

Migration efficiency sustains connectivity across agroecological networks supporting sandhill crane migration

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Abstract. Preserving avian flyway connectivity has long been challenged by our capacity to meaningfully quantify continental habitat dynamics and bird movements at temporal and spatial scales underlying long-distance migrations. Waterbirds migrating hundreds or thousands of kilometers depend on networks of wetland stopover sites to rest and refuel. Entire populations may rely on discrete wetland habitats, particularly in arid landscapes where the loss of limited stopover options can have disproportionately high impacts on migratory cost. Here, we examine flyway connectivity in water-limited ecosystems of western North America using 108 GPS tagged greater sandhill cranes. Bird movements were used to reconstruct wetland stopover networks across three geographically unique sub-populations spanning 12 U.S.–Mexican states and Canadian provinces. Networks were monitored with remote sensing to identify long-term (1988–2019) trends in wetland and agricultural resources supporting migration and evaluated using network theory and centrality metrics as a measure of stopover site importance to flyway connectivity. Sandhill crane space use was analyzed in stopover locations to identify important ownership and landscape factors structuring bird distributions. Migratory efficiency was the primary mechanism underpinning network function. A small number of key stopover sites important to minimizing movement cost between summering and wintering locations were essential to preserving flyway connectivity. Localized efficiencies were apparent in stopover landscapes given prioritization of space use by birds where the proximity of agricultural food resources and flooded wetlands minimized daily movements. Model depictions showing wetland declines from 16% to 18% likely reflect a new normal in landscape drying that could decouple agriculture–waterbird relationships as water scarcity intensifies. Sustaining network resilience will require conservation strategies to balance water allocations preserving agricultural and wetlands on private lands that accounted for 67–96% of habitat use. Study outcomes provide new perspectives of agroecological relationships supporting continental waterbird migration needed to prioritize conservation of landscapes vital to maintaining flyway connectivity.

Key words: agricultural irrigation; agroecology; flyway connectivity; migratory networks; network analysis; North America; sandhill crane; water scarcity; waterbirds; wetlands.

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INTRODUCTION

Migration is fundamental to avian ecology allowing birds to move between breeding and wintering locations to capitalize on favorable food and weather conditions (Gauthreaux 1982). Birds link their movements along continental flyways covering hundreds to thousands of kilometers using a distinct network of stopover sites to rest and refuel. Although occupied for only short periods over an entire avian annual cycle (i.e., migration, breeding, and wintering), stopover sites can be crucial to a large proportion of a population. Thus, loss of a relatively small amount of habitat can have disproportionately high impacts (Weber et al. 1999, Baker et al. 2004, Murray et al. 2018). Recent work shows 91% of migratory bird species lack adequate protected area coverage for some portion of their annual cycle, particularly stopover sites that are poorly understood despite considerable focus of conservation need in the literature (Runge et al. 2015). Acceleration of global ecological impacts brought on by changing climate and natural resource consumption (Butchart et al. 2010) raises concerns over declining flyway connectivity and the effect stopover habitat loss may have on migratory bird populations (Kirby et al. 2008, Small-Lorenz et al. 2013, Culp et al. 2017).

Shaped by water scarcity, human settlements have long been connected to migratory flyways in arid and semi-arid continental interiors where migrating waterbirds and historic agriculture concentrate around a limited number of ecologically important wetland and riparian resources (Morrison and Myers 1989, Haig et al. 2019). Water development associated with these sites today drives irrigation and urban development supporting metropolitan centers and agricultural economies that account for 40% of global food production (UNESCO-UN-Water 2020). While most wetland and riparian ecosystems have been significantly altered, they remain fundamental to biological processes sustaining waterbird migration. Populations in some flyways have adapted to landscape change and offset habitat loss in part

by utilizing abundant agricultural food resources that now support energetically demanding migrations (Elphick and Oring 2003, Gauthier et al. 2005, Fox et al. 2017). Long-term sustainability of waterbird migratory flyways will require a better understanding of underlying agriculture and wetland relationships to inform policy and conservation measures that balance economic and ecosystem benefits (Wada et al. 2013).

Arid and semi-arid mid-latitudes of western North America are among the most important inland waterbird flyways in the Western Hemisphere (Oring and Reed 1997, Wilsey et al. 2017). In this region, migratory flyways are structured around distinct wetland basins and riparian drainages that support large terminal lakes and freshwater palustrine wetlands. These habitats collectively make up a stopover network supporting 94 migratory waterbird species and millions of individual birds during breeding, wintering, and migration (Drewien and Bizeau 1974, Jehl 1994, Oring and Reed 1997, Paul and Manning 2002, Drewien et al. 2003, IWJV 2013). Wetland and riparian hydrology is heavily influenced by surface and groundwater reclamation supporting agriculture through complex storage and delivery systems overlaying migratory flyways. Two-thirds of wetlands are associated with agriculture (Donnelly et al. 2020), supporting valuable waterbird habitat, mainly consisting of flooded irrigated riparian wet meadows (McWethy and Austin 2009, Fleskes and Gregory 2010, Moulton et al. 2013).

Preserving flyway connectivity has long been challenged by our capacity to meaningfully quantify continental habitat dynamics and bird movements at the temporal and spatial scales underlying seasonal migration. In western North America, we used greater sandhill crane (*Antigone canadensis tabida*, hereafter sandhill crane) migration as a model system to evaluate waterbird flyway connectivity by reconstructing their migratory networks and examining landscape change associated with agriculture and wetland stopover habitats. Sandhill cranes are an iconic waterbird species that rely on shallowly flooded

emergent palustrine wetland and riparian habitats for roosting and foraging during migration (Drewien and Bizeau 1974, Littlefield et al. 1994). As with several other waterbird species, sandhill cranes have adapted to agriculturally dominated landscapes by supplementing dietary needs with waste grain (e.g., barley, corn, oats, and wheat) remaining in cultivated fields post-fall harvest (Austin 2012). The abundance of flood-irrigated riparian hay meadows maintained for livestock ranching also provides important wetland habitats used by sandhill cranes for roosting and foraging (McWethy and Austin 2009).

Spring and fall migratory stopover networks were derived from seasonal sandhill crane

movements spanning 12 U.S.–Mexican states and Canadian provinces in western North America (Fig. 1). Network analysis and centrality metrics were used to evaluate stopover site importance to flyway connectivity (McRae et al. 2008, Jacoby et al. 2012). Changes to network habitat availability were measured over 31 yr (1988–2019) using satellite imagery to monitor wetland surface water trends. Wetland monitoring was linked to agricultural cropping and land ownership patterns to provide a new flyway scale perspective of agroecological relationships supporting continental migration. Study outcomes provide guidance that prioritizes landscapes vital to preserving waterbird flyway connectivity. Although

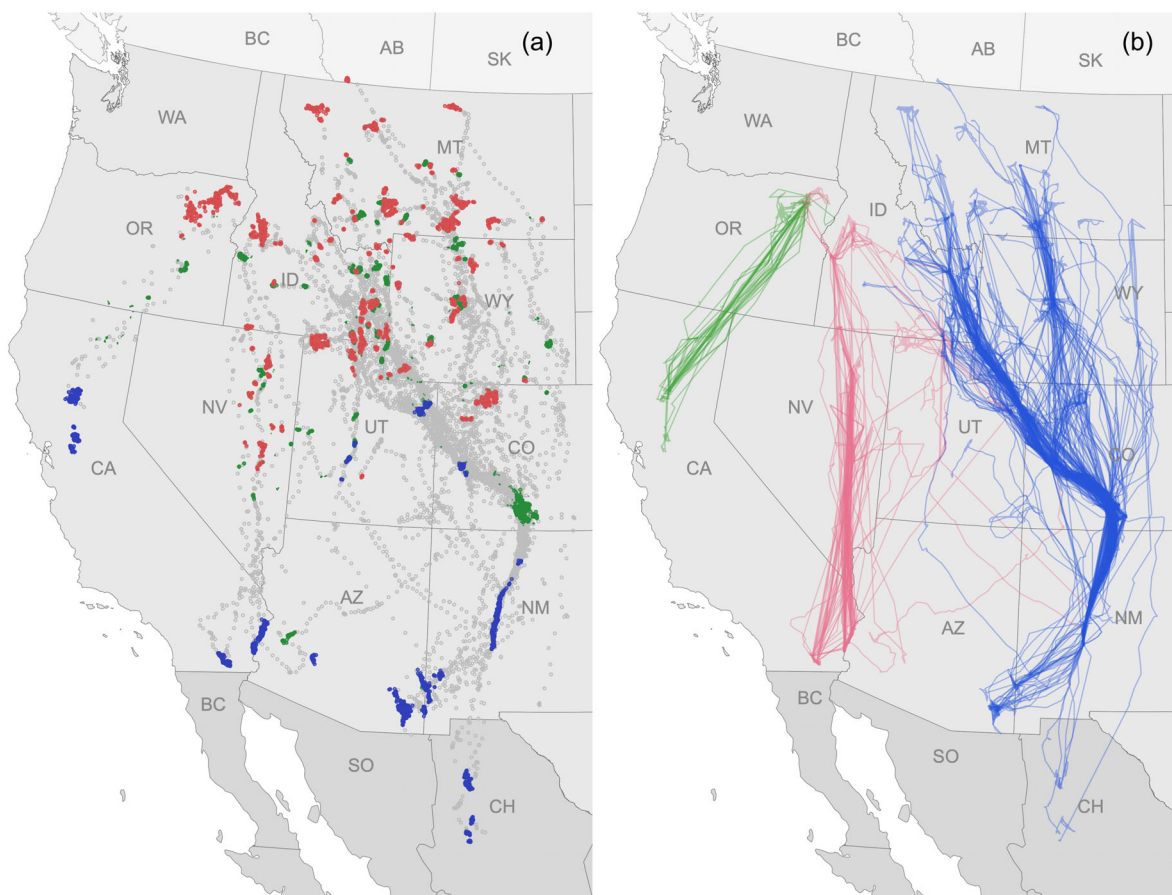


Fig. 1. Sandhill crane GPS locations (a) classified by annual cycle as summering (red), migration (gray), stopover (green), and wintering (blue). Associated satellite tracks (b) for Central Valley (green), Lower Colorado River Valley (red), and Rocky Mountain (blue) population segments. Data acquired from 108 individual birds from fall 2014 to spring 2020. Movements encompass 187 and 150 complete spring and fall migration cycles. Some summer and winter locations also functioned as stopover locations.

concentrated in North America, this research has application to all eight global waterbird flyways (Wetlands International 2012), all of which must balance changing water demands for irrigated agriculture and sustainability of wetland habitats supporting waterbird migration.

MATERIAL AND METHODS

Study area

Movements of GPS-tagged sandhill cranes in western North America defined the projects' geographic extent (Fig. 1). In this arid to semi-arid region, wetlands make up only 1–3% of the landscape footprint (Tiner 2003). Most wetlands are concentrated in valley bottoms along riparian flood plains and closed basin terminal lakes where associated water resources support irrigated agriculture on surrounding private lands. Publicly owned wetlands occur on U.S. Fish and Wildlife, National Wildlife Refuges and state wildlife areas, hereafter "wildlife refuges," managed to support sandhill cranes and other migratory waterbird populations. Private wetlands are primarily associated with flood-irrigated riparian hay meadows used for livestock forage production. Other prominent agricultural land uses include irrigated cultivation of small grain (e.g., barley, corn, oats, and wheat), alfalfa, and row crops (e.g., potatoes and chillies). Climate patterns in northern regions of the study area are characterized by cold wet winters and hot dry summers. Wetland flooding is induced by spring runoff tied to high-elevation snowmelt. Most wetlands are flooded seasonally, early spring through mid-summer, after which evaporative drying reduces surface water availability. Southern portions of the study area (Arizona, New Mexico, Mexico) exhibit mild winter conditions and hydrology heavily influenced by summer monsoonal air masses and thunderstorms that produce intermittent surface water flows supporting freshwater terminal lakes and wetlands.

Crane capture and GPS deployment

Sandhill crane movements were derived from 108 individual birds captured and fitted with GPS leg bands. Band deployments were partitioned among summer (35) and winter (78) areas covering three geographically distinct population segments; Central Valley (CV), Lower Colorado

River Valley (LCRV), and Rocky Mountain (RM; Collins et al. 2016a; Fig. 1b, Appendix S1). The majority of band deployments were staggered from November to January within large aggregations of wintering birds to increase assurances monitoring results were distributed among geographically distinct cohorts. Deployments were partitioned among individual population segments to capture differences in migratory routes. Band deployments in summering areas were focused strategically in regions that closed monitoring gaps in underrepresented portions of known migratory pathways. Breeding status and sex of adult banded sandhill cranes ($n = 100$) were unknown, but assumed to have minimal influence on our broadscale assessment of migratory networks. Because sandhill cranes form life-long pair bonds and maintain close contact family groups throughout annual summering, migration, and wintering periods, bird movements were considered similar among sexes. Additionally, birds marked as colts ($n = 8$) in summering areas exhibited migration patterns similar to adult birds during their first and successive migrations ($n = 18$) when they are typically forced out of family groups and function as unpaired non-breeders. Migratory networks derived from these movements were consistent with the movement ecology and distribution of the three population segments sampled (Collins et al. 2016a). Marked birds from the CV represented eastern portions of the population's extent due to band deployments targeting a summering region in northeastern Oregon (Pacific Flyway Council 1997).

Location acquisition rates of individual bands varied from four to 45 points per day. Location data encompassed approximately 81,000 bird-use days acquired from spring 2014 to spring 2020 (Appendix S1: Fig. S2) with over 75% of days containing seven or more acquisitions per 24 h. In total, 187 unique northward spring migrations and 150 southward fall migrations were spatially inventoried. Detailed capture and GPS deployment procedures are provided in Collins et al. (2016b), Nowak et al. (2018), and Boggie et al. (2018).

Movement classification

First passage time analysis (FPT) was used as a metric to classify annual sandhill crane

movements as summering, migration, stopover, or wintering (Fig. 1a; Johnson et al. 1992). This approach made it possible to measure sandhill crane space-use over time and identify the spatiotemporal scales at which birds interacted with landscapes (Fauchald and Tveraa 2003). Because FPT is scale dependent, we calculated sandhill crane movement variance at radii from 1 to 100 km to distinguish slow localized movements from rapid long-distance migration (sensu Le Corre et al. 2014). We segmented FPT results temporally using Behavioral Change Point Analysis (BCPA; Lavielle 1999, Lavielle and Teysnière 2006). This method optimized segmentation of seasonal space use by minimizing a contrast function (i.e., a function measuring the discrepancy between rapid long-distance migration and an underlying model characterized by slow localized movements). We applied BCPA using a mean contrast function and minimum location use parameter of 10. Differences in GPS acquisition rates among birds did not influence BCPA segmentation due to large-scale migration vs. localized movements that were distinguished. Both FPT and BCPA were implemented with R-package *adehabitatLT* (Calenge 2011).

Movement segments were classified for individual birds using a rule-based approach linked to seasonal timing and duration of unique space-use patterns. Summering and wintering segments were identified as prolonged localized movements beginning in early spring and late fall, respectively. Migration was classified as segments occurring between these periods. Stopover segments were classified as localized movements occurring for greater than 48 h during migration. Forty-eight hours was used as a temporal delimiter of stopovers, considering prolonged localized space use was indicative of migratory bird settling or refueling behaviors (Drent et al. 2006). Stopover sites identified in this manner were used consistently with >98% of locations occupied over multiple migrations. Overall stopover distribution and use were consistent with a hopping migration strategy observed in LCRV sandhill cranes (Conring et al. 2019) where birds tend to travel relatively short distances before stopping due to availability of predictable food resources and/or loafing and roost locations (Warnock 2010). We acknowledge that stochastic events such as weather or hunting had the potential to influence

stopover durations; however, the consistency of stopover reuse suggests these factors were limited in structuring broader network movements.

To ensure bird movements were comprehensive of sandhill crane migration networks, discovery of novel stopover locations were monitored annually from 2014 to 2020. Steeply declining discovery rates nearing zero in 2019 and 2020 (Appendix S1: Fig. S3) suggested our network encompassed the majority of stopover locations. Stopover sites identified were predictive of all previously known stopover locations within the study area (Drewien and Bizeau 1974, Nowak et al. 2018, Thorpe et al. 2018, Conring et al. 2019).

Mean total migration-stopover days between summering and wintering locations were calculated for each population segment during spring-fall migration. All classified BCPA results were exported to a GIS for visual inspection and editing to ensure classifications aligned with observed bird movements.

Migration networks

Utilization distributions for summering, wintering, and stopover segments were generated for individual birds with a dynamic Brownian bridge movement model (dBBMM; Kranstauber et al. 2012). A window size of 11 and margin of three locations were used as dBBMM input parameters with output resolution set to 100 × 100 m. To define the extent of local space use, 95% isopleths were extracted from utilization distributions. Isopleths for individual birds were imported to a GIS as polygons and areas of overlap merged to identify cumulative space-use patterns representing distinct sandhill crane summering, wintering, and stopover areas. R-package *move* was used to implement dBBMM (Kranstauber et al. 2019).

Migration lags for sandhill cranes were defined as all non-stop flight distances between summering and wintering locations, excluding localized movements <20 km. All distances were measured under a universal transverse mercator projection. Maximum and median lags were calculated separately for individual population segments and spring-fall migrations (Appendix S1: Fig. S4).

Summering, wintering, and stopover polygons were used as nodes to construct migration networks. Networks were generated separately for

individual sandhill crane population segments and spring–fall migrations. Nodes were connected when separated by distances less than the maximum migration lag for each population segment and seasonal migration. Connections and measurements were made from geographic centroids of stopover polygons. Connectivity was assumed to be seasonally directional, where outbound node connections during spring migration (low to high latitude) were made only for headings $>270^\circ$ and $<90^\circ$. Criteria were inverted for fall migration (high to low latitude); that is, outbound node connections were only made for headings $<270^\circ$ and $>90^\circ$.

Following an approach similar to Xu et al. (2019), we assumed longer migration distances were associated with an increased cost of movement and weighted node connections using a dispersal probability. Cost was calculated using a decreasing exponential function (Keitt et al. 1997) that assumed greater distances lowered the probability of sandhill crane movement between nodes. Calculations were implemented as follows:

$$P_{ij} = e^{-kd_{ij}},$$

where P_{ij} is the dispersal probability between nodes i and j , d_{ij} is the distance between nodes i and j , and k is a constant defined by associated sandhill crane migration lags. We set k to obtain a dispersal probability of 50% when d_{ij} equaled the median migration lag of each population segment during spring or fall migration.

Network metrics

Network connectivity values for individual summering, wintering, and stopover nodes were generated using centrality metrics: betweenness, degree, and effective resistance.

The shortest weighted paths between nodes were calculated for each network using the Dijkstra algorithm (Dijkstra 1959). All network connections were weighted using dispersal cost probabilities (see *Migration networks*). Betweenness for individual nodes was calculated as the total number of shortest paths they supported (Freeman 1978, Opsahl et al. 2010). For comparison among networks, betweenness measures were normalized as a proportion of that network's highest betweenness value. Degree for individual nodes was calculated as the sum of

their connections. Effective resistance for individual nodes was determined using the inverse sum of their contribution to overall network redundancy, that is, alternative migratory pathways connecting summering and wintering areas (McRae et al. 2008). All network calculations were implemented using R-package tidygraph (Pedersen 2019).

Importance of individual metrics was compared using a network sensitivity site removal process that eliminated stopover nodes one at a time in descending order of betweenness, degree, and effective resistance (sensu Xu et al. 2019). Random node removal was also simulated ($n = 100$). Network sensitivity was measured for each metric using a stepwise approach that quantified effective resistance during removal. The use of effective resistance in this manner provided a measure of network resilience that accounted for both migration cost (i.e., distance) and redundancy of migratory pathways (McRae et al. 2008). Results were plotted as line graphs for each population segment and spring–fall migration network and provided as supplemental material (Appendix S1: Fig. S5).

Node removal results were compared using an effect index to identify network metrics most characteristic of stopover site importance:

$$E_m = \frac{N_0 \times \ln\left(\frac{R - R_{mm}}{RR_n}\right)}{N_c},$$

where E_m is the effect index of network metrics ($m =$ betweenness, degree, or effective resistance), R_{sum} is the sum of network effective resistance and R_{mm} is the inverse sum of effective resistance when n nodes are removed in sequence of m , N_0 is the total number of nodes in the network, and N_c is the number of nodes removed upon network collapse. Because effect index results were not normally distributed (Kolmogorov-Smirnov test, $D = 0.34$, $P < 0.001$), they were evaluated using a Kruskal-Wallis test and a post hoc nonparametric multiple comparison Dunn test to differentiate E_m . Overall results showed betweenness (i.e., number of shortest migratory paths associated with a stopover node) to be significantly more important ($P \leq 0.05$) to network evaluation (Appendix S1: Fig. S6) and therefore was the centrality metric used to assess flyway connectivity. This outcome

is consistent with sandhill crane observations that suggest birds generally minimize migration by moving between nearest stopover site locations (Drewien and Bizeau 1974). We considered nodes with betweenness scores $\geq 70\%$ to be representative of key stopover sites, essential to maintaining flyway connectivity. Nodes with betweenness scores $\geq 10\%$ and $< 70\%$ were considered important, but were not viewed as essential to maintaining overall flyway connectivity. Network effect index results for individual CV, LCRV, and RM sandhill crane population segments are provided in supplemental materials (Appendix S1: Fig. S7).

Landscape trends

Inside migratory networks, we monitored wetland and agricultural resources (e.g., small grain cultivation) important to sandhill cranes (Pearse et al. 2017, Boggie et al. 2018). Wetland surface water extent was used as a proxy to wetland availability. Following a remote sensing approach outlined by Donnelly et al. (2019), wetland conditions were measured monthly (February–November) from 1988 to 2019 as a rolling five-year mean using Landsat satellite imagery. Normalizing estimates in this way moderated annual climate variability that influenced wetland conditions (Rajagopalan and Lall 1998), increasing detectability of long-term trends. Monthly monitoring also allowed wetlands to be separated into annual hydrologic regimes by totaling monthly presence of surface water within years. Wetlands were classified as temporary (flooded ≤ 2 months), seasonal (flooded > 2 and ≤ 8 months), or semi-permanent (flooded > 8 months) using standards similar to Cowardin et al. (1979).

Wetland monitoring results were summarized annually by hydrologic regime as two-month averages during spring (March–April) and fall (September–October) migration periods from 1988 to 2019. Change was measured by dividing wetland patterns temporally into equal periods, P1 (1988–2003) and P2 (2004–2019), and applying a nonparametric Wilcoxon test to compare trends (Siegel 1957). A P value of < 0.05 was used to represent statistical significance. Accuracy of surface water area determinations was estimated to be 93–98% by comparison with $\sim 20\%$ of stopover areas that overlapped previous work and identical methods used by Donnelly et al. (2019).

Accuracy was comparable to similar time-series wetland inundation studies using Landsat data (Jin et al. 2017).

Distribution and abundance of small grain cultivation (e.g., barley, corn, oats, wheat) were monitored annually from 2008 to 2019 using National Agricultural Statistics Service (NASS) cropland datasets (NASS 2019). Small grain crops are known to provide important food resources utilized by sandhill cranes during migration (Reinecke and Krapu 1986). Summaries were conducted spatially within sandhill crane stopover space-use polygons. Availability of NASS cropland data restricted monitoring prior to 2008. In a post hoc analysis, we also monitored fall tilling of harvested small grain crops (2008–2019); because this farming practice is known to reduce the availability of waste grain food resources (Krapu et al. 2004), our analysis identified as important to sandhill cranes (see *Network habitat importance*).

Tillage rates were measured annually from 2008 to 2019 using normalized difference soil indices (NDSI) using Landsat satellite imagery:

$$\text{NDSI} = \frac{(\text{band5} - \text{band4})}{(\text{band5} + \text{band4})}$$

From satellite imagery, we generated annual maximum NDSI images representing conditions from 1 September to 30 November. Because high NDSI values correlate with areas of bare soil, it was possible to distinguish tilled vs. non-tilled agriculture. We masked maximum NDSI images spatially using small grain (e.g., barley, corn, oats, and wheat) areas extracted from annual NASS cropland datasets. Small grain areas coincident with high soil reflectance (NDSI > 0.25) were classified as tilled. Tilled agricultural fields visible in Landsat imagery were overlaid with fall maximum NDSI images to identify the threshold value used in our analysis. To ensure outcomes were representative of landscape conditions, results were evaluated by overlaying tillage results on Landsat imagery in randomly selected stopover areas ($n = 20$) independent of model training inputs. Overall accuracy was estimated at 90%.

Network habitat importance

Wetland and agricultural monitoring results were used to generate a suite of spatially explicit

resource variables (Appendix S2: Table S1) important to structuring localized sandhill crane space-use patterns (Pearse et al. 2017, Boggie et al. 2018). Variables were ranked as predictors of local bird densities within stopover sites using randomForestSRC regression tree analysis (Ishwaran and Kogalur 2019) as a nonparametric measure of variable importance (VIMP). Variables identified as important were used as requisites to monitor long-term trends of network stopover habitats. Confidence intervals for VIMP were calculated using double bootstrap subsampling ($n = 500$, $\alpha = 0.05$; Ishwaran and Lu 2019) to provide a quantitative view of relative importance for each variable in the model. The Breiman-Cutler (i.e., permutation) method of VIMP calculations was applied to all random forest analysis (Breiman 2001). Model runs were conducted using 5000 trees. Sandhill crane densities were quantified spatially within a continuous 1-km hexagonal grid used to summarize bird distributions and environmental variables. Grid size was determined through visual inspection of sandhill crane space use and set to encompass typical spatial clustering patterns observed. Density calculations were normalized by stopover area, year, and season to account for variance in bird abundance throughout the network and for differences in GPS acquisition rates. Timing of bird locations and variable measures were aligned temporally to account for annual and seasonal changes to landscape conditions.

Space use

Proportional space use of public and private lands was estimated for sandhill cranes within stopover areas as a measure of land ownership reliance. A similar approach was applied to wetlands, where bird space use was allotted by landownership and wetland class (i.e., temporary, seasonal, and semi-permanent). Wetland availability was derived following methods previously outlined, but without use of a five-year rolling mean to estimate surface water conditions. Wetland availability was summarized annually as a two-month average during spring (March–April) and fall (September–October) migrations. Monitoring was completed from spring 2014 to spring 2020. Proportional estimates of public–private lands and wetland space use were made by spatially intersecting sandhill

crane locations with ownership (BLM 2004) and wetland delineations using a GIS. Wetland results were temporally aligned with sandhill crane location data to account for changing patterns of habitat availability and bird use over time. To normalize differences among GPS acquisition rates, land ownership and wetland space-use calculations were applied to individual birds and derived as a proportion of their daily point location totals. Results are presented as an overall estimate of space use by CV, LCRV, and RM population segments.

Data processing

All image processing and raster-based analyses were conducted using Google Earth Engine cloud-based geospatial processing platform (Gorelick et al. 2017). All GIS analyses were performed using QGIS (QGIS Development Team 2020). Plotting and statistical analyses were conducted using the R environment (R Core Team 2019, RStudio Team 2019), including R-packages not previously cited, Tidyverse (Wickham et al. 2019).

RESULTS

Migration networks

Classification of seasonal sandhill crane movements (2014–2020) identified 71 unique stopover locations used to construct spring–fall migratory networks connecting birds to summering and wintering grounds (Appendix S3: Fig. S1). Using betweenness as a network centrality measure, we found the San Luis Valley, Colorado (RM, fall and spring); Pahrnagat Valley, Nevada (LCRV, fall); and Lund, Nevada–LCRV (LCRV, spring) to be key stopover sites essential to maintaining flyway connectivity (Fig. 2, see Appendix S3: Fig. S2 for map of named stopover locations). Results indicate that removal of these sites would substantially alter existing migratory pathways by increasing travel distances and associated migratory cost. Additionally, we identified Cokeville, Wyoming (RM); Delta, Colorado (RM); Malad Valley, Idaho (LCRV); Middle Rio Grande Valley, New Mexico (RM); and Wilcox Playa, Arizona (RM) as sites important to maintaining spring flyway connectivity. Cache Valley, Utah (LCRV); Cliff, New Mexico (RM); Harney Basin, Oregon (CV); Middle Rio Grande Valley, New

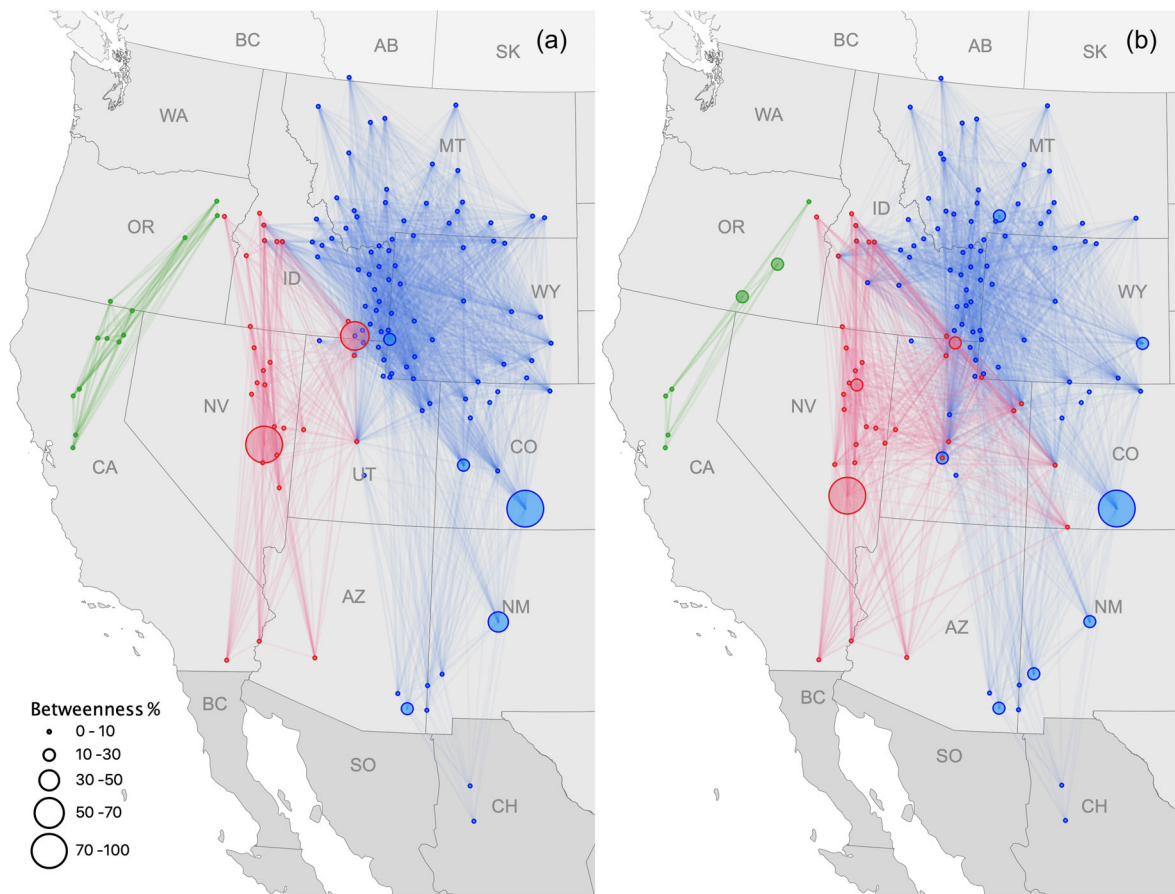


Fig. 2. Sandhill crane spring (a) and fall (b) migration networks for Central Valley (green), Lower Colorado River Valley (red), and Rocky Mountain (blue) population segments. Node size scaled by relative network centrality metric of betweenness as measure of stopover site importance to maintaining sandhill crane flyway connectivity.

Mexico (RM); Paradise Valley, Montana (RM); Ruby Valley, Nevada (LCRV); Richfield, Utah (RM); Three Forks, Montana (RM); Warner Valley, Oregon (CV); Wheatland Wyoming (RM); and Wilcox Playa, Arizona (RM) were identified as important sites for maintaining connectivity of fall migration. Patterns of network betweenness implied that stopover sites identified as important functioned to reduce migration cost regionally within networks, whereas key stopover sites influenced bird migration cost network-wide.

Central Valley, LCRV, and RM population segments exhibited spring migration networks consisting of 8, 20, and 44 stopover sites and fall migration networks of 2, 26, and 44 stopover sites, respectively (Appendix S3: Fig. S1). All

stopover sites identified were associated with wetland or riparian habitats. Lower Colorado River Valley and RM population segments shared eight common stopover sites during fall migration (Cache Valley, Utah [UT]; Great Salt Lake, UT; Jensen, UT; Malad Valley, Idaho [ID]; Ouray, UT; Payette Valley, ID; Richfield, UT; and Yuba Lake, UT) and three common sites during spring migration (Cache Valley, UT; Jensen, UT; and Payette Valley, ID).

The abundance of small grain cultivation (i.e., barley, corn, oats, wheat) and its proximity to flooded wetlands were the most important landscape predictors of sandhill crane distributions within stopover networks (Fig. 3). Birds consistently occupied areas where the location of waste

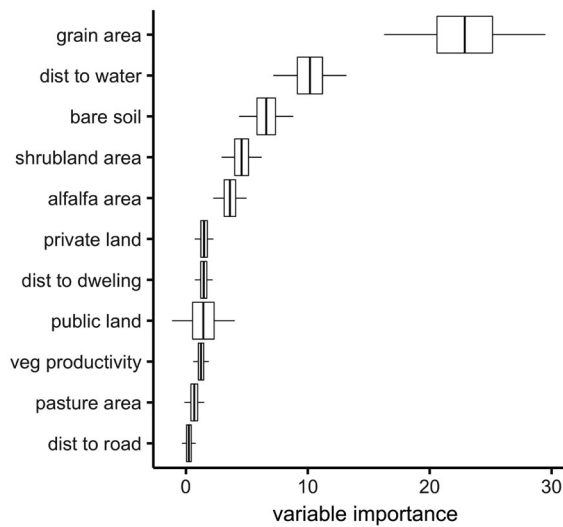


Fig. 3. Landscape factor importance in predicting sandhill crane distributions within stopover locations derived from randomForestSRC regression analysis. Box: 25th, 50th (center vertical line), and 75th percentiles, whiskers: 5th and 95th percentiles.

grain and wetlands maximized energetic efficiency by minimizing local movements between food and water resources. Space-use patterns were consistent with North American mid-continent lesser sandhill crane (*Antigone canadensis canadensis*) stopover behaviors that showed bird concentrations in areas where harvested grain fields and wetland roost locations were most proximal (Anteau et al. 2011). Factors associated with disturbance (e.g., distance to roads and human dwellings) known to influence wintering sandhill crane distributions (Boggie et al. 2018) were less important to birds during migration.

Differences in migration duration were evident among individual networks and spring–fall movements (Table 1). For example, LCRV and RM population segments took twice as many days to move through networks in fall compared with spring, with RM birds taking 60% and 100% longer on average than LCRV birds to complete spring and fall migrations. Shorter overall travel distances in CV networks limited bird migration days that were similar in number during spring and fall. Spring–fall non-stop migratory flight distances were similar among sandhill crane population segments except for fall CV flights that were double other distances observed (Table 1).

Table 1. Total days and non-stop flight distances (km) during sandhill crane spring–fall migration through the Central Valley (CV), Lower Colorado River Valley (LCRV), and Rocky Mountain (RM) regions.

Population segment	No. days (mean ± SD)	Flight distance (km)	
		Median	Maximum
CV, spring	13 ± 9	222	855
CV, fall	5 ± 3	469	819
LCRV, spring	18 ± 14	240	1405
LCRV, fall	39 ± 20	226	1279
RM, spring	36 ± 19	209	1069
RM, fall	63 ± 29	214	1022

Land use

Sandhill cranes were heavily reliant on private lands during migration, as evidenced by the importance of agriculture (i.e., small grain cultivation) in predicting high bird concentrations within stopover sites (Fig. 3). During spring migration, 67%, 96%, and 78% of CV, LCRV, and RM sandhill crane space use occurred on private lands. Patterns were similar during fall migration with private lands accounting for 90%, 95%, and 85% of CV, LCRV, and RM space use, respectively. Wetlands made up 30% of sandhill crane space use during spring migration with “seasonal” wetlands accounting for 86% of overall spring wetland use (Table 2). Only seven percent of sandhill crane space use occurred in wetlands during fall migration. Of this use, 58% was attributed to semi-permanent wetlands overall; however, use was mixed among population segments with birds favoring multiple wetland classes (Table 2; Appendix S4: Table S1). Although wetland use made up a smaller proportion of

Table 2. Sandhill crane percentage of wetland use by ownership (pub, public; pvt, private) and hydrologic regime (temporary, flooded <2 months; seasonal, >2 and ≤8 months); semi-permanent, flooded >8 months).

Regime	Spring	Fall	Pub-pvt spring	Pub-pvt fall
Semi-perm	12	58	48/52	24/76
Seasonal	86	23	20/80	21/79
Temporary	1	20	41/59	60/40

Note: Use represents seasonal means for spring (March–April) and fall (September–October) migration from 2014 to spring 2020.

sandhill crane space-use budgets, 77% and 69% of overall wetland use were associated with private lands during spring and fall migration (Table 2). The majority (>80%) public land and wetland use by sandhill cranes during migration occurred on wildlife refuges.

Landscape change

Overall wetland availability declined across network stopover sites 16–18% during sandhill crane spring–fall migration (Table 3, Fig. 4). Declines were attributed to functional wetland loss due to drying identified by measured reductions in surface water extent. Losses were significant in temporary and seasonal wetlands and nearly significant for semi-permanent wetlands (*P* value = 0.067) during spring migration (March–April). During fall migration (September–October), wetland declines were significant across all wetland classes. Overall temporary and seasonal wetland availability was three to five times greater in spring vs. fall migration, while semi-permanent wetland availability remained seasonally stable. Wetland data summaries for individual stopover sites are provided as supplemental material in Appendix S4: Tables S2–S19.

Wetland declines were mixed among migration networks with the majority of losses occurring in CV and LCRV migratory stopover sites

Table 3. Overall change to wetland availability in sandhill crane spring and fall stopover sites.

Hydrologic regime	1988–2003	2004–2019	Difference (%)	<i>P</i>
Spring				
Temporary	43,326	35,589	-18	0.0108
Seasonal	43,326	35,589	-18	0.0108
Semi-permanent	35,122	29,429	-16	0.0671
Fall				
Temporary	11,487	9592	-17	0.0045
Seasonal	15,873	13,250	-17	0.0005
Semi-permanent	15,873	13,250	-17	0.0005

Notes: Results summarized by hydrologic regimes: temporary (flooded ≤2 months), seasonal (flooded >2 months and <8 months), and semi-permanent (flooded >8 months). Change measured as a comparison of annual wetland surface water area (ha) means between 1988–2003 and 2004–2019 using Wilcoxon rank order tests. Statistical significance measured as *P* value ≤0.05. Annual surface water measures represent mean conditions during two-month spring (March–April) and fall (September–October) migration periods.

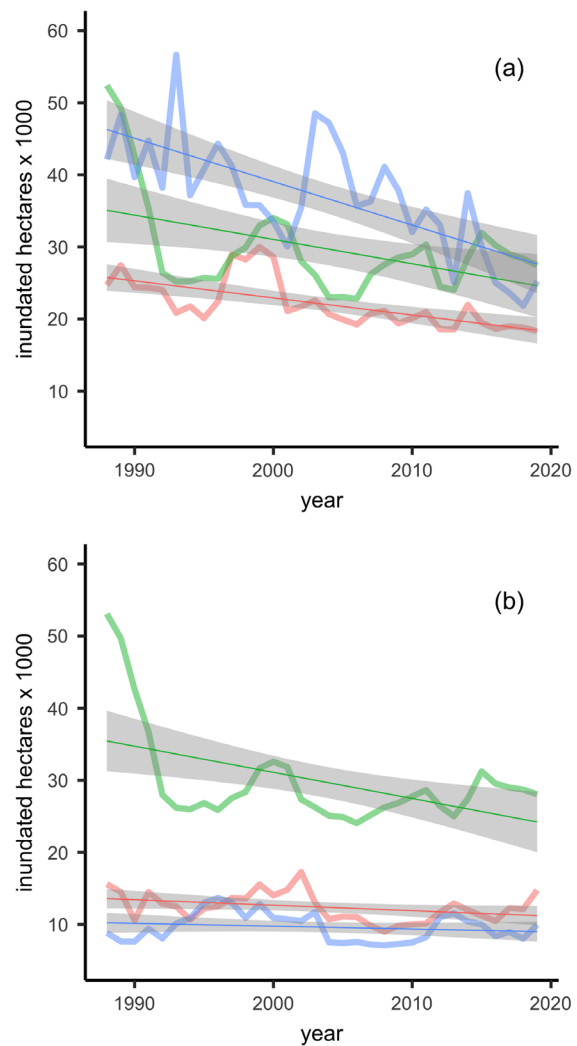


Fig. 4. Overall wetland surface water area trends for spring (a) and fall (b) sandhill crane stopover sites. Trends were measured annually as a five-year rolling mean from 1988 to 2019 and summarized by wetland hydrologic regime: temporary (blue, flooded ≤2 months), seasonal (red, flooded >2 months and <8 months), and semi-permanent (green, flooded >8 months). Surface water measures represent mean conditions during two-month spring (March–April) and fall (September–October) migration periods.

(Fig. 5). During spring migration, declines of seasonal wetlands, heavily utilized by sandhill cranes (see Table 2), occurred in 50%, 69%, and 40% of CV, LCRV, and RM stopovers with significant declines in 25%, 30%, and 18% of sites (Fig. 5a). Net loss of all wetland classes (i.e.,

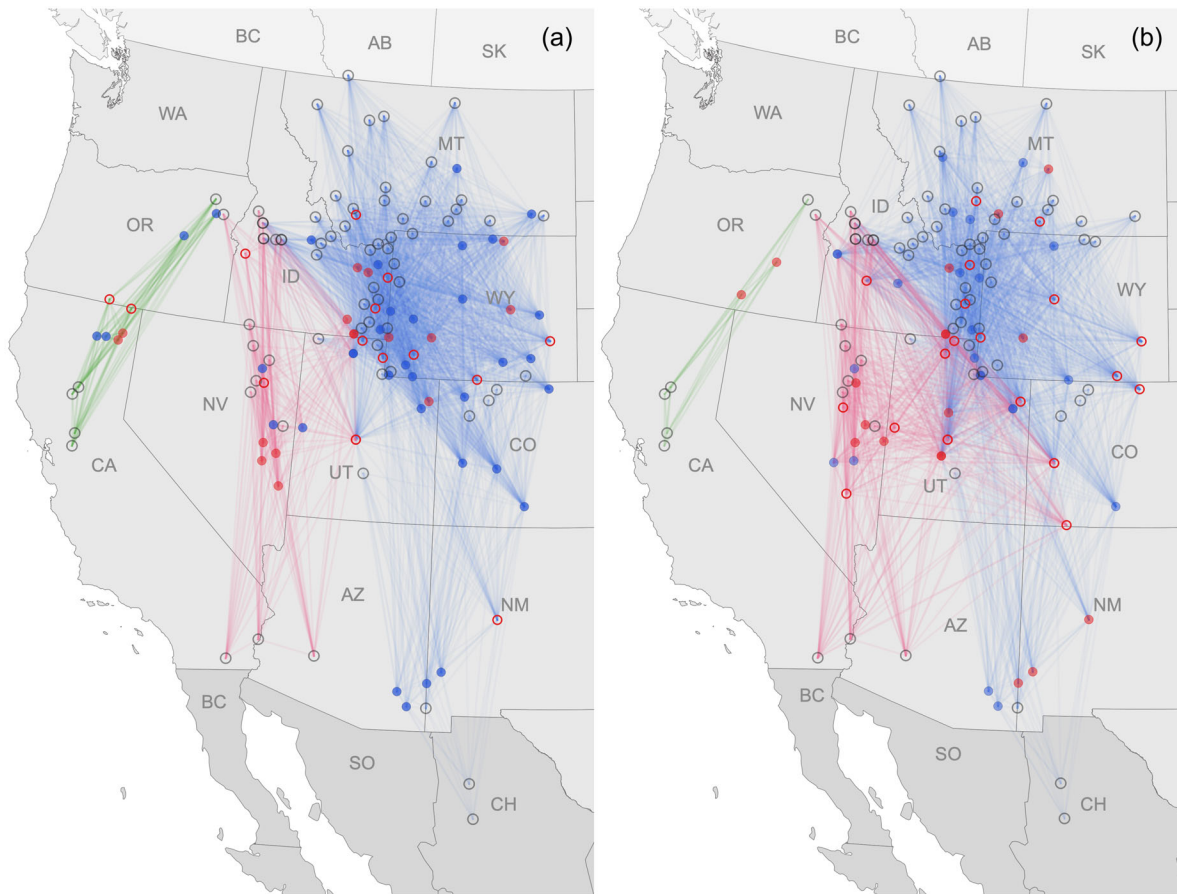


Fig. 5. Wetland change in sandhill crane migration stopover networks for Central Valley (green), Lower Colorado River Valley (red), and Rocky Mountain (blue) population segments. Changes to seasonal wetlands are shown in spring migration networks (a) due to patterns of high bird use observed in this wetland class (see Table 2). Net change for all wetland classes (temporary, seasonal, and semi-permanent) is shown in fall migration networks (b) to depict impacts of mixed wetland use exhibited by birds. Red circles indicate wetland decline, and solid red circles identify decline as significant. Blue circles indicate stable to increasing wetland availability. Gray circles identify non-stopover (i.e., wintering or breeding) locations. Change measured as a comparison of annual wetland surface water area means between 1988–2003 and 2004–2019 using a Wilcoxon rank order test. Statistical significance measured as P value ≤ 0.05 .

temporary, seasonal, and semi-permanent) during fall migration occurred in 100%, 72%, and 59% of CV, LCRV, and RM sandhill crane stopovers with significant declines in 100%, 23%, and 18% of sites (Fig. 5b).

Significant declines in seasonal wetlands occurred in one of two sites essential to maintaining spring network connectivity (Lund, Nevada [LCRV]) and in two of six sites designated as important (Malad, ID [LCRV], and Cokeville, Wyoming [RM]). Net declines in temporary,

seasonal, and semi-permanent wetlands were significant in seven of twelve stopover sites important to fall network connectivity (Cliff, New Mexico [RM]; Harney Basin, Oregon [CV]; Middle Rio Grande Valley, New Mexico [RM]; Paradise Valley, Montana [RM]; Richfield, UT [RM]; Ruby Valley, Nevada [LCRV]; and Warner Valley, Oregon [CV]).

Distribution of small grain cultivation in sandhill crane migration networks was high, occurring in 89%, 69%, and 84% of spring and 100%,

71%, and 95% of fall CV, LCRV, and RM migration stopover sites (Appendix S5: Fig. S1). Overall cultivated area trends from 2008 to 2019 were stable ($\pm 8.3\%$ SD) across stopover sites (Fig. 6). From 2008 to 2019, an average of 41%, 30%, and 42% of post-harvested small grain areas were fall tilled in CV, LCRV, and RM networks, reducing access to important waste grain foraging resources during subsequent spring migration (Anteau et al. 2011). Outliers of small grain tillage included the San Luis Valley, Colorado (RM), 14%; Cache Valley, UT (LCRV-RM), 63%; and Malad, ID (LCRV-RM), 60%. Trends in overall fall tillage rates were stable ($\pm 11.8\%$ SD) from 2008 to 2019. Small grain data summaries for individual stopover sites supporting our analysis of migration network change are provided as supplemental material (Appendix S5: Table S1).

DISCUSSION

Network function

Our analysis is the first to reconstruct sandhill crane migratory networks to evaluate the connectivity of stopover habitats in western North America. The results of this study provide an important analytical tool that structures wetland and sandhill crane conservation at the flyway scale. Migratory efficiency was the primary mechanism underpinning network function where a small number of key stopover sites important to minimizing movement costs between summering and wintering locations were essential to maintaining

connectivity. Localized efficiencies were apparent in stopover landscapes given documented space-use patterns in areas where the proximity of agricultural food resources (i.e., waste grain) and flooded wetlands minimized daily bird movements. Our continental perspective of migratory networks provides a new framework to prioritize local habitat conservation in landscapes essential to maintaining flyway connectivity for sandhill cranes and other wetland-dependent migratory birds.

Our analyses identified three key sites that were essential to maintaining flyway connectivity, and numerous others that were important to spring or fall migration. The key stopover sites supporting LCRV and RM network connectivity (San Luis Valley, Colorado; Lund and Pahrnagat Valley, Nevada) were associated with continental ecotones where ecosystem water balance transitioned semi-arid to arid as birds moved into dryer Mojave, Sonoran, and Chihuahuan desert regions. During fall migration, limited water availability and agricultural food resources acted as bottlenecks in migratory networks that concentrated birds in a small number of stopover and wintering sites (i.e., Imperial Valley, California; Middle Rio Grande Valley, New Mexico; Santa Ana, Chihuahua; Wilcox, Arizona). Conversely, key stopover sites acted as hubs for migratory dispersal in spring when birds were able to take advantage of increased network redundancy resulting from greater wetland and agricultural abundance as they moved north. The lack of key stopover sites during spring CV migration was attributed to relatively short overall migration distance and consistent availability of wetland and agricultural resources that distributed connectivity equally across the network. Longer more direct migratory movements and seasonal reductions to wetland availability were likely contributing factors that limited the CV network to two important stopover sites (Warner Valley and Harney Basin, Oregon) during fall migrations.

Observed patterns of continental movement indicated sandhill crane migration is dependent on a distinct ecological patchwork of wetland and riparian areas in water-limited landscapes. Although bird use of these sites likely preceded agricultural development (*sensu* Emory 1848), networks aligned spatially with farming and



Fig. 6. The area of small grain cultivated (blue line) across sandhill crane stopover sites from 2008 to 2019 (blue line) and untilled post-harvest small grain remaining during spring migration (red line).

ranching industries reliant on irrigation water generated from associated wetland and riparian systems. Casual observations of habitat space-use through our analysis showed that during migration, sandhill cranes took advantage of agricultural food resources to offset seasonal changes to wetland availability. Higher rates of agricultural field use during fall migration coincided with lower seasonal and temporary wetland availability caused by excessive evaporation and summer drying (see Fig. 4). Traditionally, birds may have relied more heavily on terrestrial foraging strategies in fall when wetlands were naturally limited. However, availability of high energy agricultural foods (i.e., waste grain) coupled with wetland-riparian declines is likely to have increased terrestrial habitat dependence. Conversely, we speculate that the sixfold higher use of wetlands in spring vs. fall migration is due to greater wetland availability and shifts to protein-based foraging strategies to meet the energetic demands of egg production prior to breeding (Nowald et al. 2018). High concurrent use of agricultural fields in spring (70%) also underscored the value birds continued to place on waste grain to support energetic demands during migration.

Codependence of water resources linking sandhill cranes and agriculture suggests network function is, in part, made possible by a balance between irrigation that supports crop production (i.e., waste grain availability) and water needs that maintain resilience of important wetland and riparian habitats used by birds. Since the onset of modern cultivation, agriculture has provided high energy food resources for migratory waterbirds and is credited as an important surrogate to historic habitat loss that supports numerous species globally (Czech and Parsons 2002, Elphick and Oring 2003, Gauthier et al. 2005, Fox et al. 2017). The importance of agricultural lands to sandhill crane networks was clearly evident, as the proximity of small grains to wetlands was the most important driver of sandhill crane land use at stopover sites. Furthermore, 67–96% of space use by birds occurred on private lands. Donnelly et al. (2020) found that in important waterbird landscapes, coincident with sandhill crane migration networks, nearly two-thirds of wetlands occurred on private lands, the majority of which were flood-irrigated wet meadows that

support sandhill crane habitat (Drewien and Bizeau 1974, Littlefield et al. 1994).

While our findings clearly outlined sandhill crane reliance on agriculture, underlying mechanisms supporting this relationship were more complex. In the western USA and Mexico, >89% of surface water rights are dedicated to agriculture, with demand in many regions exceeding availability (Maupin et al. 2010, Vélez and Saez 2011). More frequent irrigation shortfalls due to climate change can exacerbate wetland loss (Downard and Endter-Wada 2013) and accelerate patterns of unsustainable groundwater pumping meant to offset surface water declines that further degrade wetland function supporting migratory waterbird networks (Scott et al. 2014, Cody et al. 2015). It has been acknowledged that irrigation development has influenced wetland change (Lemly 1994), although the magnitude of wetland change attributed to agriculture in this study is unknown. Sandhill cranes and other migrating waterbirds have largely become dependent upon agriculturally supported wetlands (Drewien and Bizeau 1974, Fleskes and Gregory 2010, Donnelly et al. 2019). As noted previously, Donnelly et al. (2020) found that nearly two-thirds of wetlands in landscapes linked to sandhill crane migration were provided by agriculture, but the same study indicated that only seven percent of irrigated lands were associated with wetland habitats. Furthermore, waste grain benefiting some migratory waterbird species (Elphick and Oring 2003, Fox et al. 2005, Gauthier et al. 2005) has also been linked to agricultural conversion and water development that historically have been the greatest driver of wetland loss (Davidson 2014). While conflicts exist between conservation and agricultural interests (Lemly et al. 2000), government natural resource programs in Canada and the USA (Rewa 2005, Tyrchniewicz and Tyrchniewicz 2007) have provided substantial benefits for migratory waterbirds through financial support targeting wetland protections in agricultural landscapes (O'neal et al. 2008, Beatty et al. 2014, Tapp and Webb 2015).

Landscape change

Migratory network dependence on a limited number of key wetland and riparian systems raises concerns over intensifying patterns of water scarcity in western North America

(Scanlon et al. 2012, Donnelly et al. 2020, Richter et al. 2020). Publicly managed wildlife refuges offer protections to some stopover sites, but are often dwarfed in comparison with habitats available on surrounding private lands. These inequalities are compounded in landscapes where water shortages and increasing water costs have limited wetland habitats on wildlife refuges (Mayer 2005, Griffith et al. 2009). Overwhelming reliance on private lands identifies additional vulnerability to networks linked to the uncertainty of agricultural land-use change incompatible with migratory needs. Changes in agricultural practices reducing waste grain availability (e.g., increased harvest efficiency and tillage) or shifts to crops incompatible with dietary waterbird needs can rapidly reduce access to food used to meet energetic demands of migration (Krapu et al. 2004). We found little evidence that patterns of small grain cultivation or tillage have changed within stopover sites since 2008. However, intensifying irrigation demands and increasing water scarcity due to climate change (Snyder et al. 2019) raise questions over long-term sustainability of existing agricultural practices (Richter et al. 2020).

Our model depictions of declining surface water trends likely reflect a new normal in wetland drying that could impact connectivity of continental migration, particularly in CV and

LCRV networks where stopover sites exhibited significant wetland loss. A recent assessment of climate projections encompassing sandhill crane migration networks by Snyder et al. (2019) suggests that regional temperature by 2020–2050 will be $\sim 1^{\circ}\text{C}$ to $\sim 3^{\circ}\text{C}$ above the historical baseline of 1980–2010. Increasing temperatures are predicted to decrease snowpack runoff supporting wetland function while simultaneously increasing agricultural water needs through elevated evaporative demand from crops (Mix et al. 2009, Elliott et al. 2014). Impacts to riparian function were already apparent in the Middle Rio Grande Valley, New Mexico, identified as an important stopover site and known wintering location (Drewien and Bizeau 1974), where diminished river flows exacerbated by more frequent drought and woody species encroachment have resulted in channel constriction, dramatically reducing roost site availability for sandhill cranes (Fig. 7).

Growing urban water demands are likely to compound projected climate shortfalls by negatively impacting wetlands and irrigated agriculture in some stopover sites (Schaible and Aillery 2017). Efforts in areas of Colorado, for example, have proposed rotational agricultural fallowing through purchase and repurposing of rural irrigation water for municipal use (Dilling et al. 2019). Such scenarios frequently require out-of-basin water transfers, reducing local wetland

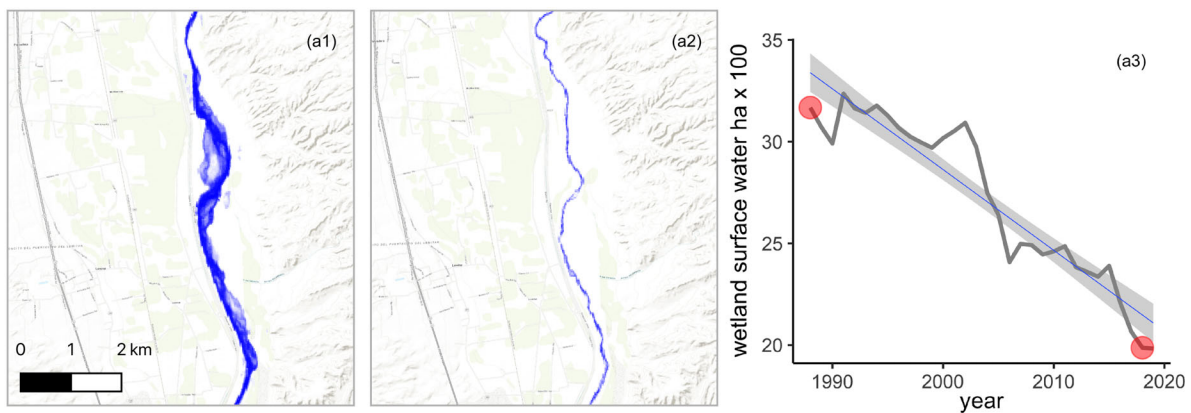


Fig. 7. Model example: Middle Rio Grande Valley, New Mexico, surface water area change images (a1–2) depict river channel constriction caused by long-term impact of woody invasive plant encroachment and flow reductions. Graph (a3) illustrates annual surface water decline from 1988 to 2019 as five-year rolling mean. Least squares regression (a3; blue line) with 0.95% confidence interval of slope shown in gray fill. Red dots identify timing of surface water conditions depicted by images; fall 1988 (a1) and 2018 (a2).

availability supported through irrigation while eliminating important agricultural food resources for birds. Additionally, loss of irrigation can increase subdivision risk that removes wildlife compatible land-use practices in rural landscapes as producers sell off land for development due to its reduced agricultural value (Dozier et al. 2017).

Sustaining flyway connectivity

Results from our analysis clearly demonstrate the need for continental land protection strategies considerate of flyway connectivity. The success of migratory networks is a result of connectivity at key stopover sites. Network collapse can occur when stopover sites have poor habitat conditions or are spaced at distances too large to maintain a positive energetic balance for migrating birds. All key stopover sites identified in this study have been impacted or have the potential to be impacted, by current or proposed water use decisions. However, the underlying drivers of water availability and solution matrices differ among sites. For example, in the San Luis Valley, a key stopover site for RM sandhill cranes, water policy decisions have led to groundwater pumping surcharges meant to curb overuse affecting senior surface water rights (Cody et al. 2015). While this action may be viewed as a net positive for wetland sustainability, the economic consequences have unintentionally suppressed conservation efforts by dramatically increasing the value of limited surface water stores. In turn, these actions have driven up wetland restoration and management costs on private lands and public wildlife refuges (Kelley 2017). Similarly, economic pressure to obtain long-term water security for the city of Las Vegas, Nevada, has prompted planning to transport groundwater from rural basins encompassing the majority of LCRV stopover sites in the state, including key network sites at Pahrana-gat Valley, and Lund, Nevada. Planning projections identify extraction of 223 million cubic meters of groundwater annually that are predicted to reduce spring discharge supporting waterbird habitats throughout the region (Deacon et al. 2007).

Water-conservation, while necessary to meet long-term human demands (Sabo et al. 2010, Richter et al. 2020), can conflict with preservation

of migratory networks. Inefficient water use by agriculture (e.g., flood irrigation) is often associated with wetland habitats supporting large waterbird populations in landscapes where few natural wetlands remain (Elphick and Oring 2003, Moulton et al. 2013). For example, flood irrigation of hay meadows confined to riparian floodplains mimic once natural hydrologic processes that today maintain habitat essential to sandhill cranes and other migratory waterbirds. Such practices, however, are frequently deemed an inefficient use of water (Richter et al. 2017), and if replaced with more efficient irrigation (e.g., sprinkler), can result in unintentional wetland loss. Improved irrigation efficiency seldom results in net water savings, but instead can encourage the expansion of irrigated lands or planting of more water-intensive crops, thus reducing water infiltration supporting aquifer recharge and riparian flows (Ward and Pulido-Velazquez 2008, Pfeiffer and Lin 2014). While the loss of individual agricultural wetlands through irrigation efficiency measures can influence wildlife use locally, the cumulative effects can negatively impact connectivity of waterbird migration at the flyway scale.

Sustainability of flyway connectivity will hinge on the balance of water allocations that preserve agricultural and wetland-riparian function. Limited distribution of publicly protected wildlife refuges indicates meaningful conservation strategies must include private landowners that made up an overwhelming majority of agricultural and wetland areas used by sandhill cranes. Conservation efforts providing long-term protections for agricultural land-use practices that sustain wetland habitats can benefit sandhill cranes substantially. As our analyses indicate, the location of available wetlands relative to others in the flyway network can amplify their value to migratory waterbirds.

Although this work focuses on sandhill cranes, our analysis provides a model system for flyway conservation applicable to all waterbirds in western North America (Miller et al. 2005, Haukos et al. 2006). Conserving connectivity will require adaptive changes to existing conservation priorities that to date have targeted wintering and breeding locations associated with the greatest bird and habitat concentrations (e.g., North American Wetlands Conservation Act 1989),

rather than stopover sites supporting migration (Arzel et al. 2006). Quantity and quality of spring migration habitat are known to influence waterbirds' breeding propensity and recruitment (Gunnarsson et al. 2005, Morrison et al. 2007, Devries et al. 2008). Inadequate protections in key stopover sites could significantly alter network efficiency by increasing the distance and energetic cost of migration. If not addressed, this reduction in flyway connectivity could manifest as new and powerful cross-seasonal effects that limit survivorship and population growth (Baker et al. 2004, Iwamura et al. 2013, Hua et al. 2015).

To accelerate continental network protections, we make our data available to natural resource planners and wildlife managers as a framework to prioritize conservation of key migratory landscapes (<https://jp4932539.shinyapps.io/craneShinyApp2/>). Consideration of specific social, ecological, and economic factors will be necessary to accurately identify impacts and provide opportunities to protect wetland stopover habitats. As highlighted in this study, the conservation value of irrigated agriculture and wetlands is manifested in the context of both local habitat needs and their contribution to processes supporting broader flyway connectivity for waterbirds. We encourage the use of our results to inform conservation solutions through collaborative and proactive decision-making among local and regional stakeholders throughout western North America.

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LITERATURE CITED

- Anteau, M. J., M. H. Sherfy, and A. A. Bishop. 2011. Location and agricultural practices influence spring use of harvested cornfields by cranes and geese in Nebraska. *Journal of Wildlife Management* 75:1004–1011.
- Arzel, C., J. Elmberg, and M. Guillemain. 2006. Ecology of spring-migrating Anatidae: a review. *Journal of Ornithology* 147:167–184.
- Austin, J. E. 2012. Conflicts between Sandhill Cranes and farmers in the Western United States: evolving issues and solutions. Pages 131–139 in *Proceedings of the Workshop “Cranes, Agriculture and Climate Change”*. International Crane Foundation, Baraboo, Wisconsin. savingcranes.org
- Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. de Lima Serrano do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings Biological Sciences/The Royal Society* 271:875–882.
- Beatty, W. S., D. C. Kesler, E. B. Webb, A. H. Raedeke, L. W. Naylor, and D. D. Humburg. 2014. The role of protected area wetlands in waterfowl habitat conservation: implications for protected area network design. *Biological Conservation* 176:144–152.
- Boggie, M. A., D. P. Collins, J. P. Donnelly, and S. A. Carleton. 2018. Land Use, anthropogenic disturbance, and riverine features drive patterns of habitat selection by a wintering waterbird in a semi-arid environment. *PLoS One* 13:e0206222.
- Breiman, L. 2001. Random forests. *Machine Learning* 45:5–32.
- Bureau of Land Management (BLM). 2004. Land ownership in the Western United States. http://sagemap.wr.usgs.gov/westUS_own.shp
- Butchart, S. H. M., et al. 2010. Global biodiversity: indicators of recent declines. *Science* 328:1164–1168.
- Calenge, C.. 2011. Analysis of animal movements in R: the adehabitatLT package. <https://cran.r-project.org/web/packages/adehabitatLT/index.html>
- Cody, K. C., S. M. Smith, M. Cox, and K. Andersson. 2015. Emergence of collective action in a ground-water commons: irrigators in the San Luis Valley of Colorado. *Society & Natural Resources* 28:405–422.
- Collins, D., T. Cooper, J. Dubovsky, and D. Fronczak. 2016a. Priority information needs for Sandhill cranes II. Association of Fish and Wildlife Agencies' Migratory Shore and Upland Game Bird Support Task Force, Washington, District of Columbia.

- https://www.fws.gov/migratorybirds/pdf/surveys-and-data/Info-Needs-Sandhill-Crane-II_2016.pdf
- Collins, D. P., B. A. Grisham, C. M. Conring, J. M. Knetter, W. C. Conway, S. A. Carleton, and M. A. Boggie. 2016b. New summer areas and mixing of two greater sandhill crane populations in the Inter-mountain West. *Journal of Fish and Wildlife Management* 7:141–152.
- Conring, C. M., K. Brautigam, B. A. Grisham, D. P. Collins, and W. C. Conway. 2019. Identifying the migratory strategy of the Lower Colorado River Valley population of Greater Sandhill Cranes. *Avian Conservation and Ecology* 14:11.
- Cowardin, L. M., F. C. Carter, and E. T. Golet. 1979. Classification of wetlands and deepwater habitats of the United States. United States Department of the Interior, Fish and Wildlife Service, Washington, District of Columbia. <https://www.fws.gov/wetlands/Documents/Classification-of-Wetlands-and-Deepwater-Habitats-of-the-United-States.pdf>
- Culp, L. A., E. B. Cohen, A. L. Scarpignato, W. E. Thogmartin, and P. P. Marra. 2017. Full annual cycle climate change vulnerability assessment for migratory birds. *Ecosphere* 8:e01565.
- Czech, H. A., and K. C. Parsons. 2002. Agricultural wetlands and waterbirds: a review. *Waterbirds/The Waterbird Society* 25:56–65.
- Davidson, N. C. 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research* 65:934–941.
- Deacon, J. E., A. E. Williams, C. D. Williams, and J. E. Williams. 2007. Fueling population growth in Las Vegas: how large-scale groundwater withdrawal could burn regional biodiversity. *BioScience* 57:688–698.
- Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in Mallards (*Anas platyrhynchos*). *The Auk* 125:618–628.
- Dijkstra, E. W. 1959. A note on two problems in connexion with graphs. *Numerische Mathematik* 1:269–271.
- Dilling, L., J. Berggren, J. Henderson, and D. Kenney. 2019. Savior of rural landscapes or Solomon's choice? Colorado's experiment with alternative transfer methods for water (ATMs). *Water Security* 6:100027.
- Donnelly, J. P., S. L. King, N. L. Silverman, D. P. Collins, E. M. Carrera-Gonzalez, A. Lafón-Terrazas, and J. N. Moore. 2020. Climate and human water use diminish wetland networks supporting continental waterbird migration. *Global Change Biology*. 26:2042–2059.
- Donnelly, J. P., D. E. Naugle, D. P. Collins, B. D. Dugger, B. W. Allred, J. D. Tack, and V. J. Dreitz. 2019. Synchronizing conservation to seasonal wetland hydrology and waterbird migration in semi-arid landscapes. *Ecosphere* 10:1–12.
- Downard, R., and J. Endter-Wada. 2013. Keeping wetlands wet in the western United States: adaptations to drought in agriculture-dominated human-natural systems. *Journal of Environmental Management* 131:394–406.
- Dozier, A. Q., M. Arabi, B. C. Wostoupal, C. G. Goemans, Y. Zhang, and K. Paustian. 2017. Declining agricultural production in rapidly urbanizing semi-arid regions: policy tradeoffs and sustainability indicators. *Environmental Research Letters* 12:085005.
- Drent, R. H., A. D. Fox, and J. Stahl. 2006. Travelling to breed. *Journal of Ornithology* 147:122–134.
- Drewien, R. C., and E. G. Bizeau. 1974. Status and distribution of greater Sandhill cranes in the Rocky Mountains. *Journal of Wildlife Management* 38:720–742.
- Drewien, R. C., A. L. Terrazas, J. P. Taylor, J. M. O. Baraza, and R. E. Shea. 2003. Status of lesser snow geese and Ross's geese wintering in the Interior Highlands of Mexico. *Wildlife Society Bulletin* 31:417–432.
- Elliott, J., et al. 2014. Constraints and potentials of future irrigation water availability on agricultural production under climate change. *Proceedings of the National Academy of Sciences of the United States of America* 111:3239–3244.
- Elphick, C. S., and L. W. Oring. 2003. Conservation implications of flooding rice fields on winter waterbird communities. *Agriculture, Ecosystems & Environment* 94:17–29.
- Emory, W. H. 1848. Notes of a military reconnaissance: from Fort Leavenworth, in Missouri, to San Diego, in California, including parts of the Arkansas, Del Norte, and Gila Rivers. Wendell and Van Benthuy-sen, Washington, District of Columbia.
- Fauchald, P., and T. Tveraa. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288.
- Fleskes, J. P., and C. J. Gregory. 2010. Distribution and dynamics of waterbird habitat during spring in southern Oregon–northeastern California. *Western North American Naturalist* 70:26–38.
- Fox, A. D., J. Elmberg, I. M. Tombre, and R. Hessel. 2017. Agriculture and herbivorous waterfowl: a review of the scientific basis for improved management. *Biological Reviews of the Cambridge Philosophical Society* 92:854–877.
- Fox, A. D., J. Madsen, H. Boyd, E. Kuijken, D. W. Nor-riss, I. M. Tombre, and D. A. Stroud. 2005. Effects

- of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. *Global Change Biology* 11:881–893.
- Freeman, L. C. 1978. Centrality in social networks conceptual clarification. *Social Networks* 1:215–239.
- Gauthier, G., J.-F. Giroux, A. Reed, A. Bechet, and L. Belanger. 2005. Interactions between land use, habitat use, and population increase in greater snow geese: What are the consequences for natural wetlands? *Global Change Biology* 11:856–868.
- Gauthreaux, S. A. Jr. 1982. The ecology and evolution of avian migration systems. Pages 93–168 in D. S. Farner, J. R. King, and K. C. Parkes, editors. *Avian biology*. Academic Press, New York, New York.
- Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* 202:18–27.
- Griffith, B., J. M. Scott, R. Adamcik, D. Ashe, B. Czech, R. Fischman, P. Gonzalez, J. Lawler, A. D. McGuire, and A. Pidgora. 2009. Climate change adaptation for the US National Wildlife Refuge System. *Environmental Management* 44:1043–1052.
- Gunnarsson, T. G., J. A. Gill, J. Newton, P. M. Potts, and W. J. Sutherland. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society Biological Sciences* 272:2319–2323.
- Haig, S. M., S. P. Murphy, J. H. Matthews, I. Arismendi, and M. Safeeq. 2019. Climate-altered wetlands challenge waterbird use and migratory connectivity in arid landscapes. *Scientific Reports* 9:4666.
- Haukos, D. A., M. R. Miller, D. L. Orthmeyer, J. Y. Takekawa, J. P. Fleskes, M. L. Casazza, W. M. Perry, and J. A. Moon. 2006. Spring migration of northern pintails from Texas and New Mexico, USA. *Waterbirds* 29:127–136.
- Hua, N., K. Tan, Y. Chen, and Z. Ma. 2015. Key research issues concerning the conservation of migratory shorebirds in the Yellow Sea region. *Bird Conservation International* 25:38–52.
- Intermountain West Joint Venture (IWJV). 2013. 2013 Implementation plan – strengthening science and partnerships. Intermountain West Joint Venture, Missoula, Montana. <https://iwjv.org/resource/2013-implementation-plan-chapter-3-strengthening-the-biological-foundation/>
- Ishwaran, H., and U. B. Kogalur. 2019. Fast unified random forests for survival, regression, and classification (RF-SRC). R package version 2. <https://cran.r-project.org/package=randomForestSRC>
- Ishwaran, H., and M. Lu. 2019. Standard errors and confidence intervals for variable importance in random forest regression, classification, and survival. *Statistics in Medicine* 38:558–582.
- Iwamura, T., H. P. Possingham, I. Chadès, C. Minton, N. J. Murray, D. I. Rogers, E. A. Treml, and R. A. Fuller. 2013. Migratory connectivity magnifies the consequences of habitat loss from sea-level rise for shorebird populations. *Proceedings. Biological Sciences/The Royal Society* 280:20130325.
- Jacoby, D. M. P., E. J. Brooks, D. P. Croft, and D. W. Sims. 2012. Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses: network analyses of animal movement. *Methods in Ecology and Evolution* 3:574–583.
- Jehl, J. R. Jr. 1994. Changes in saline and alkaline lake avifaunas in western North America in the past 150 years. *Studies in Avian Biology* 15:258–272.
- Jin, H., C. Huang, M. W. Lang, I. Yeo, and S. V. Stehman. 2017. Monitoring of wetland inundation dynamics in the Delmarva Peninsula using Landsat time-series imagery from 1985 to 2011. *Remote Sensing of Environment* 190:26–41.
- Johnson, A. R., J. A. Wiens, B. T. Milne, and T. O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* 7:63–75.
- Keitt, T. H., D. L. Urban, and B. T. Milne. 1997. Detecting critical scales in fragmented landscapes. *Conservation Ecology* 1:17.
- Kelley, K. 2017. A Tough economic choice for water rights holders in the San Luis Valley. University of Denver Water Law Review at the Sturm College of Law. Denver, Colorado. <https://duwaterlawreview.com/a-tough-economic-choice-for-water-rights-holders-in-the-san-luis-valley/>
- Kirby, J. S., A. J. Stattersfield, S. H. M. Butchart, M. I. Evans, R. F. A. Grimmett, V. R. Jones, J. O'Sullivan, G. M. Tucker, and I. Newton. 2008. Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conservation International* 18:S49–S73.
- Kranstauber, B., R. Kays, S. D. Lapoint, M. Wikelski, and K. Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology* 81:738–746.
- Kranstauber, B., M. Smolla, and A. K. Scharf. 2019. move: visualizing and Analyzing Animal Track Data. Cran.r.project. <https://CRAN.R-project.org/package=move>
- Krapu, G. L., D. A. Brandt, and R. R. Cox Jr. 2004. Less waste corn, more land in soybeans, and the switch to genetically modified crops: trends with important implications for wildlife management. *Wildlife Society Bulletin* 32:127–136.

- Lavielle, M. 1999. Detection of multiple changes in a sequence of dependent variables. *Stochastic Processes and their Applications* 83:79–102.
- Lavielle, M., and G. Teyssi re. 2006. Detection of multiple change-points in multivariate time series. *Lithuanian Mathematical Journal* 46:287–306.
- Le Corre, M., C. Dussault, and S. D. C t . 2014. Detecting changes in the annual movements of terrestrial migratory species: using the first-passage time to document the spring migration of caribou. *Movement Ecology* 2:19.
- Lemly, A. D. 1994. Irrigated agriculture and freshwater wetlands: a struggle for coexistence in the western United States. *Wetlands Ecology and Management* 3:3–15.
- Lemly, A. D., R. T. Kingsford, and J. R. Thompson. 2000. Irrigated agriculture and wildlife conservation: conflict on a global scale. *Environmental Management* 25:485–512.
- Littlefield, C. D., M. A. Stern, and R. W. Schlorff. 1994. Summer distribution, status, and trends of greater Sandhill Crane populations in Oregon and California. *Northwestern Naturalist* 75:1–10.
- Maupin, M. A., J. F. Kenny, S. S. Hutson, O. K. Lovelace, N. L. Barber, and K. S. Linsey. 2010. Estimated use of water in the United States in 2010. U.S. Geological Survey, Reston, Virginia. <https://pubs.usgs.gov/circ/1405/>
- Mayer, T. D. 2005. Water-quality impacts of wetland management in the Lower Klamath National Wildlife Refuge, Oregon and California, USA. *Wetlands* 25:697–712.
- McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* 89:2712–2724.
- McWethy, D. B., and J. E. Austin. 2009. Nesting ecology of greater Sandhill cranes (*Grus canadensis tabida*) in riparian and palustrine wetlands of Eastern Idaho. *Waterbirds* 32:106–115.
- Miller, M. R., J. Y. Takekawa, J. P. Fleskes, D. L. Orthmeyer, M. L. Casazza, and W. M. Perry. 2005. Spring migration of Northern Pintails from California’s Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. *Canadian Journal of Zoology* 83:1314–1332.
- Mix, K., W. Rast, and V. L. Lopes. 2009. Increases in growing degree days in the Alpine Desert of the San Luis Valley, Colorado. *Water, Air, and Soil Pollution* 205:289.
- Morrison, G. R. I., N. C. Davidson, and J. R. Wilson. 2007. Survival of the fittest: body stores on migration and survival in red knots *Calidris canutus islandica*. *Journal of Avian Biology* 38:479–487.
- Morrison, R. I. G., and J. P. Myers. 1989. Shorebird flyways in the new world. *in* H. Boyd, and J. Y. Piro, editors. *Flyways and reserve networks for water birds*. International Waterfowl and Wetlands Research Bureau, Slimbridge, England, UK.
- Moulton, C., J. Carlisle, K. Brenner, and R. Cavallaro. 2013. Assessment of foraging habitats of white-faced ibis near two important breeding colonies in Eastern Idaho. Idaho Fish and Game, Boise, Idaho. <https://ibo.boisestate.edu/wp-content/uploads/2013/01/Upper-Snake-White-faced-Ibis-Project-Report.pdf>
- Murray, N. J., et al. 2018. The large-scale drivers of population declines in a long-distance migratory shorebird. *Ecography* 41:867–876.
- NASS [USDA National Agricultural Statistics Service]. 2019. USDA national agricultural statistics service cropland data layer. <https://nassgeodata.gmu.edu/CropScope>
- North American Wetlands Conservation Act. 1989. Senate and house of representatives of the United States of America. P.L. 101-233.
- Nowak, C., M. Mougey, J. Krista, D. P. Collins, and B. A. Grisham. 2018. Mixing of two greater sandhill crane populations in northeast Oregon. Pages 110–114 *in* Proceedings of the North American Crane Workshop. University of Nebraska, Lincoln, Nebraska. <https://digitalcommons.unl.edu/nacwgproc/355/>
- Nowald, G., J. Fanke, and M. M. Hansbauer. 2018. Linking crane life history and feeding ecology with natural habitats and agricultural lands. Pages 18–35 *in* J. E. Austin, K. L. Morrison, and J. Harris, editors. *Cranes and agriculture: a global guide for sharing the landscape*. International Crane Foundation, Baraboo, Wisconsin.
- O’Neal, B. J., E. J. Heske, and J. D. Stafford. 2008. Waterbird response to wetlands restored through the conservation reserve enhancement program. *Journal of Wildlife Management* 72:654–664.
- Opsahl, T., F. Agneessens, and J. Skvoretz. 2010. Node centrality in weighted networks: generalizing degree and shortest paths. *Social Networks* 32:245–251.
- Oring, L. W., and J. M. Reed. 1997. Shorebirds of the western Great Basin of North America: overview and importance to continental populations. *International Wader Studies* 9:6–12.
- Pacific Flyway Council. 1997. Pacific Flyway management plan for the Central Valley Population of greater sandhill cranes. US Fish and Wildlife Service, Portland, Oregon. http://www.pacificflyway.gov/Documents/Cvgsc_plan.pdf
- Paul, D. S., and A. E. Manning. 2002. Great Salt Lake waterbird survey five-year report (1997–2001).

- Great Salt Lake Ecosystem Project, Utah Division of Wildlife Resources, Salt Lake City, Utah. <https://wildlife.utah.gov/gsl/waterbirdssurvey/>
- Pearse, A. T., G. L. Krapu, and D. A. Brandt. 2017. Sandhill crane roost selection, human disturbance, and forage resources. *Journal of Wildlife Management* 81:477–486.
- Pedersen, T. L. 2019. tidygraph: a tidy API for graph manipulation.
- Pfeiffer, L., and C.-Y.-C. Lin. 2014. Does efficient irrigation technology lead to reduced groundwater extraction? Empirical evidence. *Journal of Environmental Economics and Management* 67:189–208.
- QGIS Development Team. 2020. QGIS. Open source geospatial foundation project.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Rajagopalan, B., and U. Lall. 1998. Interannual variability in western US precipitation. *Journal of Hydrology* 210:51–67.
- Reinecke, K. J., and G. L. Krapu. 1986. Feeding ecology of Sandhill cranes during spring migration in Nebraska. *Journal of Wildlife Management* 50:71–79.
- Rewa, C. A. 2005. Wildlife benefits of the wetlands reserve program. Pages 133–145 in J. B. Haufler, K. E. M. Galley, and W. R. Rooney, editors. Fish and wildlife benefits of farm bill programs. 2000–2005, Beltsville, Maryland. USA. <https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1105&context=usdafsfacpub>
- Richter, B. D., D. Bartak, P. Caldwell, and K. F. Davis. 2020. Water scarcity and fish imperilment driven by beef production. *Nature* 3:319–328.
- Richter, B. D., J. D. Brown, R. DiBenedetto, A. Gorsky, E. Keenan, C. Madray, M. Morris, D. Rowell, and S. Ryu. 2017. Opportunities for saving and reallocating agricultural water to alleviate water scarcity. *Water Policy* 19:886–907.
- RStudio Team. 2019. RStudio: integrated development environment for R. RStudio Inc, Boston, Massachusetts. <https://www.R-project.org/>
- Runge, C. A., J. E. M. Watson, S. H. M. Butchart, J. O. Hanson, H. P. Possingham, and R. A. Fuller. 2015. Protected areas and global conservation of migratory birds. *Science* 350:1255–1258.
- Sabo, J. I., et al. 2010. Reclaiming freshwater sustainability in the Cadillac Desert. Proceedings of the National Academy of Sciences of the United States of America 107:21263–21270.
- Scanlon, B. R., C. C. Faunt, L. Longuevergne, R. C. Reedy, W. M. Alley, V. L. McGuire, and P. B. McMahon. 2012. Groundwater depletion and sustainability of irrigation in the US High Plains and Central Valley. Proceedings of the National Academy of Sciences of the United States of America 109:9320–9325.
- Schaible, G. D., and M. P. Aillery. 2017. Challenges for US irrigated agriculture in the face of emerging demands and climate change. Pages 44–79 in J. R. Ziolkowska, and J. M. Peterson, editors. Competition for water resources. Elsevier, Cambridge, Massachusetts.
- Scott, C. A., S. Vicuña, I. Blanco Gutiérrez, F. Meza, and C. Varela Ortega. 2014. Irrigation efficiency and water-policy implications for river-basin resilience. *Hydrology and Earth System Sciences* 18:1339–1348.
- Siegel, S. 1957. Nonparametric statistics. *American Statistician* 11:13–19.
- Small-Lorenz, S. L., L. A. Culp, T. B. Ryder, T. C. Will, and P. P. Marra. 2013. A blind spot in climate change vulnerability assessments. *Nature Climate Change* 3:91.
- Snyder, K. A., L. Evers, J. C. Chambers, J. Dunham, J. B. Bradford, and M. E. Loik. 2019. Effects of changing climate on the hydrological cycle in cold desert ecosystems of the Great Basin and Columbia Plateau. *Rangeland Ecology & Management* 72:1–12.
- Tapp, J. L., and E. B. Webb. 2015. Aquatic invertebrate food base for waterbirds at wetland reserve program easements in the lower Mississippi alluvial valley. *Wetlands* 35:183–192.
- Thorpe, P. P., J. P. Donnelly, and D. P. Collins. 2018. September 2018 survey of the rocky mountain population of greater Sandhill cranes. US Fish and Wildlife Service, Division of Migratory Birds, Lakewood, Colorado.
- Tiner, R. W. 2003. Estimated extent of geographically isolated wetlands in selected areas of the United States. *Wetlands* 23:636.
- Tyrchniewicz, A., and E. Tyrchniewicz. 2007. Alternative Land Use Services (ALUS) a preliminary overview of potential cost reductions and financial benefits to Canada. Alternative Land Use Services, Winnipeg, Manitoba, Canada. <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.602.5&rep=rep1&type=pdf>
- UNESCO-UN-Water. 2020. United Nations World Water Development Report 2020: water and climate change. United Nations, Paris, France. <https://en.unesco.org/themes/water-security/wwap/wwdr/2020>
- Vélez, E. P., and E. M. Saez. 2011. Water use for agriculture in Mexico. Pages 129–143 in Ú. Oswald Spring, editor. Water resources in Mexico: scarcity, degradation, stress, conflicts, management, and

- policy. Springer Berlin Heidelberg, Berlin, Heidelberg.
- Wada, Y., L. P. H. van Beek, N. Wanders, and M. F. P. Bierkens. 2013. Human water consumption intensifies hydrological drought worldwide. *The Environmentalist* 8:14. <https://doi.org/10.1088/1748-9326/8/3/034036>
- Ward, F. A., and M. Pulido-Velazquez. 2008. Water conservation in irrigation can increase water use. *Proceedings of the National Academy of Sciences of the United States of America* 105:18215–18220.
- Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. *Journal of Avian Biology* 41:621–626.
- Weber, T. P., A. I. Houston, and B. J. Ens. 1999. Consequences of habitat loss at migratory stopover sites: a theoretical investigation. *Journal of Avian Biology* 30:416–426.
- Wetlands International. 2012. Waterbird population estimates. Fifth edition. Wetlands International, Wageningen, The Netherlands. <https://www.wetlands.org/wp-content/uploads/2015/11/Waterbird-Populations-Estimates-Fifth-Edition.pdf>
- Wickham, H., et al. 2019. Welcome to the tidyverse. *Journal of Open Source Software* 4:1686.
- Wilsey, C. B., N. Taylor, M. Stockdale, and K. Stockdale. 2017. Water and birds in the arid west: habitats in decline. National Audubon Society, New York, New York. https://www.audubon.org/sites/default/files/wbaw_report_5july17_updated.pdf
- Xu, Y., Y. Si, J. Takekawa, Q. Liu, H. H. T. Prins, S. Yin, D. J. Prosser, P. Gong, and W. F. de Boer. 2019. A network approach to prioritize conservation efforts for migratory birds. *Conservation Biology: the Journal of the Society for Conservation Biology*. 34:416–426.

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