Lake), as another strategy to ensure shallow-water wetlands are available for migratory shorebirds when drought occurs.

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