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Research Paper

Whooping Crane (*Grus americana*) use patterns in relation to an ecotop classification in the Central Platte River Valley, Nebraska, USA

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ABSTRACT. A portion of the Aransas-Wood Buffalo population of Whooping Cranes (*Grus americana*) stopover within the Central Platte River Valley (CPRV) annually. Past studies have found Whooping Cranes select herbaceous wetlands over agricultural fields when evaluated at a migration-corridor scale. However, recent studies conducted within the CPRV have reported Whooping Cranes selected agricultural fields and avoided herbaceous landcover classes. We hypothesized that much of this discrepancy was due to differences in landcover classifications used in previous studies, particularly those related to wetland designations. We used multiple existing, fine-scale geospatial data sources considering both landcover and hydrological factors to define unique and regionally specific ecotopes, which are the smallest homogenous and biologically relevant mappable units of analysis in landscape ecology (e.g., meadow-marsh, upland agriculture, etc.). We examined whether ecotop-based landcover, when evaluated at multiple spatial scales (i.e., 400 m and 1000 m), predicted terrestrial Whooping Crane occurrence within the CPRV. We used generalized linear mixed models within an information-theoretic approach to assess Whooping Crane occurrence within the CPRV. We found distinct ecotopes at the 1000-m scale explained nearly 40% of the variation in Whooping Crane occurrence. Ecotop models outperformed models including only their component parts such as flooding frequency and wetland designation. Whooping Cranes occurred more frequently within wetland portions of both agricultural fields and natural herbaceous communities and were less likely to use analogous upland components. We also found that occurrence was positively associated with proximity to the main channel of the Platte River and that Whooping Cranes avoided roads and developed areas, as several other studies have reported. Our findings indicate herbaceous and agricultural wetland areas should be targeted for Whooping Crane conservation efforts within the CPRV and perhaps regionally.

La grue blanche (*Grus americana*) utilise des modèles liés à un classement d'écotop dans la vallée de la rivière Central Platte, dans l'état américain du Nebraska.

RÉSUMÉ. Une partie de la population de grues blanches Aransas-Wood Buffalo (*Grus americana*) fait escale dans la vallée de la Central Platte River (CPRV) Des études passées ont démontré que les grues blanches sélectionnent des zones humides herbeuses de préférence aux champs agricoles lorsqu'elles sont surveillées à l'échelle de leur couloir de migration. Toutefois, des études récentes réalisées dans la CPRV ont indiqué que les grues blanches sélectionnaient les champs cultivés et évitaient les zones terrestres herbeuses. Nous avons supposé que cet écart tenait en grande partie aux différences des classifications de terres utilisées dans les études précédentes, en particulier celles qui concernent les désignations des terres humides. Nous avons utilisé de multiples sources de données géospatiales existantes à échelle fine en tenant compte à la fois de la végétation et des facteurs hydrologiques pour définir des écotopes uniques et spécifiques à la région, qui sont les unités d'analyse cartographiables les plus petites homogènes et biologiquement pertinentes dans l'écologie des paysages (par ex. prés marécageux, agriculture de montagne, etc.). Nous avons cherché à savoir si la végétation basée sur l'écotop, lorsqu'elle est évaluée à différentes échelles spatiales (par ex. 400 m et 1 000 m), permettait de prédire l'occurrence terrestre de grues blanches dans la CPRV. Nous avons utilisé des modèles mixtes linéaires généralisés dans une approche d'information-théorique pour évaluer l'occurrence des grues blanches dans la CPRV. Nous avons constaté que les écotopes distincts à l'échelle de 1 000 m expliquait près de 40 % des variations de l'occurrence des grues blanches. Les modèles d'écotopes surperformaient les modèles qui ne tenaient compte que de leurs éléments composants, comme la fréquence des inondations et la désignation de terres humides. Les grues blanches étaient plus nombreuses dans les parties de terres humides des champs agricoles comme des espaces herbacés naturels et étaient moins susceptibles de fréquenter des secteurs analogues en altitude. Nous avons également constaté que leur occurrence était associée positivement à la proximité de la branche principale de la Platte River et que les grues blanches évitaient les routes et les zones développées, comme l'ont indiqué plusieurs autres études. Nos résultats indiquent que les terres humides herbacées et agricoles devraient être ciblées dans le cadre des efforts de conservation de la grue blanche dans la CPRV et peut-être à l'échelle régionale.

Key Words: *ecotop; Grus americana; habitat selection; landcover classification; Whooping Crane*

INTRODUCTION

Precise mapping of ecologically relevant landcover characteristics represents a critical component for assessing wildlife habitat associations accurately (Roloff and Kernohan 1999, Gallant 2009). However, widely available geospatial landcover databases regularly differ in their demarcation of fine-scale but ecologically relevant features such as riparian corridors and associated wetlands (Cunningham 2006, Gergel et al. 2007, Fremgen-Tarantino et al. 2021). Differences in landscape definitions and classifications, as well as mapping scale, mapping techniques, and when the data were collected can result in misleading conclusions and, ultimately, poor management decisions (Langford et al. 2006, Kleindl et al. 2015). Integrating several geospatial data sources can increase mapping accuracy of finer-scale habitat features and therefore improve wildlife habitat models (Gallant 2009). This approach can also help identify distinct and biologically relevant ecotopes, which are the smallest homogenous mappable units of analysis in landscape ecology considering spatially explicit abiotic (e.g., flooding) and biotic (e.g., vegetation) factors (Klijn and Udo de Haes 1994, Naveh 1994, Hong et al. 2004, Ingegnoli 2013). Ecotope-level landscape classifications have been helpful in demarcating potential habitat for wildlife species that require a relatively specific set of conditions (Hong et al. 2004, Caven et al. 2017).

Whooping Cranes (*Grus americana*) were once at the precipice of extinction when fewer than 20 individuals were in existence in the mid-20th century, but numbers in the Aransas-Wood Buffalo population (AWBP) have slowly increased because of concerted long-term conservation efforts (Urbanek and Lewis 2020). The AWBP of Whooping Cranes, the only wild, self-sustaining population in the world, migrates through Central Flyway twice annually. Migration is an important life history event for many birds, and it is critically important that individuals are able to locate safe resting areas with sufficient food resources that will fuel migration and ensure birds arrive at breeding sites in good physical condition (Piersma et al. 2005, O'Neal et al. 2012). In the Great Plains, the Central Platte River Valley (CPRV) serves as an important stopover area for Whooping Cranes, where, between 1995 and 2015, more than 27% of all Whooping Crane records in Nebraska have been recorded (U.S. Fish and Wildlife Service, *unpublished data*). The CPRV is one of only five areas designated as Critical Habitat in the Central Flyway for the endangered Whooping Crane (CWS and USFWS 2005). The CPRV is important to Whooping Cranes and other migratory birds, both historically and currently, because of the diverse array of landcover classes and rich food resources it provides (NRC 2004, Caven et al. 2021). The CPRV is now dominated by row-crop agriculture (Dappen et al. 2008). Natural landscapes, including palustrine wetlands such as wet meadows, are limited but serve as important foraging sites for Whooping Cranes and Sandhill Cranes (*Antigone canadensis*) based on studies throughout the Central Flyway (Reinecke and Krapu 1986, Lingle et al. 1991, Austin and Richert 2005, Geluso et al. 2013, Baasch et al. 2019). Recent research by Howlin and Nasman (2017) in the CPRV did not detect a significant association between wet meadow landcover and Whooping Crane use. This result raises questions as to whether Whooping Crane habitat use in the CPRV is different than elsewhere in the Central Flyway.

Herbaceous plant communities in the CPRV are influenced by ground water levels and vary meaningfully across relatively small elevational gradients (e.g., < 2.0 m; Currier 1989, Henszey et al. 2004). Sub-irrigated herbaceous landcovers in the CPRV have been classified multiple ways. Brie and Bishop (2008) categorized the drier portions of these sub-irrigated herbaceous systems dominated by big bluestem (*Andropogon gerardi*) and switchgrass (*Panicum virgatum*) as xeric wet meadows. By contrast, Rolfsmeier and Steinauer (2010) defined these systems as Sandhills mesic tallgrass prairies. Brie and Bishop (2008) categorized the wetter portions of sub-irrigated herbaceous landcovers that are dominated by sedges, such as Emory's sedge (*Carex emoryi*) and woolly sedge (*C. pellita*), as mesic wet meadows. Additional terms used to classify these wetter ecotopes include eastern sedge meadows (Rolfsmeier and Steinauer 2010), wet meadows (Currier 1982, Chávez-Ramírez and Weir 2010), and sedge meadows (Henszey et al. 2004).

Considering nationally recognized wetland definitions, wet meadows represent a subtype of palustrine wetland dominated by emergent herbaceous vegetation that are sustained by fluctuating moisture regimes (Wilcox et al. 2007, Tiner 2016). Annually, these ecosystems experience periodic surface inundation or saturation during the growing season for durations long enough to allow the development of wetland soil profiles (Tiner 2016). Regionally, most wet meadows are sustained by fluctuating groundwater levels linked to riparian corridors (Hurr 1981, Wesche et al. 1994, Brinley Buckley et al. 2021). Variable hydrology is a key feature of this landcover type because sustained inundation or a lack of periodic inundation results in the system transitioning to an alternative community (i.e., shallow marsh or lowland tallgrass prairie; Boswell and Olyphant 2007, Wilcox et al. 2007, Tiner 2016). In Nebraska, Platte River wet meadows are classified into the hydro-geomorphic subclass of riverine floodplain, rapid permeability with minimal out of bank flooding (LaGrange 2015). The plant and soil profiles used by Brie and Bishop (2008) to map mesic wet meadow correspond closely to the conception of a wet meadow put forth by Tiner (2016) as a subtype of palustrine wetland with a seasonally saturated water regime. Brie and Bishop's (2008) definition of xeric wet meadow similarly corresponds to the general description of sub-irrigated lowland tallgrass prairie put forth by Kaul et al. (2006) as well as Rolfsmeier and Steinauer (2010).

Recent research suggests that Whooping Cranes select for aquatic and wetland habitats for diurnal use over all other land cover types including cornfields (Baasch et al. 2019). Howlin and Nasman's (2017) contradictory conclusion that Whooping Cranes do not select wet meadows over agricultural lands in the CPRV may be the result of imprecise regional definitions, mapping, or spatial consideration of wetland components (i.e., wet meadows and shallow marshes) embedded within a lowland tallgrass prairie matrix. Howlin and Nasman (2017) employed a highly inclusive and arguably arbitrary definition of wet meadow following the Platte River Recovery Implementation Program's (PRRIP 2012) definition that did not correspond to standard wetland classification schemes (Tiner 2016). The Platte River Recovery Implementation Program (2012) considered nearly all grasslands that possessed some proportion of sub-irrigated herbaceous vegetation entirely as wet meadow, regardless of its overarching

hydrologic regime (Howlin and Nasman 2017). However, many of the landscapes classified by PRRIP (2012) as wet meadow were defined as non-wetland habitats (e.g., lowland tallgrass prairie and sand ridge prairie) via alternative habitat classification and mapping efforts (Currier 1989, Henszey 2001, Henszey et al. 2004, Brei and Bishop 2008, Rolfmeier and Steinauer 2010, Kaul et al. 2006). Brei and Bishop's (2008) map of the CPRV, as well as 2011 National Wetland Inventory mapping, may help us better assess the degree to which Whooping Cranes select for herbaceous wetland components (e.g., wet meadows, shallow marsh, etc.) compared to analogous upland land cover types. As Chávez-Ramírez and Weir (2010) noted, wet meadows have been variously conceptualized within the CPRV but have always been considered important as diurnal Whooping Crane habitat.

We used multiple fine-scale geospatial data sources to reassess Whooping Crane occurrence in the CPRV at the ecotope level. We also examined landscape features associated with diurnal terrestrial occurrence at multiple spatial scales to determine which was most predictive of Whooping Crane occurrence (Johnson 1980, Mayor et al. 2009, Niemuth et al. 2018). We hypothesized that wetland landcover types would be predictive of Whooping Crane terrestrial habitat use at multiple spatial scales considering recent studies in other areas of the Great Plains (e.g., Niemuth et al. 2018, Baasch et al. 2019). Results of our study will help conservation practitioners and decision makers prioritize areas that provide important resources to Whooping Cranes during migratory stopovers and could guide future conservation actions regionally.

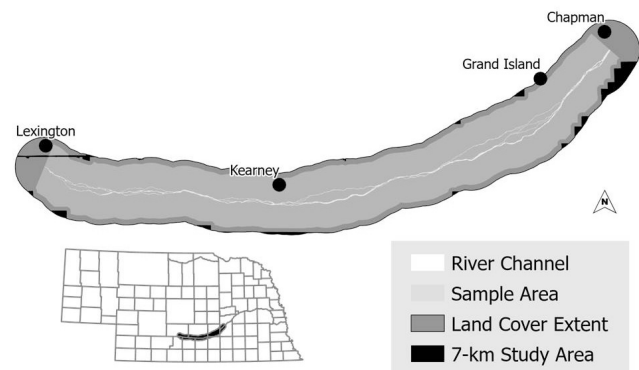
METHODS

Study area

Our study area included a 7 km buffer surrounding a 56 km reach of the main channel of the Platte River between Lexington (40° 73' N, 99°74' W) and Chapman (40°98' N, 98°15' W) Nebraska, USA (184,776 km²; Fig. 1). A large portion of this reach has been designated as Critical Habitat for the endangered Whooping Crane (USFWS 1978). Our study area is entirely encompassed within the current 95% migration corridor (Pearse et al. 2018) and is located 1500 km north of wintering grounds and 2500 km south of the breeding grounds. The CPRV is dominated by row-crop and other agriculture including corn (*Zea mays*), soybeans (*Glycine max*), alfalfa (*Medicago sativa*), sorghum (*Sorghum bicolor*), and wheat (*Triticum aestivum*; Dappen et al. 2008). However, native herbaceous landcover types, including wet meadows and lowland tallgrass prairies, are distributed throughout the study area and have been protected, enhanced, and restored for 40 years as part of cooperative conservation efforts by non-governmental organizations, government agencies, and private landowners (Currier and Henszey 1996, Krapu et al. 2014). Research indicates that meadow-marsh landcover is more abundant in the eastern portion of the CPRV (Krapu et al. 2014, Caven et al. 2019). The CPRV extends the range of tallgrass prairie westward into the central mixed-grass eco-region of the Great Plains by providing sub-irrigated moisture to a deep-rooted herbaceous perennial plant community (Currier 1989, Henszey et al. 2004, Kaul et al. 2006). Drier portions of these sub-irrigated herbaceous systems (i.e., lowland tallgrass prairies) are dominated by big bluestem and switchgrass, whereas the wetter portions of

sub-irrigated herbaceous ecosystems (i.e., wet meadows) are dominated by prairie cordgrass (*Spartina pectinata*) and sedges, such as Emory's sedge and woolly sedge. The CPVR is also an area of sustained restoration and management action by conservation organizations (e.g., Crane Trust, Audubon, and The Nature Conservancy) and state and federal natural resource agencies (e.g., U.S. Fish and Wildlife Service and Nebraska Game and Parks Commission) to improve Whooping Crane habitat conditions since the mid-1970s as well as the ongoing Platte River Recovery Implementation Program (Currier and Pfeiffer 2005, PRRIP 2006, Renfrew et al. 2006, Meyer et al. 2010).

Fig. 1. Map depicting our study area within the Central Platte River Valley (CPRV), which was delineated by placing a 7-km buffer around the main channel of the Platte River between Lexington and Chapman, Nebraska, USA. The map also highlights the location of the CPRV within the state of Nebraska, USA.



Locational data

We used the U.S. Fish and Wildlife Service (USFWS) public sightings database, which included verified sightings of Whooping Cranes reported by the public, state and federal agencies, conservation organizations, and others from 1995–2015 to determine Whooping Crane use locations (Austin and Richert 2005, Tacha et al. 2010, Caven et al. 2020). All sightings in the public sightings database were confirmed via visual verification of photos, videos, or in-field assessment by a qualified observer including biologists, natural resource professionals, or experienced bird watchers (Austin and Richert 2005, Tacha et al. 2010, Caven et al. 2020). We updated the associated geodatabase by digitizing secondary, tertiary, and additional use locations that previously existed only in hard copy reports because most analyses to date have simply used the first observed use location (Tacha et al. 2010, Niemuth et al. 2018). We undertook this effort because most of the first documented use locations in the CPRV correspond to night roosts; therefore, diurnal use locations important to foraging were not well represented within the primary geodatabase.

The USFWS public sightings database contains inherent biases (Tacha et al. 2010, Hefley et al. 2013). For instance, Niemuth et al. (2018) found that Whooping Cranes had a higher probability of being sighted near roads and population centers. Within our statistical models, we included distance to nearest paved road and

developed area as fixed effects and population density within a 2.6 km² area of use and random locations as random effects to account for the variation explained by these variables in our modeling effort (Seirup and Yetman 2006, Niemuth et al. 2018). We also included unbiased use locations from Platform Transmitter Terminal-marked (PTT) cranes, collected during 2010 to 2015, to make up a comprehensive set of known use locations and increase the size of our database (Baasch et al. 2019, Pearse et al. 2017, 2018, 2020). To facilitate our analysis, we generated 20 random locations distributed throughout the study area per use location for a total of 6940 random locations per 306 public sightings and 41 PTT-marked crane locations, which equates to 3.8 random locations per km² and generally reflects or exceeds the number of random points relative to study area size or known use location number used in similar space-use studies (e.g., Aarts et al. 2007, Hebblewhite and Merrill 2008). Use locations were included in the analysis based on three criteria: location > 10 m outside of the high banks of any river channel, data quality (location accuracy estimated at ≤ 400 m), and data within 10 years of 2005 (i.e., 1995-2015), which was when the CPRV landcover was mapped by Brei and Bishop (2008).

Landcover mapping

To assess Whooping Crane occurrence in relation to landscape characteristics, we used secondary data sources including the 2005 vegetation and landcover classifications created by the Rainwater Basin Joint Venture (Brei and Bishop 2008), the National Wetlands Inventory Project (NWI; Wilen and Bates 1995, USFWS 2021; Tande and Michaelson 2011, *unpublished data*), and flooding frequency data from the USDA-NRCS (2019, 2020; Table 1). All input data were converted to 10-m raster to match the USDA-NRCS (2020) gridded soil survey geographic database. All palustrine wetland types, with the exception of excavated pits, stock ponds, and impoundments, were dissolved together to get total palustrine wetland area and overlaid with the 2005 landcover (Wilen and Bates 1995, USFWS 2021). Soil survey data included the following flooding frequency categories: never, very rarely, rarely, occasionally, frequently, and very frequently, which we assessed in relation to terrestrial Whooping Crane occurrence patterns (USDA-NRCS 2019, 2020). Frequently and very frequently flooded categories were merged into one category because very frequently flooded landcover types were rarely observed in the study area. We hypothesized that Whooping Cranes would be more likely to use wetter components of the landscape per hydrological mapping efforts. However, we further hypothesized that landscape designations that integrated landcover types (e.g., herbaceous, woodland, etc.) with hydrological categorizations (e.g., flooding frequency, wetland designation, etc.) into ecotone classifications would better predict Whooping Crane use locations. Meadow-marsh was intended to represent wetland herbaceous landcover thought to be preferred by Whooping Cranes (Baasch et al. 2019). The meadow-marsh landcover class combined multiple categories from Brei and Bishop (2008) including mesic wet meadow, floodplain marsh, and warm-water slough (Table 1). We defined categorically non-wetland herbaceous landcovers in the CPRV as prairie, which included meadow sand ridge, xeric wet meadow, upland grassland, and undisturbed grassland per Brei and Bishop (2008; Table 1). However, some landcover types classified as prairie were defined as wetlands through the NWI (USFWS 2021; Tande and Michaelson 2011, *unpublished data*). As Rolfsmeier and Steinauer

(2010) noted, the Platte Valley contains a significant amount of eastern cordgrass wet prairie, which can serve as a transitional landcover type between sub-irrigated lowland tallgrass prairies and wet meadows. Therefore, we defined the prairie landcover type per Brei and Bishop (2008) with a wetland footprint per the NWI (Tande and Michaelson 2011, *unpublished data*) as wet prairies (Table 1). Given rotational practices of farming within the CPRV (i.e., soybean and cornfields are frequently rotated on an annual basis), all agricultural landcover types were lumped together and classified as agricultural wetlands or agricultural uplands based on flooding frequency. Binary rasters were generated for each landscape variable and the mean of each binary was calculated at 400 m (minimum locational accuracy of our data) and 1000 m (relevant to Whooping Cranes per Belaire et al. 2014, Niemuth et al. 2018, Baasch et al. 2019, Caven et al. 2022) radius scales with the focal statistics tool in ArcGIS version 10.6.1 (Environmental Systems Research Institute, Redlands, CA.) using a circular moving window. The mean values were multiplied by 100 to give the percent of landcover at each scale. Scaled ecotone, flood frequency, and palustrine wetland values were extracted to Whooping Crane use and available locations for statistical analysis.

Table 1. Landcover classes used by Brei and Bishop (2008) to map the Central Platte River Valley, Nebraska as well as our adjustments to them to facilitate an investigation of the likelihood of Whooping Crane (*Grus americana*) occurrence.

Landcover Classes	
<i>Brei and Bishop 2008</i>	<i>Our Classifications</i>
Upland Agriculture	Agricultural
Agricultural + Palustrine Wetland*	Agricultural Wetland*
Roads	Development
Rural Developed	
Urban/Suburban	
Phragmites	Invasive Dominated Wetland
Purple Loosestrife	
Floodplain Marsh	Meadow-Marsh**
Mesic Wet Meadow	
Basin Wetland**	
Warmwater Slough	
Canal/Drainage	Open Water
Irrigation Reuse Pit	
Lagoon	
Reservoir	
Sand Pit	
Stock Pond	
Bareground/Sparse Veg	Other
Meadow Sand Ridge	Prairie
Undisturbed Grassland	
Upland Grassland	
Xeric Wet Meadow	
Xeric Wet Meadow + Palustrine Wetland*	Wet Prairie*
River Channel	River Channel
River Early Successional	
Unvegetated Sandbar	
Riparian Shrubland	Shrubland
River Shrubland	
Upland Shrubland	
Riparian Woodland	Woodland
Upland Woodland	

* Indicates a classification partially based on mapping data from the National Wetlands Inventory (USFWS 2021). ** Indicates a classification partially based on mapping data from the Rainwater Basins (Bishop et al. 2015).

Statistical analyses

We used binomial family Generalized Linear Mixed-Effects Models (GLMM) within the lme4 package of Program R with a logit link function and a BOBYQA nonlinear optimizer to assess the effects of ecotone composition, flooding frequency, and wetland status on the probability of Whooping Crane occurrence across multiple spatial scales (Dean and Nielsen 2007, Powell 2009, Bates et al. 2015, Bates et al. 2021). Using the scale function in Program R version 4.2.0 (R Core Team 2020), all integer and continuous predictor variables were scaled to z-scores (standard deviations above or below the mean) and centered at zero to improve model convergence (Bring 1994). This approach had the added benefit of producing standardized coefficients with model results, which provide a coarse indication of each covariate's relative importance within a statistical model (Bring 1994, Afifi et al. 2020). To avoid issues of multicollinearity, we examined bivariate relationships between all ordinal, interval, and continuous predictor variables using Pearson product-moment correlation coefficients with the cor function in the stats package (R Core Team 2020). No two variables with $> |0.6|$ correlation or association (binary) were included in the same model (Dormann et al. 2013) but, rather, were tested in separate models. To ensure that standard errors in our models were not inflated as a result of collinearity between more than two variables, we conducted variance inflation tests on each candidate model using the vif function in the car package and dropped all models scoring > 5.0 from our analyses (Fox and Weisberg 2019).

We developed 54 a priori candidate models based on landscape mapping efforts that separated the study area across gradients of wetness to determine if Whooping Cranes differentially utilized the wetland components of herbaceous or agricultural habitats in the CPRV. Candidate models were based on three themes including ecotone, flooding frequency, and palustrine wetland models. Models included all possible uncorrelated variable combinations within each model theme. Like models were run at two scales including landcover within 400-m and 1000-m buffers around each use or random location to determine which landcovers were most predictive of terrestrial Whooping Crane occurrence. All models shared a common structure including a set of uncorrelated and thematically related (e.g., flooding frequency) predictor variables at the same spatial scale (i.e., 400 m or 1000 m) along with developed landcover and distance to nearest road as fixed effects control variables as well as landcover classification and categorical human population density as random effects control variables. Our model structure allowed for intercepts to vary across categories of landcover and population, which helped ensure that these variables potentially associated with detection probability did not represent a large amount of unexplained variance that could have biased independent variable parameter estimates. Population was converted to a categorical variable and treated as a random effect because it was highly correlated to developed landcover at both spatial scales. We used natural breaks from a histogram analysis to derive population categories from local census data (Seirup and Yetman 2006). Abundance categories included population as 0 people (15.8% of observations), 1 person (35.0%), 2 people (21.6%), 3–5 people (16.0%), 6–10 people (3.6%), 11–30 people (3.4%), 31–100 people (2.2%), and > 100 people (2.4%) per 2.6 km². In total, 26 models

were run at each scale in addition to two null models, including one with random effects ($y \sim 1 + (1|Landcover\ Class) + (1|Categorical\ Population)$) and a simple null model ($y \sim 1$). Models were compared using AIC corrected for small sample sizes (AICc) using the model.sel function in the MuMIn package (Burnham and Anderson 2002, Wagenmakers and Farrell 2004, Barton 2020). We assessed the model fit of top models using marginal and conditional R^2 values per Nakagawa and Schielzeth (2013). We also used predictor effects plots from the effects package (Fox and Weisberg 2018, 2019) and conditional density plots from the graphics package (R Core Team 2020) to describe the relationship between key predictor variables and Whooping Crane occurrence.

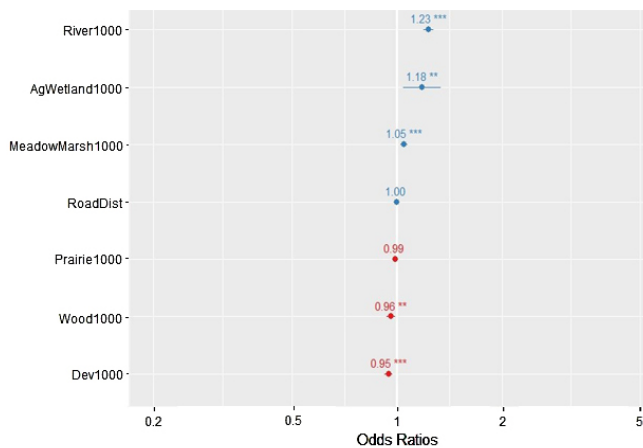
RESULTS

Ecotone-based models at the 1000-m scale performed the best and represented the top eight of 54 a priori models tested (Appendix 1). They were followed by palustrine wetland models at the 1000-m scale and ecotone models at the 400-m scale, which in total accounted for the top 19 of 54 models (Appendix 1). However, all flooding frequency models also outperformed both null models, which ranked 53rd and 54th out of the 54 models, respectively. Scales were intermixed for flooding frequency models, but the top couple flooding frequency models were at the 400-m scale and the four lowest ranked flooding frequency models corresponded to the 1000-m scale. The top six models overall, which all corresponded to ecotone models at the 1000-m scale, represented 100% of the cumulative model weight (Appendix 1).

The top model included agricultural wetland ($B \pm SE = 0.090 \pm 0.034$, $p = 0.008$), meadow-marsh ($B \pm SE = 0.193 \pm 0.053$, $p < 0.001$), prairie ($B \pm SE = -0.155 \pm 0.091$, $p = 0.086$), river channel ($B \pm SE = 0.541 \pm 0.042$, $p < 0.001$), woodland ($B \pm SE = -0.195 \pm 0.067$, $p = 0.004$), development ($B \pm SE = -0.770 \pm 0.190$, $p < 0.001$), and distance to nearest road ($B \pm SE = 0.094 \pm 0.058$, $p = 0.104$) as fixed effects and landcover class and categorical population density as random effects (Appendix 1, Fig. 2). The only other model with a $\Delta AICc \leq 2$ represented the same set of predictors with prairie removed.

Predictor effect plots (Fig. 3) and our probability of occurrence heat map (Fig. 4) clearly demonstrate an increasing likelihood of Whooping Crane occurrence with increasing values of meadow marsh, agricultural wetland, and riverine landcovers and a decreasing likelihood of occurrence with increased woodland and developed landcovers within a 1000-m buffer. Top model results indicate that a 1% increase in meadow-marsh landcover would increase the probability of Whooping Crane use by 5.1% (Fig. 3). Our top model indicates that a 1% increase in agricultural wetland landcover would result in a 17.4% increase in the probability of Whooping Crane occurrence (Fig. 3). Our top model predicted that a 1% increase in riverine landcover would result in a 27.9% increase in Whooping Crane occurrence (Fig. 3). A 1% increase in woodland was predicted to result in a 3.8% decrease in the probability of Whooping Crane use (Fig. 3). Similarly, a 1% increase in developed landcover was predicted to result in a 3.9% decrease in Whooping Crane occurrence (Fig. 3). Theoretical pseudo R^2 values were 0.39 for the model as a whole including random effects (conditional) and 0.19 regarding fixed effects only (marginal).

Fig. 2. Odds ratios with 95% confidence intervals for fixed effects variables from the top model controlling for landcover class and categorical human population density as random effects. The proportion of landcover classes within 1000 m of each use and available location that were evaluated included river (River1000), agricultural wetland (AgWetland1000), meadow marsh (MeadowMarsh1000), prairie (Prairie1000), woodland (Wood1000), and human development (Dev1000). RoadDist was a measure of the Euclidian distance between any paved road and each use or available location. Models were ranked via Akaike information criterion corrected for small sample sizes (AICc) and are presented with coefficient estimates and significance levels (** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$) for individual covariates in the top model.



DISCUSSION

Similar to other studies, we found areas with increased wetland components (i.e., meadow-marsh and wetland agriculture) located near the Platte River and decreased densities of roads and development had a higher likelihood of occupancy for diurnal use by Whooping Cranes than drier components of the landscape (Krapu 1981, Belaire et al. 2014, Hefley et al. 2015, Baasch et al. 2019). Our top model explained 39% of the variance in Whooping Crane occurrence within terrestrial landscapes in the CPRV. This indicates that finer scale habitat features, defined here as ecotopes, are likely an important factor in defining migratory stopover habitat for Whooping Cranes. Contrastingly, Howlin and Nasman (2017) found Whooping Cranes avoided wet meadows as compared to agricultural fields within the CPRV. However, their demarcations of wet meadows were based on PRRIP's (2012) delineations, which included all riparian grassland landcover types regardless of relative wetland composition or wetland size. Contrastingly, we found Whooping Crane occurrence was positively associated with meadow-marsh and negatively linked to upland prairie habitats. Therefore, the coarser mapping scale used by Howlin and Nasman (2017) likely masked ecologically important differences in landcover types that are predictive of Whooping Crane occurrence. We found nuanced differences in ecotope classification that captured variations in wetness (e.g., prairie, wet prairie, and meadow-marsh) were

important to consider when determining the likelihood of Whooping Crane occurrence. Whooping Cranes appear to be more likely to occupy wetland components of both herbaceous and agricultural landscapes, so occurrence and selection models that treat all grasslands or agricultural lands equally likely fail to detect important and biologically relevant habitat associations for this species.

Our study demonstrates the importance of using biologically relevant mapping approaches when evaluating species' habitat use patterns. This is especially important when individual species depend on finer-scale habitat features, such as wetlands, that are challenging to precisely map (Cunningham 2006, Roloff and Kernohan 1999, Gallant 2009, Fremgen-Tarantino et al. 2021). Our ecotope classifications considered not only broad landcover categories, but also included hydrologically significant gradients of wetness (Brei and Bishop 2008, USDA-NRCS 2019, 2020, Tiner 2016; Tande and Michaelson 2011, *unpublished data*). Accordingly, ecotope classifications were more predictive of Whooping Crane occurrence than their component parts including flooding frequencies, wetland status, and landcover designations alone. Most studies do not adequately consider the effects of classification precision and accuracy on model results (Cunningham 2006, Gergel et al. 2007, Gallant 2009, Lechner et al. 2012, Howlin and Nasman 2017, Fremgen-Tarantino et al. 2021). Recent research suggests that the landcover classifications and resolutions selected for use in modeling can impact estimates of species distributions (Lawler et al. 2004, Roloff and Kernohan 1999, McKerrow et al. 2018, Neimuth et al. 2018, Fremgen-Tarantino et al. 2021). A potential limitation of our study is that all agricultural landcovers were lumped, which could have masked the effects of different crop types on Whooping Crane occurrence. However, most sites were farmed rotationally, and several different cycles of annual crops were likely planted on each field across the study period. Additionally, Whooping Cranes generally respond positively to most herbaceous agricultural landcover classes, especially pre- and post-harvest (Caven et al. 2022). Ecologically relevant and accurate mapping is expressly important when studies are focused on a critically endangered species and when findings can influence management decisions with significant long-term implications (e.g., land protection and restoration). Our finding that the 1000-m buffer scale was most predictive of Whooping Crane occurrence was similar to Niemuth et al. (2018), which suggested that landcover classifications at the 1200-m scale were most predictive. Future research should attempt to assess variations in Whooping Crane occurrence at an ecotope scale including real-time information regarding habitat conditions (e.g., grazing, flooding, etc.) and behavior (e.g., foraging, preening, etc.; Rasool et al. 2021). In addition, assessing food resource availability within different ecotopes in conjunction with behavioral studies may provide valuable insights into the provisions provided to Whooping Cranes by different ecotopes (e.g., diet, rest, etc.; Lingle et al. 1991, Jorgensen and Dinan 2016, Hou et al. 2021).

Given that we used opportunistically collected data obtained through public sightings, consistent information does not exist regarding the condition of habitats during the time birds were using them (i.e., whether the landscape was inundated or not). Furthermore, data used in our study do not include Whooping Crane behaviors associated with each use location. Whereas use

Fig. 3. Likelihood of Whooping Crane (*Grus americana*) occurrence based on the proportion of meadow marsh (top left), agricultural wetland (top right), riverine (middle left), woodland (middle right), and developed (bottom left) landcover within a 1000-m buffer holding all other model covariates constant at their mean and including 95% confidence intervals. Tick marks on the X axis represent observed values on which the model was based.

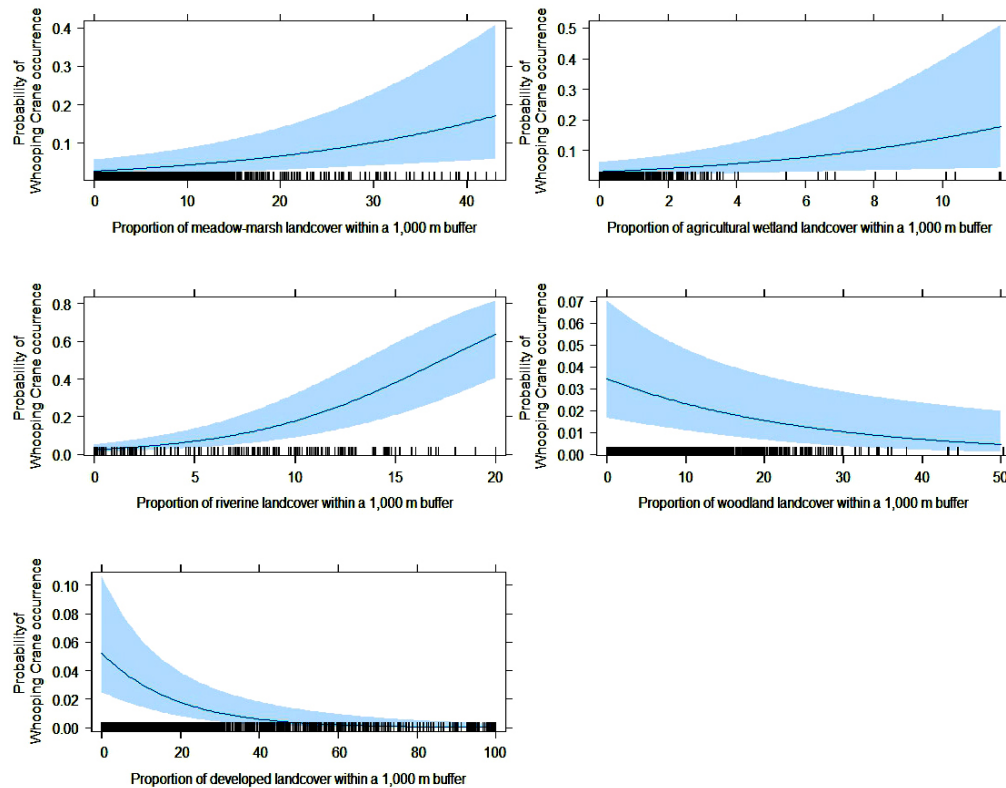
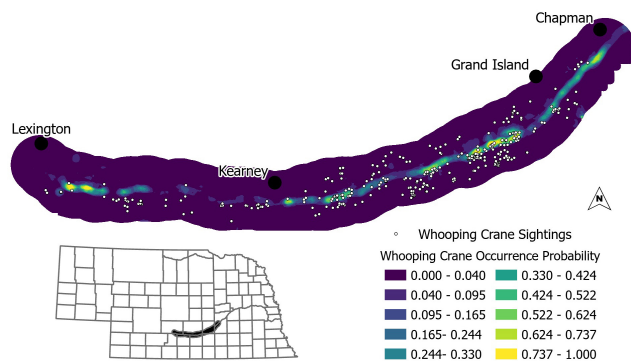


Fig. 4. Heat map depicting areas within the Central Platte River Valley most likely to be occupied by Whooping Cranes (*Grus Americana*) based on the top model from our analysis including terrestrial Whooping Crane locations (white circles) documented between 1995 and 2015 that were included in our study.



of one landcover class over another is an indication of its importance for Whooping Cranes, behavioral activities performed in various landcover classes, such as foraging or loafing, represent other important considerations when assessing the relative importance of each landcover class with regards to fitness and survival during migration (Lingle et al. 1991, Jorgensen and Dinan 2016, Hale et al. 2020). Research from the CPRV suggests that Sandhill Cranes spend a higher proportion of their time foraging while using lowland grasslands (i.e., lowland tallgrass prairie and wet meadows combined) as compared to other landscapes in the CPRV (i.e., agricultural fields; Sparling and Krapu 1994, VerCauteren 1998, Davis 2003). Davis and Vohs (1993) found Sandhill Cranes exhibited differential use patterns within the CPRV in that they extensively used areas composed of wet meadow and lowland tallgrass prairie but minimally used areas composed entirely of lowland tallgrass prairie, highlighting the importance of wetland components in supporting Sandhill Crane diets, which may serve as a useful indicator of their dietary value for Whooping Cranes as well. Research suggests that corn cannot meet a crane's daily physiological needs in terms of nutrients, such as protein, calcium, and phosphorus, necessary for successful migration and reproduction (Reinecke and Krapu 1986, Sparling and Krapu 1994, Caven et al. 2021). Neri (2011) demonstrated that plant matter, such as seeds and berries, are high

in calories but low in protein, whereas animal matter is low in calories but high in protein value for Whooping Cranes. Wetland habitats provide access to an array of animal protein sources, such as invertebrates, fish, amphibians, and reptiles (Neri 2011, Geluso et al. 2013, Urbanek and Lewis 2020, Caven et al. 2021). Recent behavioral research conducted in Nebraska indicates Whooping Cranes spend a disproportional amount of time foraging in wetland landcover classes, including wet meadows (Jorgensen and Dinan 2016, Baasch et al. 2021). Although waste grains are known to provide essential caloric requirements to complete migration, recent studies have also documented the importance of aquatic vertebrates and invertebrates in the diets of migrating Whooping Cranes (Neri 2011, Geluso et al. 2013, Urbanek and Lewis 2020, Caven et al. 2021).

Stopover habitats with quality foraging opportunities are thought to be essential for migrating Whooping Cranes to build energy reserves that enable them to complete their 4000 km biannual migration and to arrive at the breeding ground in adequate fitness for successful reproduction (Baasch et al. 2019, Caven et al. 2022). Interestingly, Caven et al. (2022) found that stopover duration was predicted by landcover classes associated with what appear to be important Whooping Crane foraging habitats (e.g., palustrine wetlands). Lingle (1987) described diurnal habitat use from 51 Whooping Crane sightings within the CPRV and reported that corn stubble received 37% of the documented diurnal use whereas tilled and natural wetlands received 35%. Given there are wetlands that are farmed, many of these wetland areas may have a more diverse set of food resources because they can sometimes be too wet to successfully produce a crop and become more grass- and forb-dominated, especially during wet years. Though we did not directly observe or study foraging behaviors, wetland portions of low-elevation grasslands, such as wet meadows and wetland areas in agricultural fields, clearly provide important food resources for Whooping Cranes during migration (Neri 2011, Geluso et al. 2013, Urbanek and Lewis 2020). However, lowland grasslands and embedded wetlands have experienced substantial losses and degradation because of agricultural expansion and development during the past half century (Sidle et al. 1989, Samson and Knopf 1994, Noss et al. 1995, Ricketts et al. 1999, Samson et al. 2010; WWFC 1988, *personal communication*). Protection of these landscapes, as well as the hydrological regime that sustains them, remain critical objectives for Whooping Cranes and, broadly, waterbird conservation in the CPRV and similar riverine ecosystems throughout the Great Plains (Currier 1989, Henszey et al. 2004, Baasch et al. 2019, Caven et al. 2020, Brinley Buckley et al. 2021).

Protecting expanses of agricultural and herbaceous landcovers free of human development with limited woodland landcover near to the Platte River that contains significant and functional wetland footprints may provide the most desirable set of conditions for supporting Whooping Cranes during migration stopovers in the CPRV. Similar to other research, we found having riverine landcover within 1000-m buffer had a strong influence on the likelihood of Whooping Crane occurrence (Howe 1989, Austin and Richert 2005, Niemuth et al. 2018, Baasch et al. 2019). Conversely, we found woodland and developed landcover, including both structures and roads, within a 1000-m buffer had a negative association with the likelihood of Whooping Crane occurrence. These findings are similar to other studies that

reported Whooping Cranes generally select foraging and roosting locations that are located away from woodland edges, roads, and human development (Pearse et al. 2017, Neimuth et al. 2018). This suggests that maintaining relatively treeless and undeveloped expanses of land, especially adjacent to wetland habitats and the main channel of the Platte River, could increase the likelihood of Whooping Crane occurrence. Protecting or restoring large expanses of habitat near key Whooping Crane use sites through easement or purchase will be essential to ensure that the CPRV remains a valuable stopover site for the Aransas-Wood Buffalo population of Whooping Cranes. Whooping Cranes do not exhibit a significant association with upland agricultural landcover and have a marginal negative association with upland prairie landcover. Nonetheless, protecting these habitats with the goal of preserving embedded wetlands and limiting human development is probably necessary to effectively maintain undisturbed Whooping Crane habitat within the CPRV.

The historic drainage and conversion of wetland to agricultural landcover and human development in the CPRV have reduced the availability of terrestrial wetland habitats that are most likely to be occupied by Whooping Cranes (Krapu 1981, Currier et al. 1985, Sidle et al. 1989, NRC 2004). Additional reductions in stream flows resulting from water development will continue to reduce the frequency and duration of wetland inundation, which will further reduce the availability and productivity of wetland landcovers (Brinley Buckley et al. 2021). Conservation efforts have retained remnant native wet meadows within the CPRV and restored other areas back to a prairie-wetland mosaic (Pfeiffer 1999, Meyer et al. 2010). Management efforts during the last 50 years have focused on the restoration of native plants and wetland topography to former agricultural lands, as well as the conversion of forest-dominated accretion to herbaceous habitats adjacent to the Platte River (Pfeiffer 1999, Krapu et al. 2014). To date, little research has been implemented to compare and evaluate wet meadow restoration efforts to determine whether they contain functional components found in native wet meadows (Pfeiffer 1999, Meyer and Whiles 2008, Meyer et al. 2010). Future efforts should evaluate if remnant wet meadow and shallow marsh landcover is more predictive of Whooping Crane occurrence than restored analogs as well as the length of time required for successful restoration of functional wetlands, both of which may influence long-term regional conservation strategies.

MANAGEMENT IMPLICATIONS

Given the continued developmental pressures, the protection of undeveloped landcover near the main channel of the Platte River may be essential for maintaining the long-term importance of the CPRV to Whooping Cranes. In addition, wetland components of agricultural fields provide an important resource to Whooping Cranes. As such, draining or filling these wetlands to improve agricultural production generally reduces the suitability of these landcover types for Whooping Cranes. Similarly, degradation of base flows or future water development, which decreases groundwater levels in adjacent wetlands, may also reduce the suitability of Whooping Crane habitats in the CPRV. Conservation efforts in the CPRV should not abandon investments in the conservation of herbaceous wetland habitats but, rather, focus such efforts on protecting and enhancing landscapes with a higher proportion landcovers with a diverse

array of seasonal, shallow wetland habitats (e.g., wet meadows and shallow marshes). Our results also indicate that Whooping Crane terrestrial occurrences take place primarily in areas of lower human development near the Platte River, where most Whooping Cranes roost within the CPRV. As such, protecting these lands from development through the use of land acquisitions and conservation easements may be the best way to ensure functional Whooping Crane habitat within the CPRV into the future. Our findings also emphasize the importance of the scale of landscape considered when assessing habitat use and species occurrence. These findings could be used to prioritize landcover types for intensified conservation efforts and further study to ensure functional critical habitat is maintained within the CPRV for the Aransas-Wood Buffalo Whooping Crane population.

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Appendix 1. Model selection table including the 54 models tested in our study and model theme with fixed effects predictors and control variables as well as random effects control variables, the model degrees of freedom (df), log likelihood (Log Lik.), Akaike Information Criterion corrected for small sample sizes (AICc), Δ AICc, and AIC model weight (Wt.). Model themes included ecotope classifications within 1000-m or 400-m buffers of use and available locations (Ecotope1000m or Ecotope400m), wetland landcover classifications within 1000-m or 400-m buffers of use or available locations (Wetland1000m or Wetland400m), and the proportion of landcover within 1000-m or 400-m buffers of use or available locations with various flooding frequencies. Fixed predictor effects included the proportion of each landcover class within a 1000-m or 400-m buffer of use or available locations including agricultural wetland (AgWetland1000 or AgWetland400), meadow marsh (MeadowMarsh1000 or MeadowMarsh400), prairie (Prairie1000 or Prairie400), riverine (River1000 or River 400), woodland (Wood1000 or Wood400), open water (OpenWater1000, or OpenWater400), wet prairie (WetPrairie1000 or WetPrairie400), invasive vegetation (Invasive1000 or Invasive400), and shrubland (Shrub1000 or Shrub400). Fixed effects also included the proportion of landcover within a 1000-m or 400-m buffer with flooding frequencies from the National Wetland Inventory including none, very rare, rare, occasional, and frequently (FloodNone1000, FloodVeryRare1000, FloodRare1000, FloodOccasional1000, and FloodFreq1000, or FloodNone400, FloodVeryRare400, FloodRare400, FloodOccasional400, and FloodFreq400, respectively). Controlled fixed effects included proportion of developed landcover within 1000 m or 400 m of use and available locations (Dev1000 or Dev400) as well as the Euclidean distance to the nearest paved road (RoadDist). Random effects included categories of landcover class (LandcovClass) and categories of population density within a 2.6 km² buffer (PopCat).

Model Theme	Fixed Effects (Predictors)	Fixed Effects (Controls)	Random Effects (Controls)	df	Log Lik.	AICc	Δ	
							AICc	Wt.
Ecotope 1000m	AgWetland1000 + MeadowMarsh1000 + Prairie1000 + River1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	10	-1226.1	2472.3	0.00	0.503
Ecotope 1000m	AgWetland1000 + MeadowMarsh1000 + River1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	9	-1227.6	2473.3	1.05	0.298
Ecotope 1000m	AgWetland1000 + MeadowMarsh1000 + OpenWater1000 + Prairie1000 + River1000 + WetPrairie1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	12	-1225.6	2475.2	2.96	0.115
Ecotope 1000m	AgWetland1000 + AgUpland1000 + MeadowMarsh1000 + OpenWater1000 + River1000 + WetPrairie1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	12	-1226.6	2477.2	4.90	0.043

Ecotope 1000m	MeadowMarsh1000 + Prairie1000 + WetPrairie1000 + River1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	10	-1228.7	2477.4	5.17	0.038
Ecotope 1000m	AgUpland1000 + AgWetland1000 + Wood1000 + River1000	Dev1000 + RoadDist	LandcovClass + PopCat	9	-1232.3	2482.5	10.26	0.003
Ecotope 1000m	AgWetland1000 + Invasive1000 + MeadowMarsh1000 + OpenWater1000 + Prairie1000 + WetPrairie1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	12	-1234.8	2493.7	21.41	0.000
Ecotope 1000m	AgUpland1000 + AgWetland1000 + Invasive1000 + MeadowMarsh1000 + OpenWater1000 + WetPrairie1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	12	-1236.1	2496.3	24.03	0.000
Wetland 1000m	Palustrine1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	7	-1253.5	2521.0	48.70	0.000
Wetland 1000m	Palustrine1000	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1256.1	2524.1	51.87	0.000
Ecotope 400m	AgWetland400 + MeadowMarsh400 + River400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	9	-1265.1	2548.2	75.91	0.000
Ecotope 400m	AgWetland400 + MeadowMarsh400 + Prairie400 + River400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	10	-1264.9	2549.7	77.48	0.000
Ecotope 400m	AgWetland400 + MeadowMarsh400 + OpenWater400 + Prairie400 + River400 + WetPrairie400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	12	-1263.7	2551.4	79.11	0.000
Ecotope 400m	AgWetland400 + OpenWater400 + MeadowMarsh400 + Prairie400 + Shrub400 + WetPrairie400	Dev400 + RoadDist	LandcovClass + PopCat	12	-1263.9	2551.8	79.54	0.000
Ecotope 400m	MeadowMarsh400 + Prairie400 + River400 + WetPrairie400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	10	-1270.4	2560.8	88.50	0.000

Ecotope 400m	AgUpland400 + AgWetland400 + River400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	9	-1273.2	2564.4	92.12	0.000
Ecotope 400m	AgUpland400 + AgWetland400 + Invasive400 + MeadowMarsh400 + OpenWater400 + WetPrairie400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	12	-1272.3	2568.7	96.43	0.000
Ecotope 400m	AgWetland400 + Invasive400 + MeadowMarsh400 + OpenWater400 + Prairie400 + WetPrairie400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	12	-1272.4	2568.8	96.58	0.000
Ecotope 1000m	AgWetland1000 + MeadowMarsh1000 + OpenWater1000 + Prairie1000 + Shrub1000 + WetPrairie1000	Dev1000 + RoadDist	LandcovClass + PopCat	11	-1280.4	2582.8	110.55	0.000
Flooding 400m	FloodFreq400 + FloodNone400	Dev400 + RoadDist	LandcovClass + PopCat	7	-1287.4	2588.7	116.46	0.000
Flooding 400m	FloodFreq400 + FloodNone400 + FloodVeryRare400	Dev400 + RoadDist	LandcovClass + PopCat	8	-1287.1	2590.3	117.98	0.000
Ecotope 1000m	AgUpland1000 + AgWetland1000 + MeadowMarsh1000 + OpenWater1000 + Shrub1000 + WetPrairie1000	Dev1000 + RoadDist	LandcovClass + PopCat	11	-1284.2	2590.4	118.18	0.000
Flooding 400m	FloodNone400	Dev400 + RoadDist	LandcovClass + PopCat	6	-1292.8	2597.6	125.31	0.000
Flooding 1000m	FloodFreq1000 + FloodNone1000	Dev1000 + RoadDist	LandcovClass + PopCat	7	-1293.2	2600.4	128.18	0.000
Wetland 400m	Palustrine400	Dev400 + RoadDist	LandcovClass + PopCat	6	-1294.7	2601.3	129.05	0.000
Wetland 400m	Palustrine400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	7	-1293.7	2601.4	129.18	0.000
Flooding 1000m	FloodFreq1000 + FloodNone1000 + FloodVeryRare1000	Dev1000 + RoadDist	LandcovClass + PopCat	8	-1293.0	2602.1	129.82	0.000

Flooding 400m	FloodOccasion400 + FloodRare400 + FloodVeryRare400	Dev400 + RoadDist	LandcovClass + PopCat	8	-1297.0	2610.1	137.83	0.000
Flooding 400m	FloodFreq400 + FloodOccasion400 + FloodRare400 + FloodVeryRare400	Dev400 + RoadDist	LandcovClass + PopCat	9	-1297.0	2612.0	139.78	0.000
Flooding 1000m	FloodNone1000	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1301.0	2614.1	141.83	0.000
Flooding 400m	FloodOccasion400 + FloodRare400	Dev400 + RoadDist	LandcovClass + PopCat	7	-1301.1	2616.3	144.03	0.000
Ecotope 400m	AgWetland400 + MeadowMarsh400 + OpenWater400 + Prairie400 + Shrub400 + WetPrairie400	Dev400 + RoadDist	LandcovClass + PopCat	11	-1299.1	2620.2	147.96	0.000
Ecotope 400m	AgUpland400 + AgWetland400 + MeadowMarsh400 + OpenWater400 + Shrub400 + WetPrairie400	Dev400 + RoadDist	LandcovClass + PopCat	11	-1299.9	2621.8	149.52	0.000
Flooding 400m	FloodRare400	Dev400 + RoadDist	LandcovClass + PopCat	6	-1308.7	2629.4	157.16	0.000
Flooding 1000m	FloodOccasion1000 + FloodRare1000 + FloodVeryRare1000	Dev1000 + RoadDist	LandcovClass + PopCat	8	-1310.1	2636.2	163.89	0.000
Flooding 1000m	FloodOccasion1000 + FloodRare1000	Dev1000 + RoadDist	LandcovClass + PopCat	7	-1311.1	2636.2	163.90	0.000
Ecotope 1000m	MeadowMarsh1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	7	-1311.2	2636.4	164.18	0.000
Flooding 1000m	FloodFreq1000 + FloodOccasion1000 + FloodRare1000 + FloodVeryRare1000	Dev1000 + RoadDist	LandcovClass + PopCat	9	-1309.6	2637.2	164.95	0.000
Ecotope 1000m	MeadowMarsh1000	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1313.5	2639.0	166.76	0.000

Ecotope 400m	MeadowMarsh400	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1318.6	2649.2	176.92	0.000
Ecotope 400m	MeadowMarsh400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	7	-1318.6	2651.2	178.92	0.000
Flooding 1000m	FloodRare1000	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1321.8	2655.6	183.35	0.000
Flooding 400m	FloodVeryRare400	Dev400 + RoadDist	LandcovClass + PopCat	6	-1322.4	2656.9	184.63	0.000
Flooding 400m	FloodOccasion400	Dev400 + RoadDist	LandcovClass + PopCat	6	-1322.7	2657.5	185.23	0.000
Flooding 1000m	FloodOccasion1000	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1323.3	2658.6	186.33	0.000
Ecotope 400m	AgWetland400	Dev400 + RoadDist	LandcovClass + PopCat	6	-1323.8	2659.5	187.25	0.000
Ecotope 400m	AgWetland400 + Wood400	Dev400 + RoadDist	LandcovClass + PopCat	7	-1323.7	2661.5	189.23	0.000
Flooding 400m	FloodFreq400	Dev400 + RoadDist	LandcovClass + PopCat	6	-1329.7	2671.4	199.15	0.000
Ecotope 1000m	AgWetland1000 + Wood1000	Dev1000 + RoadDist	LandcovClass + PopCat	7	-1329.0	2671.9	199.65	0.000
Flooding 1000m	FloodVeryRare1000	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1331.9	2675.8	203.51	0.000
Ecotope 1000m	AgWetland1000	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1333.8	2679.6	207.30	0.000
Flooding 1000m	FloodFreq1000	Dev1000 + RoadDist	LandcovClass + PopCat	6	-1338.0	2688.0	215.71	0.000

Null + Random	1	-	LandcovClass + PopCat	3	-1365.3	2736.6	264.32	0.000
Null	1	-	-	1	-1395.1	2792.1	319.84	0.000

WHOOPING CRANE STAY LENGTH IN RELATION TO STOPOVER SITE CHARACTERISTICS

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Abstract: Whooping crane (*Grus americana*) migratory stopovers can vary in length from hours to more than a month. Stopover sites provide food resources and safety essential for the completion of migration. Factors such as weather, climate, demographics of migrating groups, and physiological condition of migrants influence migratory movements of cranes (Gruidae) to varying degrees. However, little research has examined the relationship between habitat characteristics and stopover stay length in cranes. Site quality may relate to stay length with longer stays that allow individuals to improve body condition, or with shorter stays because of increased foraging efficiency. We examined this question by using habitat data collected at 605 use locations from 449 stopover sites throughout the United States Great Plains visited by 58 whooping cranes from the Aransas–Wood Buffalo Population tracked with platform transmitting terminals. Research staff compiled land cover (e.g., hectares of corn; landscape level) and habitat metric (e.g., maximum water depth; site level) data for day use and evening roost locations via site visits and geospatial mapping. We used Random Forest regression analyses to estimate importance of covariates for predicting stopover stay length. Site-level variables explained 9% of variation in stay length, whereas landscape-level variables explained 43%. Stay length increased with latitude and the proportion of land cover as open-water slough with emergent vegetation as well as alfalfa, whereas stay length decreased as open-water lacustrine wetland land cover increased. At the site level, stopover duration increased with wetted width at riverine sites but decreased with wetted width at palustrine and lacustrine wetland sites. Stopover duration increased with mean distance to visual obstruction as well as where management had reduced the height of vegetation through natural (e.g., grazing) or mechanical (e.g., harvesting) means and decreased with maximum water depth. Our results suggest that stopover length increases with the availability of preferred land cover types for foraging. High quality stopover sites with abundant forage resources may help whooping cranes maintain fat reserves important to their annual life cycle.

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Key words: Great Plains, *Grus americana*, habitat, machine learning, migration, stay length, stopover, wetlands, whooping crane.

The Aransas-Wood Buffalo population (AWBP) of Whooping cranes (*Grus americana*) was reduced to fewer than 20 individuals by the early 1940s as a

consequence of habitat loss and unregulated hunting and has since increased to over 500 individuals as a result of targeted species recovery efforts such as habitat conservation throughout their range, including their migratory corridor (Meine and Archibald 1996, NRC 2004, Mirande and Harris 2019, Harrell and

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Bidwell 2020). The AWBP migrates about 4,000 km twice annually spending about 20% of its annual cycle in migration (Kuyt 1992; Pearse et al. 2018, 2020). Stopover sites provide necessary food resources and secure roosting locations essential to the safe completion of migration for species of birds worldwide (Alerstam and Högstedt 1982, Hamer et al. 2006, Newton 2006). Whooping crane stopovers can range in duration from hours to more than 1 month (Faanes and Lingle 1988, Jorgenson and Bomberger Brown 2017, Pearse et al. 2020). Whooping crane stopovers average approximately 3 days in the U.S. portion of the migration corridor (\bar{x} = 2.9, SD = 5.9, Rabbe et al. 2019; \bar{x} = 2.5, SD = 3.6, Pearse et al. 2020), with the majority of stopovers lasting a single night (~12-16 hr; 77%, Pitts 1985; 64%, Pearse et al. 2020). However, extended stopovers of over 2 weeks have been documented throughout the migration corridor (Faanes and Lingle 1988, Kuyt 1992, Johns et al. 1997, Jorgensen and Dinan 2016, Rabbe et al. 2019, Urbanek and Lewis 2020).

Variation in stopover stay lengths may be explained by several factors, including the demographic composition of the migrating group and the ages of individual migrants (Ueta and Higuchi 2002, Teitelbaum et al. 2016, Pearse et al. 2020), short-term weather (Melvin and Temple 1982, Littlefield 2010, Malzahn et al. 2018), seasonal weather patterns (Wright et al. 2014, Harner et al. 2015, Caven et al. 2019a), and migration chronology (Krapu et al. 2014, Jorgenson and Bomberger Brown 2017, Caven et al. 2019a). Additional factors that potentially influence stopover stay length, such as body condition or habitat quality, have received less attention in cranes but more robust focus for other migratory birds. For example, Seewagen and Guglielmo (2010) found that fat reserves in a pooled sample of ovenbirds (*Seiurus aurocapilla*), Swainson's thrushes (*Catharus ustulatus*), and hermit thrushes (*C. guttatus*) were negatively related to stopover duration. Moreover, Hegemann et al. (2018) found that blood parasite infections prolonged stopover durations for passerines. The relationship between an individual's body condition and stopover duration has not been assessed directly for crane species. Nonetheless, Pearse et al. (2020) found that stopover stay length was negatively related to time spent at preceding migration stopovers for whooping cranes, which could indicate that the balance of an individual's energy reserves may partially influence stay length. Little information

exists regarding the relationship between stopover site characteristics or quality and an individual bird's stay length, particularly regarding cranes.

Though a substantial body of literature indicates that stopover duration is influenced by an individual's physical condition and broader weather patterns favorable or unfavorable to migration, uncertainty remains regarding the degree to which habitat availability, suitability, and quality influence avian stopover duration. Ktitorov et al. (2010) demonstrated that reed warblers (*Acrocephalus scirpaceus*) captured during migration and released into suitable habitat (marsh) stayed significantly longer than those released into unsuitable habitat (sand dune/xeric scrub). However, Liu and Swanson (2015) determined that yellow-rumped warblers' (*Setophaga coronata*) stopover duration was not influenced by habitat type (native riparian woodlands vs. anthropogenic woodlots), which may indicate relatively coarse differences in habitat did not greatly affect stay length. Even when habitat characteristics or quality influence stopover duration, taxa with distinct life histories demonstrate varying relationships. For example, Russell et al. (1994) found that stopover duration increased for rufous hummingbirds (*Selasphorus rufus*) as habitat quality, assessed in terms of nectar resources, decreased, whereas O'Neal et al. (2012) found that dabbling duck (Anatinae) stay length was positively related to foraging habitat quality. Quality sites could entice individuals to stay longer and improve body condition or could alternatively provide the same forage value with less effort and therefore precipitate shorter stay lengths. However, several crane species complete extended stopovers, often called "staging periods," at sites with predictably abundant forage resources where they tend to gain significant amounts of fat, preparing them for challenging stretches of migration (Melvin and Temple 1982; Krapu et al. 1985, 2014; Johns 1992; Warnock 2010; Prange 2012; Ilyashenko and Markin 2013; Ma et al. 2013). If whooping cranes also require acquisition of fat resources during migration, then stay length may be positively related to habitat quality or specific measures of resource abundance (e.g., land cover of documented foraging habitats).

Whooping cranes roost in a variety of wetland types, including small- to medium-sized palustrine wetlands, wide and shallow braided rivers, and lacustrine habitats throughout the southern boreal region, Canadian Prairies, and U.S. Great Plains (Faanes et al. 1992, Kuyt 1992, Johns et al. 1997, Austin and Richert 2005,

Farmer et al. 2005, Pearse et al. 2017, Farnsworth et al. 2018, Baasch et al. 2019a). Whooping cranes select for wetland habitat at multiple spatial scales as well as open sites that have wide unobstructed views, shallow water depths, and a lack of human disturbance for both night roosting and diurnal use locations (Faanes et al. 1992; Austin and Richert 2001, 2005; Richert and Church 2001; Farmer et al. 2005; Pearse et al. 2017; Niemuth et al. 2018; Baasch et al. 2019a, 2019b). Whooping cranes have diverse omnivorous diets that are largely derived from wetlands including macroinvertebrates such as crayfish, small vertebrates such as anurans and fish, and roots and tubers of wetland plants, as well as waste grain that is consumed primarily during migration and occasionally on the wintering grounds (Allen 1952, 1954; Kuyt 1987; Chavez-Ramirez 1996; Geluso et al. 2013; Thompson 2018; Caven et al. 2019b; Urbanek and Lewis 2020). Wetland availability has declined drastically throughout the U.S. Great Plains with increases in agriculture and other developments, with long-term declines being particularly stark south of the Platte River (Stahlecker 1992, Dahl 2000, Cariveau et al. 2011, Tang et al. 2012). A reduced quantity of wetland habitats within the whooping crane migration corridor could result in more long-duration stopovers at these limited sites, as successful migration and subsequent reproduction are largely dependent on the maintenance of adequate fat reserves (Krapu et al. 1985, Meine and Archibald 1996, NRC 2004, Fitzpatrick 2016, Mirande and Harris 2019). We used data collected on multiple spatial scales (site-level [third order] and landscape-level [second order]; see Johnson 1980, Mayor et al. 2009) from stopover sites used by satellite-tracked whooping cranes to examine the relationship between habitat characteristics and stay length within the U.S. Great Plains.

METHODS

Data Collection and Management

From December 2009 to February 2014, 68 whooping cranes were captured (35 juvenile, 33 adult plumage) and fitted with platform transmitting terminals (PTT; North Star Science and Technology LLC, Baltimore, MD, USA) at and surrounding Wood Buffalo National Park, Alberta and Northwest Territories, Canada, or at Aransas National Wildlife Refuge, Texas, United States, and adjacent wintering

areas (Pearse et al. 2015, 2018). Generally, only 1 crane from each family group was fitted with a PTT device. We obtained between 4 and 5 whooping crane locations per day through the Argos satellite system (Argos, Inc., Landover, MD, USA; Pearse et al. 2015, 2018). Locations were manually vetted for plausibility and eliminated if they deviated substantially from expected time sequences, having displacement rates exceeding 100 km/hour, or forming acute angles of less than 5 degrees for distances exceeding 50 km (Douglas et al. 2012, Pearse et al. 2015, 2018). We then eliminated all locations that included velocities above 2.1 m/second to ensure our database did not include sites passed over during flight (Pearse et al. 2015). Field crews visited day-use and night-roost locations used during migration within the conterminous U.S. to collect habitat related data after the whooping cranes had departed (Pearse et al. 2017). We attempted to collect data on nearly all initial roost sites as well as a broad subset of diurnal use sites; the sample was primarily constrained by physical accessibility, admission to private property, logistical constraints (e.g., travel time), and expert opinion (Pearse et al. 2017). Sites were visited within an average of 11 days following the departure of the whooping cranes, all sites were assessed within the same migration season, and >98.5% were visited within 1 month (Pearse et al. 2017). In total, field crews assessed 668 stopover use locations between October 2012 and November 2015. However, we removed use locations from this analysis that field crews were unable to physically visit, resulting in a sample of 605 stopover use locations at 449 stopover sites used by 58 individual whooping cranes. We compared the frequency distribution of stay lengths from our database to the U.S. Fish and Wildlife Service's (USFWS) whooping crane public sightings database ($n = 3,206$, 1942-2018; see Caven et al. 2020) to provide a more updated picture of stay lengths from this highly utilized data source (Pitts 1985, Tacha et al. 2010). We also compared stay length values between our database and Pearse et al. (2020) as a validation exercise given that the sample of sites we visited were not randomly selected.

Stopover sites were defined as a collection of location points for a single bird or group of birds migrating together that were separated by a movement of ≥ 15 km based on general movement patterns following Pearse et al. (2017) and Baasch et al. (2019a). Location points included initial evening roosts (R1), diurnal use sites (DU1), and subsequent night roost and day-use sites

(e.g., R2, DU2). Stopover sites included a 1.6-km buffer surrounding each use point in which land cover was assessed. Field measurements and assessments were collected at individual location points as well as within buffers surrounding them and included documentation of physical and hydrological characteristics, land use and cover, potential forage items, visual obstructions, anthropogenic disturbances, and photographs of the site (see Pearse *et al.* 2017). Distance measurements were collected in the field using a Nikon laser range finder (Laser 800 6×21 6.0°, Nikon Imaging, Tokyo, Japan) and longer measurements were validated using ArcMap 10.4.1 if necessary (Esri 2016). We used a subset of 47 site-level metrics collected following examination of data quality, completeness, and utility for measuring habitat quality and characteristics based on the existing literature (Austin and Richert 2001, 2005; Farmer *et al.* 2005; Pearse *et al.* 2017; Baasch *et al.* 2019a). We then merged our database of site-level metrics with an ArcGIS geodatabase developed from field assessments of buffers that detailed the proportional cover of 31 land-cover classes surrounding each stopover site and employed Esri World Imagery as a base map (Esri 2021). Each case of an individual bird at a unique stopover site was included as a separate data point for this analysis. This database represents habitat covariates on 2 different spatial scales with land cover data representing landscape-level (second order, Johnson 1980) and data gathered by field crews *in situ* representing site-level (third order, Johnson 1980) habitat characteristics (for a full list of variable descriptions, see Appendix A).

Statistical Analyses

We reduced the number of missing values in our dataset by assigning theoretically grounded values to information missing because of non-applicability or because observations represented extreme outlying values beyond measurability per our methods (Kwak and Kim 2017). For example, endangerments represent features such as power lines and wind turbines that can potentially harm or kill whooping cranes (see Brown *et al.* 1987). Endangerments were observed from most use sites but sometimes existed beyond the limits of our detection abilities, and thus were recorded as absent despite the fact an endangerment would ultimately be encountered at some distance. To avoid dropping observations from the dataset because of missing values, we applied the maximum observed

nearest endangerment distance to sites where no endangerment was detected, which can be considered a “Winsorization” technique (Kwak and Kim 2017). This approach was repeated to reduce missing values for other continuous variables within the database as well, such as distance to nearest standing water, with details presented in Appendix A. Following this effort, we assessed the data using the “densityplot” function in the “lattice” package in the open-source statistical software program R, which suggested that missing values were predominantly missing at random (MAR; Rubin 1976, Sarkar 2008, R Core Team 2019). All statistical analyses were performed using R version 3.6.0 (R Core Team 2019).

We handled remaining missing values via multiple imputation (MI) using predictive mean matching via the “mice” package (Van Buuren and Groothuis-Oudshoorn 2011, R Core Team 2019). We generated 4 separate databases using 25 iterations for each imputation ($m = 4$, $\text{maxit} = 25$, Van Buuren and Groothuis-Oudshoorn 2011). Employing a relatively high number of iterations (>10) generally ensures that convergence is reached, and imputed values are stable even when variables with missing information are strongly associated (White *et al.* 2011). Li *et al.* (1991) state that MI is robust to moderately large percentages of missing information ($\sim 30\%$) and generally results in valid models even under conditions of up to 50% missing data with modest power loss given the generation of a sufficient number of imputed databases ($m \geq 4$) on which to base point estimates for missing values. Seventy-two of our 79 variables (91.1 %) had less than 30% missing values ($\bar{x} = 7 \pm 14\%$ [SD]; $\text{max} = 47\%$) and no variable exceeded the 50% missing values threshold. We felt variables with $>30\%$ missing information were theoretically important enough to include in our model despite the probability that their effect sizes may be underestimated as a result of the high number of imputed cases (Li *et al.* 1991, Dong and Peng 2013). Dong and Peng (2013) demonstrated that coefficient estimates displayed similar directional relationships and effect sizes comparing data with 20% and 60% imputed values, but that standard errors were inflated in the 60% missing values condition, thus increasing the P -value of model covariates and leading to underestimated significance (i.e., Type II Error). The robustness of the imputed data was improved for our analyses because there were no missing values of the dependent variable “stopover stay length” (Von Hippel *et al.* 2007). Finally, it is worth noting that no landscape-

level covariates were missing more than 3% of case values. We evaluated pooled data from the imputed databases by comparing it to frequency distributions, associations with the dependent variable (stay length), and summary statistics, including means and variance, of raw data (Moore et al. 2009, Nguyen et al. 2017).

We analyzed data using Random Forest (RF) regression, a type of ensemble/machine learning analysis that incorporates permutations of multiple decision trees (i.e., “data forests”) via bootstrap sampling a database with replacement, to assess the importance of a set of covariates in predicting values of an outcome variable using the package “randomForest” (Breiman 2001, Liaw and Wiener 2002). Because decision-tree based models such as RF regression are constructed through repeat random sampling of a database, they do not make assumptions about data independence and therefore are relatively robust to issues of pseudoreplication (Breiman 2001, Jones et al. 2006, Prasad et al. 2006, Davidson et al. 2009). RF deals comparatively well with correlated predictor variables as well as interactions between them and nonlinear relationships (Cutler et al. 2007, Olden et al. 2008). Our models included 3,000 classification trees with either 5 (site-level) or 7 (landscape-level) variables tried for splitting at each node (Breiman 2001, Liaw and Wiener 2002, Probst et al. 2019). We included a relatively high number of trees ($n_{tree} = 3,000$) to maximize the precision of predictor variable importance estimates (Probst et al. 2019). We used a moderate number of candidate variables tried at each split ($m_{try} = 5-7$) to achieve reasonable predictive strength for individual trees while limiting correlation between them (Probst et al. 2019). Thus, the m_{try} values we employed met or exceeded recommendations for classification (\sqrt{p} , where p is the number of predictor variables) but were less than those generally applied to regression ($p/3$) in an effort to tune models to accurately estimate the importance of a broad host of potentially relevant predictor variables (Liaw and Wiener 2002, Probst et al. 2019).

We assessed predictor variables by the percent increase in the mean squared error (MSE) when each was removed from models (Breiman 2001, Liaw and Wiener 2002, Cutler et al. 2007). We then ran identical RF regression models and generated variable importance estimates for each of the 4 databases with imputed values. We averaged (mean) results across all 4 databases including standard deviations as confidence intervals surrounding variable importance estimates. We

presented standard deviations (SD) instead of standard errors (SE) because they better display importance estimate variability across datasets with unique imputed values (Altman and Bland 2005, Barde and Barde 2012). We considered this an appropriate way to pool parameter importance estimates from multiple imputed datasets given the lack of a traditional coefficient estimates provided by RF regression for averaging (see Rubin 1987). Given the importance of migration season (i.e., spring or fall) on whooping crane migratory behavior and habitat use (Johns et al. 1997; Austin and Richert 2001, 2005; Pearse et al. 2020), we included “season” along with the “type” of use location assessed (e.g., R1, DU1) in all models as control variables (Hünemann and Louw 2020). We also present the results of the same analysis completed following the listwise deletion of observations with missing information (Kwak and Kim 2017). Although listwise deletion generally produces more biased results than multiple imputation when missing values are MAR, presenting the results from both methods may better display the level of certainty surrounding variable importance estimates (Rubin 1976, 1987; Moore et al. 2009; Kwak and Kim 2017, Nguyen et al. 2017). We repeated this procedure with variables on 2 spatial scales: site-level and landscape-level. This does not represent a habitat selection analysis, per se, as we are not examining use points in reference to unused random locations (Johnson 1980, Mayor et al. 2009, Baasch et al. 2019a). However, this framework does allow us to examine which scale habitat was most predictive of stopover duration and what variables most strongly influenced stay length (Johnson 1980, Mayor et al. 2009).

We present the mean amount of variation explained in the dependent variable stopover duration by both landscape and site-level models. We also describe the most important variables within each model and their relationship to stopover stay length. Finally, we describe the relationship of select variables indicative of habitat suitability or quality in the literature (e.g., water depth; Austin and Richert 2001, 2005; Farmer 2005) that demonstrated notable importance in our analyses ($>10\%$ increase MSE) to stopover stay length (see Genuer et al. 2010, Caven et al. 2017). This process helped us determine if characteristics generally associated with habitat quality were related with extended stay lengths. Some variables may be relatively important (e.g., $>20\%$ increase MSE), yet demonstrate comparatively small predicted effect sizes (0.2-day or 4.8-hr increase in stay

length) because the results of our models are additive (Molnar 2019). We used partial dependence plots to interpret the relationship of continuous variables to stopover duration using the “randomForest” and “pdp” packages (Liaw and Wiener 2002, Auret and Aldrich 2012, Greenwell 2017, Molnar 2019), and we used boxplots to describe the variation in stopover duration across categories of nominal variables (“ggplot2” package, Wickham *et al.* 2009). Plots were based off data associated with the best performing site-level or landscape-level model for each predictor variable (*i.e.*, the imputed database related to the model in which the explanatory variable demonstrated the highest increase in the MSE when removed).

RESULTS

Mean stopover duration was 3.1 ± 4.4 days (\pm SD, $n = 605$; range = 0-27) at stopover sites used by tracked whooping cranes and assessed by ground crews from 2012 to 2015 (Fig. 1). For comparison, mean stopover duration via the USFWS public sightings database was 2.9 ± 5.9 days (\pm SD, $n = 3,206$; range = 0-53). However, the median and mode values for stopover duration in both datasets were 1 day. Over half (55%) of stopovers by tracked whooping cranes at sites assessed for habitat features were a single day or less as were 61% of publicly documented stopovers (Fig. 1). Stopover lengths of ≥ 11 days were observed at 7% of assessed sites used by tracked whooping cranes and at 5% of stopovers documented via the USFWS public sightings database. Eighty-nine percent of diurnal and nocturnal use locations assessed were ≤ 100 m from surface water, and 94% were ≤ 400 m from surface water.

Site-level variables across 4 imputed databases explained an average of $9 \pm 3\%$ of variation in stopover stay length, whereas landscape-level variables explained $43 \pm 1\%$ (Figs. 2 and 3). Random Forest analyses using databases with listwise deletion explained a similar amount of variation in stopover duration at the landscape level (43%) and slightly less than imputed databases at the site level (7%). Variable importance estimates differed between site-level models developed using imputed ($n = 605$) and listwise deleted data ($n = 192$) but were similar regarding landscape-level models ($n = 605$ and $n = 592$, respectively; Figs. 2 and 3). Eight site-level and 18 landscape-level variables produced $>15\%$ increase in the MSE of RF regression models when removed (Figs. 2 and 3). The top landscape-level

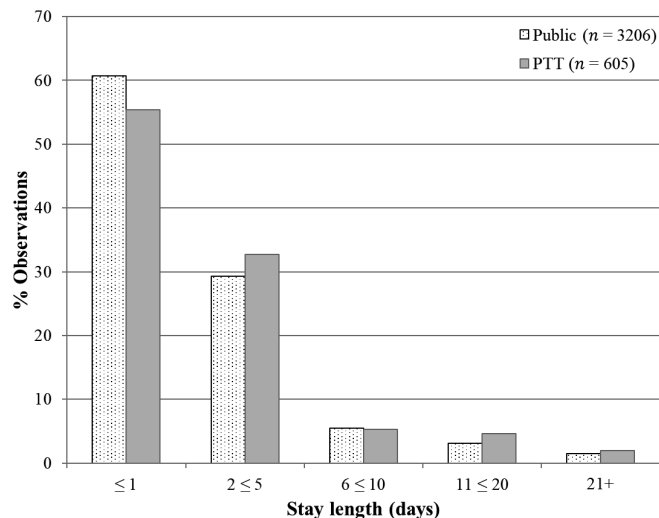


Figure 1. Stopover stay lengths from the USFWS public sightings database (Public; 1942-2018) and field crew assessed stopovers of whooping cranes from the Aransas-Wood Buffalo population tracked by platform transmitting terminals (PTT; 2012-2015).

variables included proportional land cover of open-water sloughs with emergent vegetation (OWSloughWemerg, $39 \pm 2\%$), latitude (Lat, $37 \pm 1\%$; Fig. 4), proportional land cover of alfalfa (Alfalfa, $37 \pm 2\%$; Fig. 3, Appendix A). Longitude (Lon, $36 \pm 1\%$; Fig. 4) and the proportional land cover of row crop agriculture (Ag_Sum, $32 \pm 1\%$) were also relatively important predictor variables at the landscape level (Fig. 3, Appendix A). The best site-level variables included wetted width (WettedWidthCom, $20 \pm 2\%$), the dominant land cover at the nearest terrestrial bank to wetland use locations (LandcovBank, $19 \pm 2\%$), and the distance to the nearest terrestrial bank from wetland use locations (DistBank, $19 \pm 11\%$; Fig. 2, Appendix A). Distance to nearest bank exhibited more variation in importance estimates across models than other top predictor variables with the 1-standard deviation confidence interval ranging from an 8% to a 30% increase in the model’s MSE when this variable was removed, signifying some uncertainty in the relative importance of this parameter (Fig. 2). Wetland classification (WetlandClass, $19 \pm 1\%$) and the percent of silt and/or clay present in sediment (SiltorClay, $19 \pm 13\%$) were also relatively important predictor variables at the site-level (Fig. 2, Appendix A).

Stopover duration increased with the proportion of land cover as open-water slough with emergent vegetation. Our model predicted, based on PTT and habitat data, that stopover duration would increase from

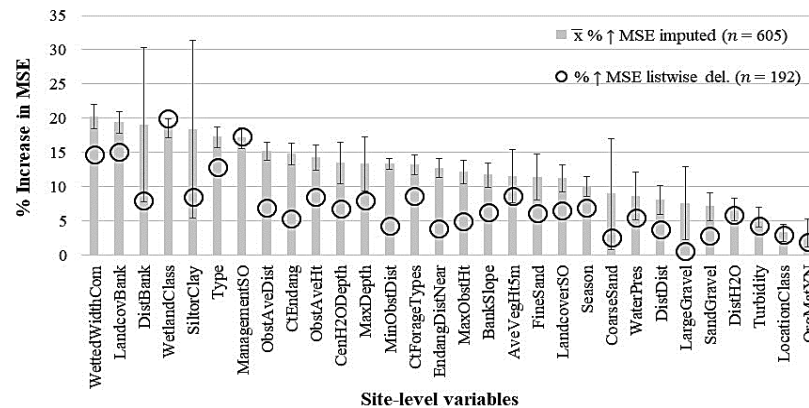


Figure 2. Importance estimates for site-level variables predicting whooping crane stopover duration measured as the increase in the mean squared error (MSE) when a variable is removed from the model with results averaged across 4 analyses using separate databases with imputed values (\bar{x} % ↑ MSE imputed) presented with confidence intervals of 1 standard deviation. Variable estimates are also presented from a similar model using data in which listwise deletion was applied to handle missing values (% ↑ MSE listwise del.). Variable names and descriptions are presented in Appendix A. Data derived from 605 locations used by 58 whooping cranes of the Aransas-Wood Buffalo population, 2012-2015.

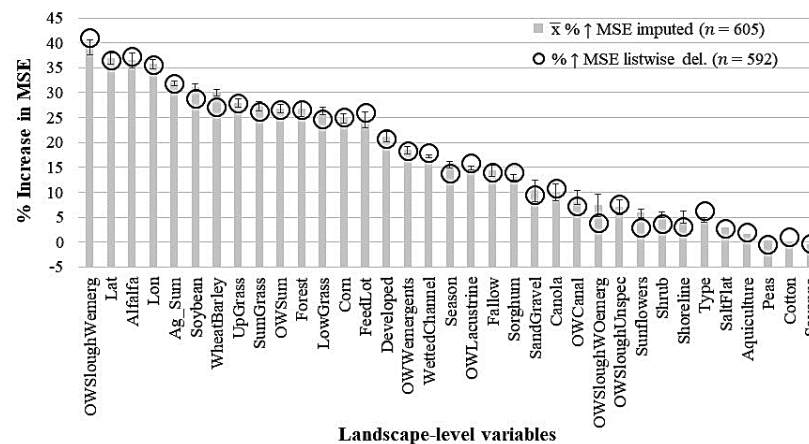


Figure 3. Importance estimates for landscape-level variables predicting whooping crane stopover duration measured as the increase in the mean squared error (MSE) when a variable is removed from the model with results averaged across 4 analyses using separate databases with imputed values (\bar{x} % ↑ MSE imputed) presented with confidence intervals of 1 standard deviation. Variable estimates are also presented from a similar model using data in which listwise deletion was applied to handle missing values (% ↑ MSE listwise del.). Variable names and descriptions are presented in Appendix A. Data derived from 605 locations used by 58 whooping cranes of the Aransas-Wood Buffalo population, 2012-2015.

an expected 3 days to >5.6 days as open-water slough with emergent vegetation habitat increased from 0% to 30% of land cover within stopover site buffers (Fig. 5a). Stopover duration increased with latitude after reaching a predicted minimum near 37°N (northern Oklahoma) with notable spikes in an otherwise relatively linear upward trend near 41°N (southcentral Nebraska) and 46-47°N (northern South Dakota, throughout North Dakota; Fig. 5b). This trend is clearly visible in Figure 4 where the stopovers in the longest duration category (stay length = 23-27 days) are distributed throughout

Nebraska, South Dakota, and North Dakota and are absent from the southern Great Plains. Stay length was predicted to increase from 3.0 to >5.5 days as proportional land cover of alfalfa within site buffers increased from 0 to nearly 30%, with the greatest gain from 10-12% land cover (Fig. 5c). Additionally, predicted stay length was positively related to proportional land cover as lowland grassland (from 3.1 to 3.7 days with an increase from 0 to 40%; Fig. 5d) and corn (from 3.2 to 3.9 days with an increase from 0 to 40%; Fig. 5e). Predicted stay length was negatively

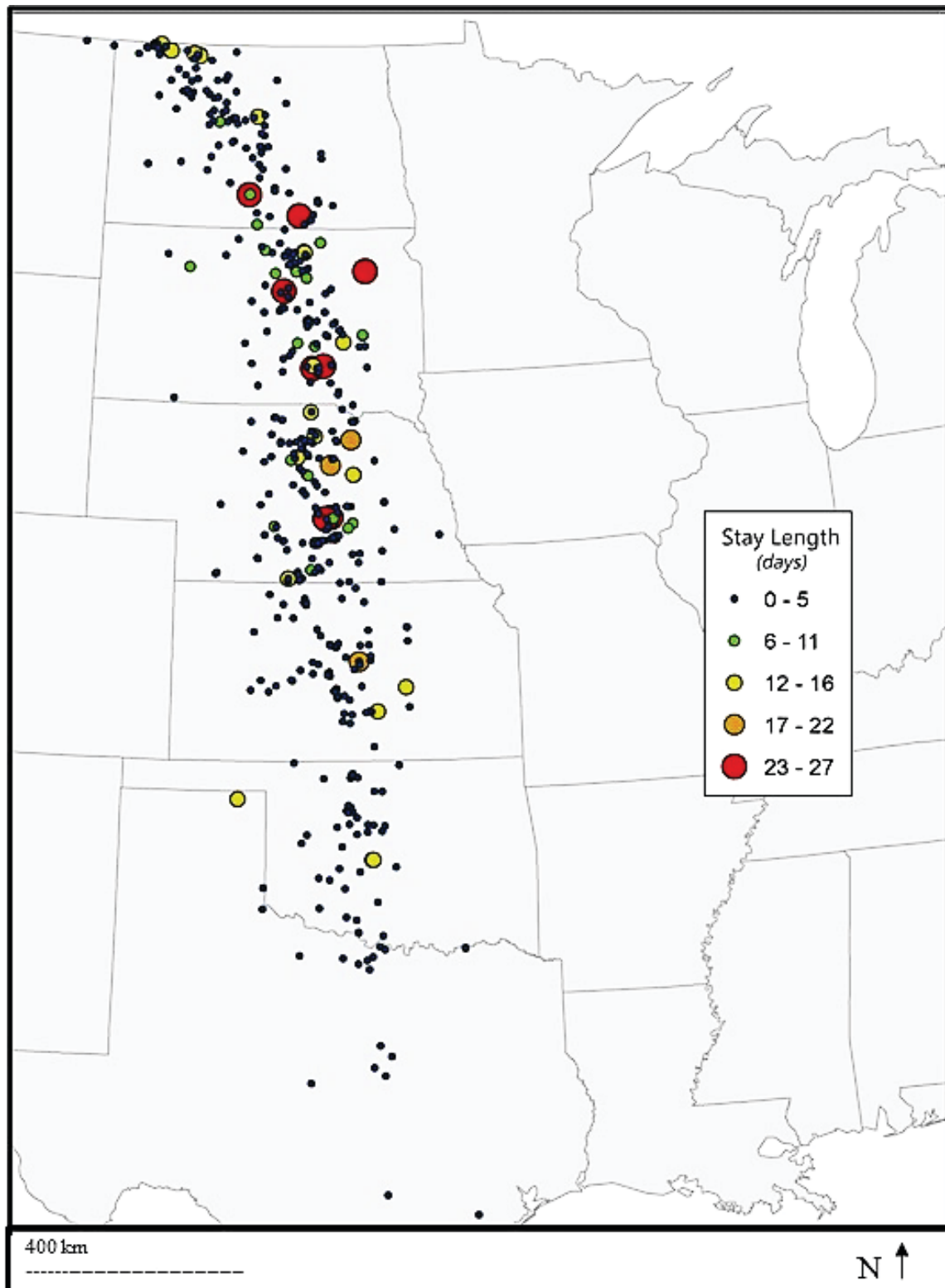


Figure 4. The distribution and associated stay lengths of PTT-tracked whooping cranes at stopover sites assessed by field crews from 2012 to 2015 throughout the Great Plains of the United States.

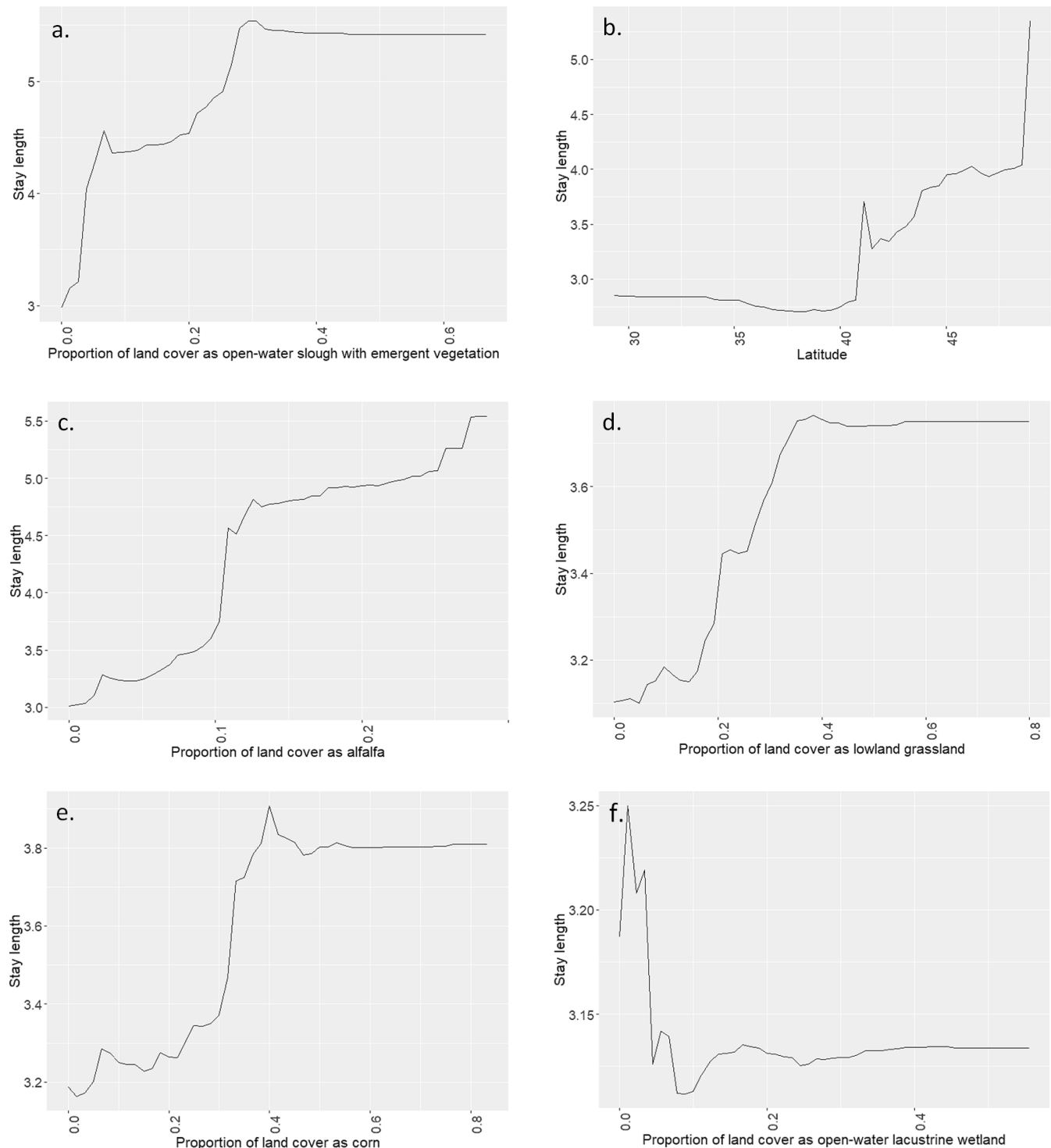
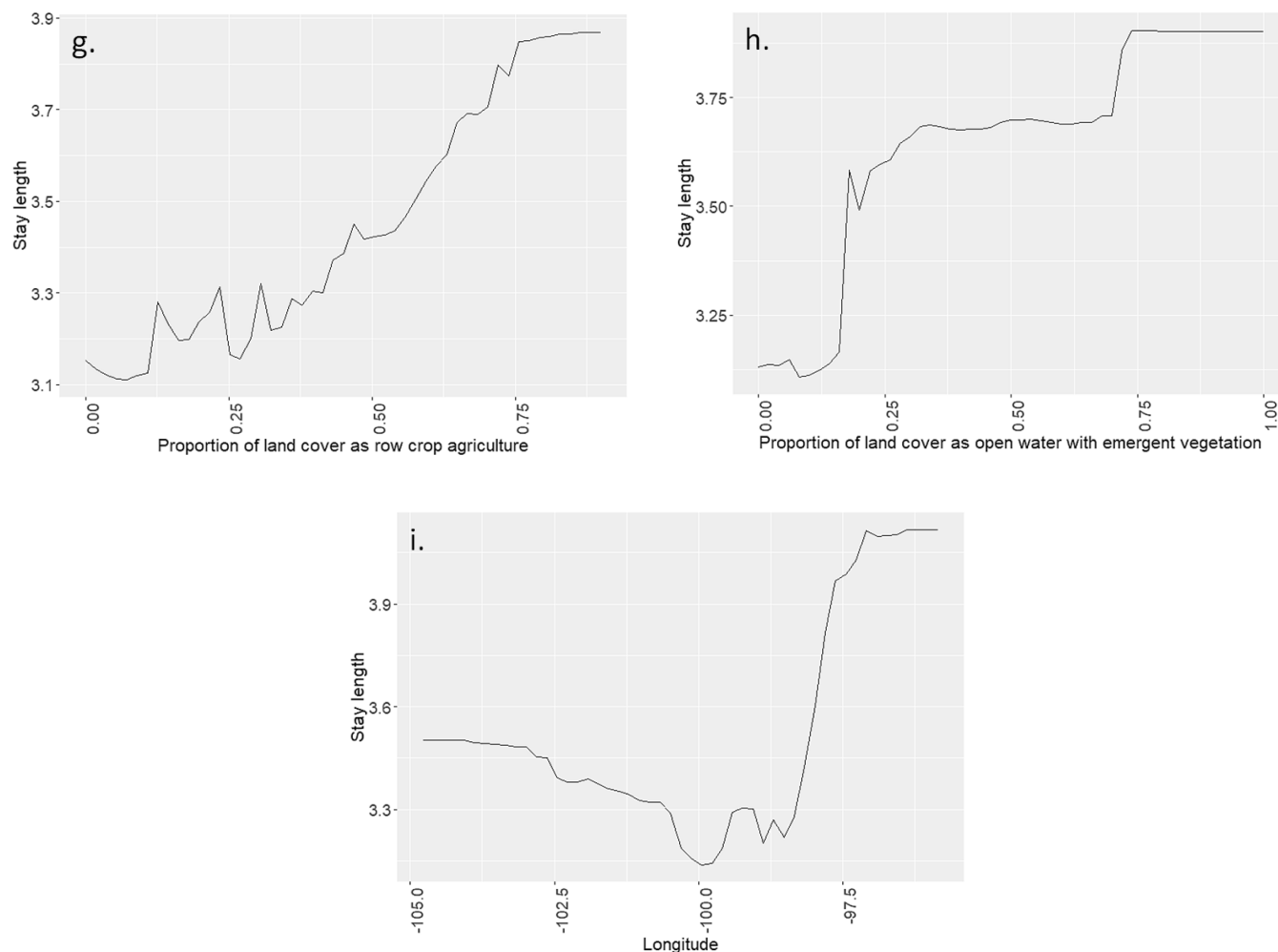


Figure 5. Partial dependence plots describing predicted stopover stay length of whooping cranes (WHCR) (y-axis) in relation to top and selected continuous landscape-level predictor variables, including the proportion of land cover within stopover buffers (x-axis) as (a) open-water slough with emergent vegetation (OWSloughWemerg), (b) latitude (Lat), (c) proportional land cover as alfalfa (Alfalfa), (d) proportional land cover as lowland grassland (LowGrass), (e) proportional land cover as corn (Corn), (f) proportional land cover as open-water lacustrine wetland (OWLacustrine), (g) proportional land cover as any row crop agriculture (Ag_Sum), (h) the proportion as open water with emergent vegetation (OWWemergents), and (i) longitude (Lon). Further variable descriptions are presented in Appendix A.

**Figure 5. Continued.**

related to open-water lacustrine land cover (from 3.3 to 3.1 days with an increase from 3 to 10%; Fig. 5f). The sum of row crop agriculture (from 3.1 to 3.9 days with an increase from 12 to 78%; Fig. 5g) and open water with emergent vegetation (from 3.1 to 3.9 days with an increase from 10 to 75%; Fig. 5h) were positively related to stay length. Finally, stay length appeared to have an inverse quadratic relationship to longitude, as predicted stopover duration was shortest near the center of the migration corridor near the hundredth meridian and increased moving outward, particularly east of -98.5° (Figs. 4 and 5i).

Whooping crane stopover duration demonstrated a system-specific response to wetted width. Stay length increased from 2.8 to 3.6 days at riverine sites as wetted width increased from 100 m to 400 m, then plateaued at about 3.7 days at widths >900 m (Fig. 6a). Stay

length at palustrine and lacustrine wetlands decreased about 0.4 days as wetted width increased >5 -fold (900 to 5,000 m; Fig. 6b). We found considerable variation in stay length at palustrine and lacustrine wetland sites with wetted widths <900 m, with a spike in stay length at around 500 m, indicating that additional site characteristics may have been more influential to stay length than wetted width at these sites (Fig. 6b). Predicted whooping crane stay length increased 1.2 days as the percent of the substrate at use points composed of silt and/or clay (SiltorClay) increased from $<5\%$ to $>90\%$, with a conspicuous spike between 26 and 35% (Fig. 6c). Predicted stay length was positively related to the mean distance of a visual obstruction from the use location (from 3.2 to 3.7 days with an increase from 200 to 5,000 m; Fig. 6d), while being negatively related to maximum depth of the wetland near or at the use

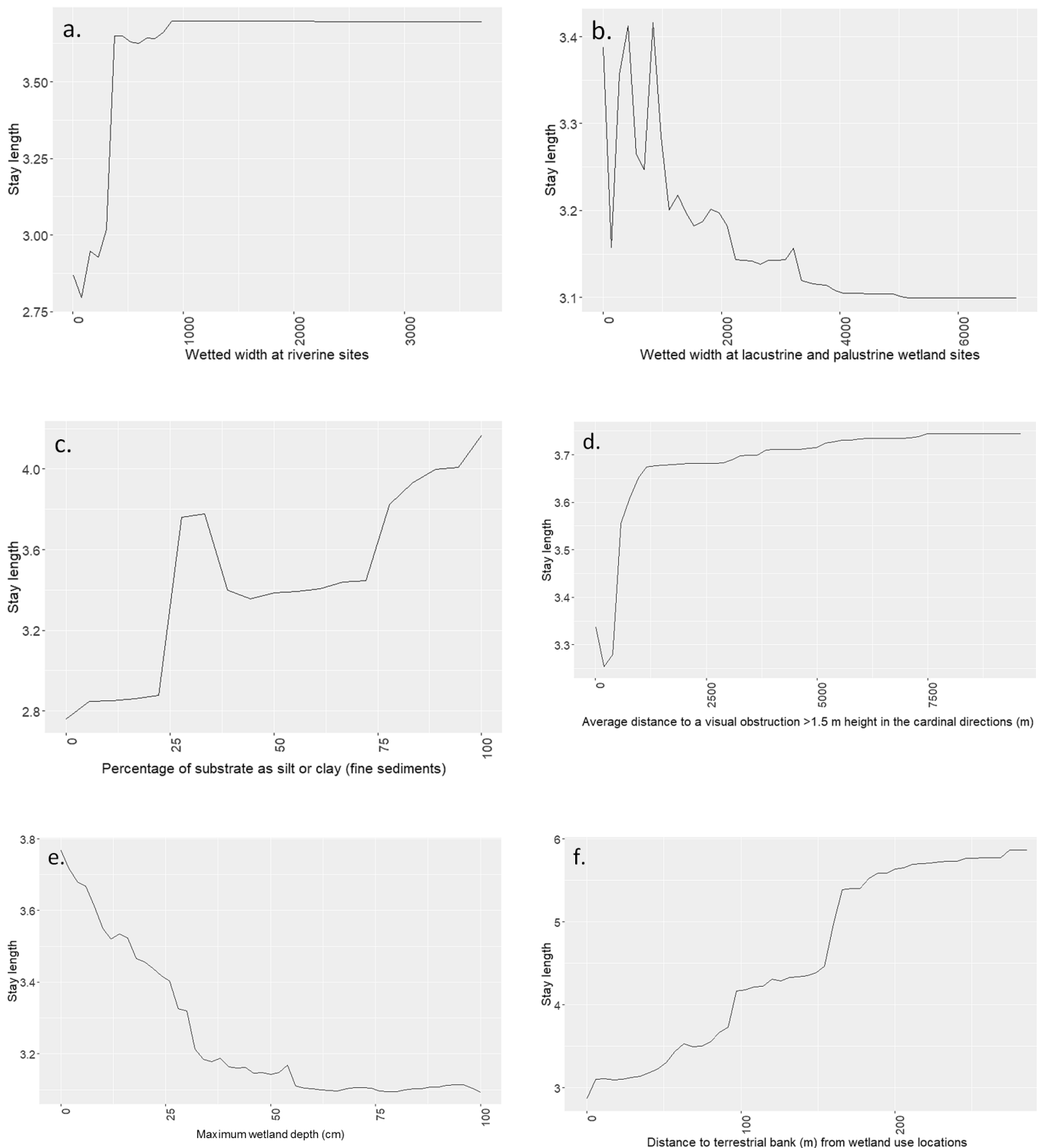


Figure 6. Partial Dependence plots describing predicted stopover stay length of whooping cranes (WHCR) (y-axis) in relation to top and selected continuous site-level predictor variables (x-axis), including (a) wetted width at riverine sites (WettedWidthCom), (b) wetted width at palustrine and lacustrine wetland sites (WettedWidthCom), (c) the percent of sediment at the use site that was silt or clay (SiltorClay), (d) average distance to a visual obstruction from the use point in the cardinal directions (ObstAveDist), (e) maximum depth of the wetland near (or at) use points (MaxDepth), (f) distance from use points to the terrestrial bank at wetland sites (DistBank), and (g) nearest endangerment (EndangDistNear). Further variable descriptions are presented in Appendix A.

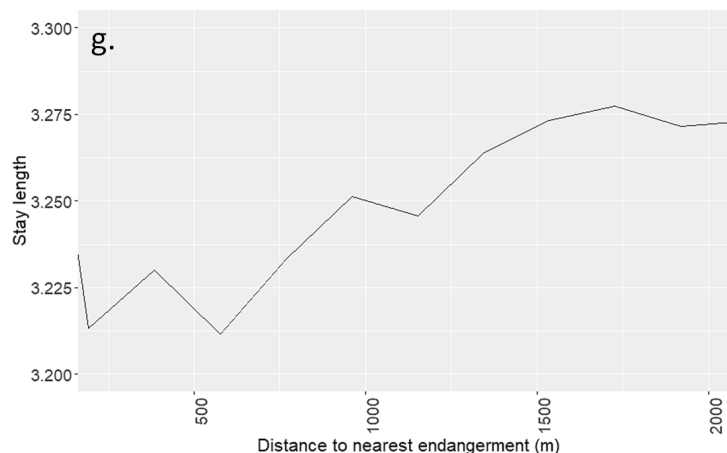


Figure 6. Continued.

site (from 3.8 to 3.1 days with an increase from 0 to 55 cm, with the starkest declines from 0 to 30 cm (Fig. 6e). Finally, distance from the wetland use point to the nearest terrestrial bank (from 2.9 to 5.8 days with an increase from 0 to 280 m; Fig. 6f) and distance to the nearest endangerment (from 3.2 to 3.3 days with an increase from 100 to 1,750 m; Fig. 6g) were positively related to stopover stay length.

Median stay lengths were longest (>4 days) at sites with open-water slough with emergent vegetation, canola, and fallow field as the terrestrial land covers of wetland banks (Fig. 7a). Additionally, sites with lowland grassland or corn as wetland bank land covers had upper interquartile range stopover durations of about 5 days and whiskers ($1.5 \times$ Interquartile Range; IQR) exceeding 10 days, indicating that extended stay lengths may be regularly observed in these contexts despite median values being comparatively shorter (Fig. 7a). Stay lengths were longest at natural permanent and natural temporary wetlands, as well as at sites where upland habitats were assessed (Fig. 7b). Random Forest models predicted that mean whooping crane stay length would be 3.5 days at natural permanent wetlands, 3.3 days at natural temporary wetlands, 3.3 days at assessed upland sites, 3.1 days at riverine sites, 2.9 days at impoundment sites, and 2.9 days at reservoirs. Stopover duration was longest at sites that had been manipulated through haying or mowing (grasslands/herbaceous wetlands), harvesting (row crop agriculture), or grazing (grasslands/herbaceous wetlands) (Fig. 7c). The median and upper interquartile range values of stay length increased with each use point assessment (Fig. 7d). First assessed roosts (R1) had a median stopover

duration of 1 day, second measured roosts (R2) were 5 days, and third measured roosts (R3) were 12 days. First measured day-use areas (DU1) had a median stopover stay length of 2 days, and second measured day-use areas were 14 days (DU2), which was expected and was the justification for including this variable in our model as a control variable (Fig. 7d). Stopover duration demonstrated less variability by season, which was our other control variable (Fig. 7e). However, it is possible that, although median stopover durations were similar across seasons, different factors were associated with extended stay lengths in each.

DISCUSSION

Characteristics measured at the landscape level explained more than 4 times more variation in stopover duration than site characteristics (Figs. 2 and 3). Our model represents an integration of spatial (i.e., land cover within 1.6-km buffer) and behavioral (e.g., feeding site) elements, which generally correspond to second- (range at stopover) and third- (use site at stopover) order habitat selection (Johnson 1980, Mayor *et al.* 2009). In some cases, selection at finer spatially or behaviorally relevant scales is constrained by choices made at broader scales, while on other occasions broad-scale habitat use patterns are simply a reflection of finer-scale preferences (Mayor *et al.* 2009). Our findings imply resources present at a relevant landscape-scale were more useful than finer-scale habitat features in predicting stay length, indicating that second-order selection may be more ecologically pertinent to whooping crane migratory behavior (Johnson 1980,

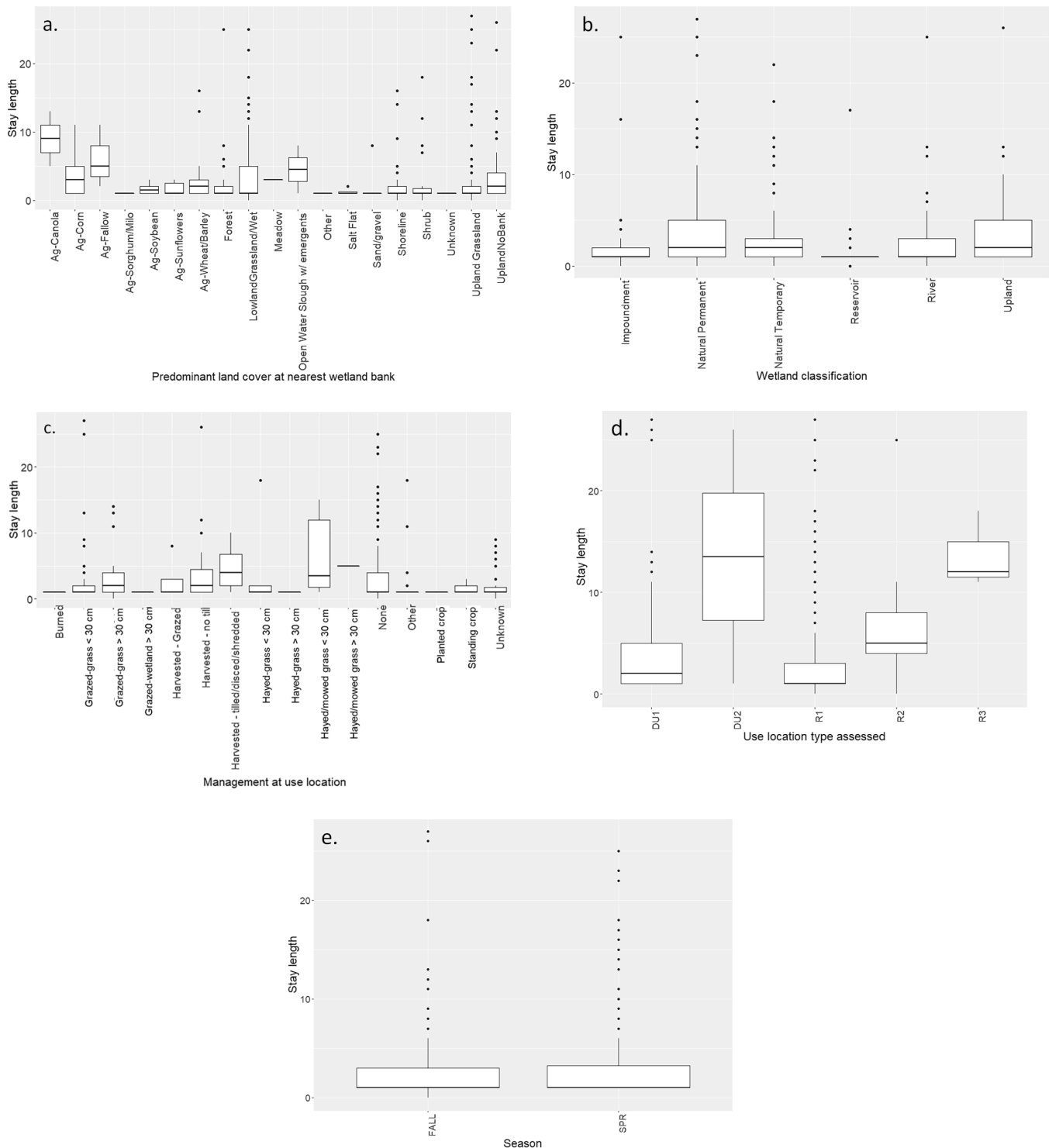


Figure 7. Box plots using data from imputed databases describing variation in stopover stay length of whooping cranes (WHCR) (y-axis) in relation to top and selected categorical site-level predictor variables including (a) land cover at the nearest terrestrial bank of a wetland (LandcovBank), (b) wetland classification (e.g., Natural Temporary) (WetlandClass), (c) active management at stopover sites (ManagementSO), (d) type of use site assessed (e.g., second day-use site = “DU2”) (Type), and (e) migration season (Season). Further variable descriptions are presented in Appendix A. The central horizontal line represents median values, the top and bottom of the box represents the interquartile ranges (25th and 75th percentiles; IQR), the extending whiskers represent 1.5x IQR, and points represent outliers.

Mayor et al. 2009, Thompson 2018). However, variation in use-site characteristics may have been constrained by lower-order habitat selection and explained stopover duration more poorly despite ultimately being relevant (Johnson 1980, Mayor et al. 2009). For instance, if most landscapes selected for use tended to have wide lateral visibility, variation in distance to the nearest visual obstruction could be preemptively constrained (i.e., it was generally wide in most cases within our data). Similarly, given that nearly 94% of use sites were within 400 m of water, the selection for wetland habitat at the landscape-level may have *de facto* limited the influence of the site-level variable “distance to nearest standing water” in determining stay length (Mayor et al. 2009, Niemuth et al. 2018, Baasch et al. 2019a). Nevertheless, proportional land covers of documented whooping crane foraging habitats were the most important habitat-related predictors of stopover duration. Relatedly, Pearse et al. (2020) found whooping cranes generally followed a defined migration corridor but demonstrated low rates of fidelity to particular stopover sites and suggested that conservation efforts may therefore be best targeted toward landscape and habitat features associated with use.

Landscape-Level Findings

Our findings indicated that land covers which best predict stopover duration corresponded directly to whooping crane habitat preferences for foraging. Our most important variable for predicting stay length was proportional land cover of open-water sloughs with emergent vegetation (Figs. 3 and 5). Whooping cranes regularly forage in this type or similar habitat when available (Kuyt 1987, 1992; Howe 1989; Lingle et al. 1991; Chavez-Ramirez 1996; Johns et al. 1997; Jorgensen and Dinan 2016; Baasch et al. 2019a). Sloughs often contain an abundance and diversity of aquatic macroinvertebrates (e.g., snails, dragonfly larvae), anurans, salamanders, small-bodied fish, snakes, and native wetland plants that whooping cranes have been recorded consuming (Howe 1989, Goldowitz and Whiles 1999, Meyer and Whiles 2008, Geluso et al. 2013, Geluso and Harner 2013, Caven et al. 2019b, Urbanek and Lewis 2020). Other land covers that exhibited a positive relationship with stay length, including alfalfa, corn, lowland prairie, and open water with emergent vegetation (palustrine wetlands *sensu lato*), are similarly well-documented as whooping crane

foraging habitats (Howe 1989; Lingle et al. 1991; Austin and Richert 2001, 2005; Nowald et al. 2018; Thompson 2018; Urbanek and Lewis 2020). Baasch et al. (2019a), found that migrating whooping cranes in the Great Plains selected for open water and semipermanent wetlands for diurnal use above all terrestrial land cover types. Our results suggest that whooping cranes are staying longer where preferred foraging habitat was relatively abundant. We also found that stay length increased with latitude throughout the U.S. Great Plains, potentially indicating that the availability of quality foraging habitat expanded moving north. This assumption is supported by a number of studies indicating wetland habitat loss in the Great Plains has been more pronounced and sustained south of the Platte River, Nebraska, than to the north (Stahlecker 1992, 1997; Dahl 2000; Cariveau et al. 2011; Tang et al. 2012; Caven et al. 2020). However, it is worth noting that wetland habitat loss has accelerated in recent years within the migratory corridor north of the Platte River as well (Johnston 2013, Wimberly et al. 2017).

Some migratory bird research has suggested that habitat characteristics are not important determinants of stopover duration and that it is predominantly a function of seasonal and immediate weather patterns as well as an individual bird's physiological condition (Seewagen and Guglielmo 2010, Liu and Swanson 2015). These are clearly important factors influencing stopover duration, including for cranes (Melvin and Temple 1982, Kuyt 1992, Littlefield 2010, Malzahn et al. 2018, Pearse et al. 2020). However, the influence of habitat quality on stopover duration likely varies as a result of an individual species' life history as well as the distribution of resources important to them throughout their migratory corridor (Russell et al. 1994, Weber et al. 1994, O'Neal et al. 2012, Vardanis et al. 2016). For instance, stopover site characteristics may be less influential for generalists that experience relatively little habitat limitation throughout their migration corridor (e.g., Liu and Swanson 2015) or for those species that do not have the physiological ability to store large amounts of fat without significant costs to flight capabilities (Witter and Cuthill 1993). By contrast, large-bodied waterbirds such as the whooping crane can carry significant fat reserves (Krapu et al. 1985, Barzen and Serie 1990, Gauthier et al. 1992, Piersma et al. 2005). This is likely an adaption to the intermittent and patchy distribution of wetland resources within their migration corridors, which fluctuates widely with

climatic variation (Skagen and Knopf 1994, Weber et al. 1994, Piersma et al. 2005, Skagen 2006). The ability to store significant amounts of fat is likely even more important for waterbirds in recent decades as wetland habitat loss has continued, particularly in the Great Plains, as a function of increasing development (Dahl 2000, Skagen 2006, Cariveau et al. 2011, Tang et al. 2012, Reese and Skagen 2017). The need to store fat reserves can be even more crucial to waterbirds that breed at higher latitudes, which often arrive on their breeding grounds before widespread food availability (Krapu et al. 1985, 2005; Gauthier et al. 1992; Piersma et al. 2005). Myers (1983) noted that long-distance migrant shorebirds depend on fat reserves to traverse lengthy stretches of inhospitable upland habitat and that the decline in wetland availability has made a handful of high-quality migratory sites bottlenecks where a number of species gather at high density. Relatedly, Caven et al. (2020) found whooping crane flocks of 10 or larger have increased as a proportion of total groups detected and that they disproportionately occurred in regions where wetland habitat availability is limited, suggesting that increased migratory flock sizes may indicate a relative scarcity of quality alternatives in the area. Our analysis suggests whooping cranes stay longer in habitats that provide quality foraging as well as roosting opportunities and it is possible this behavioral pattern could become more pronounced if palustrine wetland availability continues to decline.

Development of conservation strategies for waterbirds can benefit from an understanding of landscape structure and migratory connectivity (Haig et al. 1998). Our results support this reasoning and indicate that it is also important to understand target species' life histories as they apply to migration. The National Research Council (NRC 2004) hypothesized that whooping cranes build fat reserves during extended stopovers that allow them not only to successfully complete their biannual migrations but also to succeed across subsequent life stages (e.g., breeding, wintering). The possibility for energy supplies or deficits to persist across multiple seasons highlights the importance of protecting ecologically functional habitat throughout the whooping crane's migration corridor where they can potentially rebuild fat reserves (NRC 2004, Piersma et al. 2005, Skagen 2006, Caven et al. 2020). Though extended stay lengths represent a small minority of stopovers, they represent a significant proportion of crane use days during the migration (Johns et al. 1997;

Pearse et al. 2015, 2020). Pearse et al. (2015) found that "extended-use core intensity" sites accounted for 42% of whooping crane use days despite only making up 13% of stopovers and that these areas had a higher proportion of land under some form of conservation protection than the migration corridor at large. Relatedly, Pearse et al. (2020) found that stay length was negatively related to stopover duration at previous use sites, providing evidence that energy storage likely influences whooping crane migratory behavior. Buler and Moore (2011) suggest that stopover habitat selection is a factor of both immediate availability as well as quality following challenging portions of the migration that deplete fat reserves. Relatedly, Moore and Aborn (2000) contended that habitat selection choices are made during migration through a hierarchical decision-making process, which operates on multiple spatial scales and under temporal constraints and, as the spatial scale broadens, decisions depend less on habitat characteristics and more on additional factors (e.g., weather patterns, physical condition). Relatedly, Smolinsky et al. (2013) found that an individual songbird's physical condition influenced how it navigated an ecological barrier during migration, demonstrating how both endogenous (e.g., body condition, age) and exogenous (e.g., immediate weather, habitat availability) factors interact to influence migratory behavior. Whooping cranes' stopover decisions are likely similarly influenced by several endogenous and exogenous factors and determined through a hierarchical decision-making process (Moore and Aborn 2000, Smolinsky et al. 2013), with habitat characteristics representing a dynamic exogenous influence on migratory stopover behavior per our analyses.

Stopover duration represents a decision subordinate to the choice to stop and may be influenced by a different set of factors (Weber et al. 1994, Moore and Aborn 2000, Skagen 2006, Smolinsky et al. 2013). Whether to stop or not may be largely driven by factors such as weather, physical condition, time of day, the presence of active disturbances (e.g., traffic), and the general appearance of the site (e.g., apparently safe, suitable; Moore and Aborn 2000, Buler and Moore 2011, Smolinsky et al. 2013). However, the availability of high-quality forage resources is likely only determinable from the ground, which is why migrants likely use coarse spatial information to make initial site choices and often demonstrate exploratory movements away from these initial locations following their use (Muller et al.

1997, Moore and Aborn 2000, Sundar 2006, Buler and Moore 2011). Theoretically, there could be substantial differences between sites that are appropriate for overnight roosting and those that precipitate extended duration stopovers. Our results indicate the proportional land cover of habitats associated with whooping crane foraging were more indicative of stopover stay length than those associated with roosting. For instance, stay length was negatively related to open-water lacustrine but positively related to palustrine and corn land cover. Austin and Richert (2005) similarly found lacustrine sites comprised a higher percentage of roost (8%) and dual use (11%) sites than feeding (3%) sites. Relatedly, Howe (1989) found that palustrine wetlands were more commonly used as foraging sites while lacustrine wetlands were used more for roosting. Large lacustrine wetlands (often irrigation reservoirs in the Great Plains) may regularly provide acceptable roosting habitat but may not commonly be high value foraging sites, which may partially explain the generally shorter stay lengths.

Site-Level Findings

Site-level findings indicated that features generally associated with providing quality roosting and foraging habitat corresponded to stay length (Figs. 2 and 6). Whooping cranes select wider river channels as roosting sites (Lingle *et al.* 1986, Faanes *et al.* 1992, Farmer *et al.* 2005, Baasch *et al.* 2019b), and we found that expected stopover stay length increased by nearly 1 day as wetted width increased from 100 m to 900 m at riverine sites. Site-level findings concur with the landscape-level analysis and indicated that large lacustrine wetlands, often reservoirs in the Great Plains, were associated with reduced stay lengths. Longer stays were more frequent at natural permanent, natural temporary, and riverine use sites than at reservoirs and impoundments. Reservoirs may be less likely to provide dietary resources associated with other land cover classes linked to extended duration stopovers. Also, they are generally more likely to support recreational activities that can comprise disturbances to whooping cranes than shallow palustrine wetlands (e.g., boating; Batten 1977, Mosisch and Arthington 1998). Nonetheless, large reservoirs may provide a valuable substitute for palustrine and braided river habitats when they are unavailable and likely build resilience via increased wetland availability into the whooping crane migration corridor, particularly during drought (Chan-Woo *et al.* 2006, Ma *et al.* 2010,

Murakani *et al.* 2015). Furthermore, the value of various wetland resources to waterbirds is not static and can vary widely with management, which can be targeted to improve habitat for whooping cranes (Chan-Woo *et al.* 2006, Ma *et al.* 2010, McConnell 2018).

Our results indicated that a variety of wetland characteristics may be associated with extended duration stopovers. Stay length was greatest at wetted widths between 400 and 1,000 m in all wetland systems (riverine, palustrine, and lacustrine). Wetland habitats within this size range may be particularly likely to provide good roosting conditions (e.g., depths, unobstructed views) or dynamic foraging opportunities, as hydroperiod varies with wetland size and regulates biotic processes (Whiles and Goldowitz 2001, Greenburg *et al.* 2015, Tiner 2016). We also found that stay length increased as the distance from wetland use points to the nearest bank increased (maximized at ~280 m). This supports the assertion that wetlands of a particular size/width range (~13-79 ha; ~200-500 m radius) may be associated with extended stopovers. Austin and Richert (2005) documented frequent use of palustrine wetlands within this size range, particularly in the fall, and suggested that this was predominantly a reflection of high use of comparatively large, high-quality wetlands managed by state and federal agencies for conservation purposes, such as Quivira National Wildlife Refuge in Kansas or Funk Waterfowl Production Area in Nebraska. Our findings indicate that wetlands of a distinct depth range and substrate profile may also be associated with prolonged stopovers. We found a 0.7-day decrease in expected stay length as the maximum depth of utilized wetlands increased from about 5 to 60 cm. Research has consistently documented whooping crane use of shallow water depths (14-20 cm) for roosting and foraging (Howe *et al.* 1989, Faanes *et al.* 1992, Austin and Richert 2005, Pearse *et al.* 2017). Pearse *et al.* (2017) found that 90% of water depths at roost sites were less than 32 cm, which was similar to the 30-cm suitability threshold recommended by Armbruster (1990). Our results indicated that wetlands with wider expanses of suitable depths (maximum depth <30 cm) were associated with extended duration stopovers. Our results also predict that whooping crane stay length increases with the percent of the substrate composed of silt and/or clay. As Tiner (2016) noted, finer textured soils such as clays are more likely to support wetlands than coarsely textured soils (e.g., sands) because they are less porous and therefore can hold water under higher tension. Similarly, Austin and Richert (2005) found

that soft substrates (finer than sand) were dominant across whooping crane foraging, roosting, and dual-use sites, and were associated generally with palustrine wetlands. We also noted a spike in stay length as silt/clay ranged from 26% to 35% of sediment, which likely reflects extended stays in some riverine environments where finer substrates integrate with coarser sediments, predominantly sand (Chen 2007, Kinzel and Runge 2010).

Factors documented to describe whooping crane habitat preferences also explained duration at stopovers. Whooping cranes prefer wide viewscapes with a lack of visual obstructions >1.5 m in height (Armbruster 1990, Faanes 1992, Faanes et al. 1992, Pearse et al. 2017, Baasch et al. 2019b). Our model predicted that stay length would increase about half a day as the average distance to a visual obstruction above this height increased from around 200 m to about 5 km at use sites. However, it is notable that the majority of increase in stay length was observed as average obstruction distance increased from 200 m to 1,200 m, which may indicate a useful threshold for site management. Relatedly, the habitat management actions which increased the openness of viewscapes through some form of natural or mechanical defoliation, including the haying and grazing of grasslands or the disking and shredding of crop fields, were positively associated with extended duration stopovers. As Austin et al. (2018) noted, cranes evolved with wild ungulates throughout the grassland regions of the world and benefit not only from the structure that moderate grazing provides but also from the nutrients and macroinvertebrate communities they bring to ecosystems. However, it is important to note that very intensive grazing can have several negative impacts on cranes (Austin et al. 2018). Whooping crane stay length also increased as the distance to the nearest endangerment feature such as a power line or wind turbine increased from about 100 m to 1,750 m. Johns et al. (1992) found that use sites (\bar{x} = 687 m spring, 845 m fall) were significantly farther from power lines than random sites (\bar{x} = 319; Johns et al. 1992). Interestingly, Brown et al. (1987) demonstrated that cranes were less likely to strike power lines as their distance from them upon takeoff increased and recommended that power lines be situated >2.0 km from regular roosting and feeding sites, which is about the distance that endangerments appear to no longer influence stay length per our analysis. Though distance to nearest endangerment was positively associated with

stay length, the effect on stopover duration appeared relatively small in our data considering past research (Fig. 6). This may be a result of pooling all endangerment features for analysis (e.g., hunting blinds, wind towers). It may be beneficial to separate key endangerments (e.g., power lines) in future analyses.

Study Limitations

Our analysis involved processing a large amount of data derived from a broadly focused study to answer a relatively targeted question about the relationship between whooping crane stopover stay length and habitat characteristics. This detailed database (192 variables) was pared down, missing values were dealt with using multiple imputation, and data were analyzed using Random Forest regression, a machine learning technique. This process involved running several large models and averaging the results within various spatial scales. In short, this study could be criticized for taking a “black box” approach, for which multiple imputation and RF analyses have both been critiqued (Su et al. 2011, Molnar 2019). However, we attempted to deal with this by generally following the recommendations of Guidotti et al. (2018) to “open” the black box by describing the constructs of the model (e.g., tuning parameters), carefully interpreting the outcomes using visual plots as well as narrative descriptions, presenting a description of how we evaluated the model (particularly the multiple imputation), and providing a transparent explanation of the results.

We found indication of oversampling stay lengths >1 day for habitat assessment. For instance, using data from the same tracked individual whooping cranes, Pearse et al. (2020) found that 64% of stopovers represented a single evening, compared to 55% of those assessed here, and about 61% from the USFWS public sightings database. This bias was similarly reflected in the mean stay length (\bar{x} = 3.1 days herein, compared to \bar{x} = 2.5 in Pearse et al. 2020, and \bar{x} = 2.9 via the USFWS public sightings database). Furthermore, we evaluated day-use sites at stopover locations where total stay length was longer (Fig. 7d). Median stay length at first assessed day-use sites was 1 day longer than at first assessed roost sites; this difference was even more pronounced regarding second assessed evening roost and day-use sites (Fig. 7d). Day-use points may occur more frequently at longer duration stopover sites, but this would not likely account for the magnitude of difference

observed between median stay lengths at day-use and evening roost locations. This bias could have potentially increased the relative importance of some upland land covers and corresponding site features in explaining stopover stay length. Including site “type” (e.g., R1, DU2) within our model helped control for this bias within the data.

Another potential limit to our study is the possibility that land covers associated with stay length may have been concentrated at certain latitudes, resulting in multicollinearity between important covariates. Random Forest regression deals well with correlated covariates and overfitting compared to linear model approaches, and we feel that our analysis parsed out the influences of geospatial coordinates and land cover classes relatively well, particularly regarding the most important predictor variables (Breiman 2001, Cutler *et al.* 2007). However, considering the number of covariates, some level of overfitting is likely unavoidable despite our efforts to tune models to avoid it, and we noted some potentially spurious associations regarding less important/influential predictor variables and stay length (Segal 2004, Probst *et al.* 2019). For instance, canola is a more common crop farther north where longer stopovers occurred more frequently, and it was positively associated with stay length despite previous research indicating that it is not a preferred habitat (Johns *et al.* 1997). It is also worth noting that we received only 4-5 locations per day for each crane, and that those did not always pass accuracy assessments. Given the relatively low number of locations per day, it is likely that additional land covers were utilized without documentation at each stopover location. This may be an additional reason why landscape-level characteristics were more pertinent to stay length than site-level characteristics. Finally, our results demonstrate less certainty regarding site-level than landscape-level findings, which may be partially attributed to the amount of missing data for some variables (Li *et al.* 1991). Multiple imputation is widely seen as the least biased way in which to deal with missing data, but this process may occasionally inflate the variance of a covariate, particularly when information is missing in $\geq 30\%$ of cases (Dong and Peng 2013). A like analysis was conducting following listwise deletion of cases with missing information to provide further clarification of uncertainty (Rubin 1976, Moore *et al.* 2009). However, these results should be assessed with caution as the comparative site-level analysis ultimately relied on a relatively small (31.7%) and potentially non-random

subset of data (Rubin 1976, 1987; Moore *et al.* 2009).

MANAGEMENT IMPLICATIONS

Whooping cranes spent longer periods of time at stopover sites where land covers associated with preferred foraging habitats were present (e.g., open-water sloughs with emergent vegetation, alfalfa, corn) and where site-level characteristics reflected previously determined whooping crane habitat preferences (e.g., shallow water depths). High-quality sites with abundant resources likely make up a minority of stopovers, but account for a much higher percentage of crane-use days during migration (Pearse *et al.* 2015). If stay length reflects resources gained, then maintaining wetland habitats in preferred condition, and not just above minimum thresholds, may have the largest positive influence on whooping crane condition during migration (see Pearse *et al.* 2017, Pearse 2020). Ideal habitat to encourage long-duration stopovers would likely be comprised of natural wetland with a semi-permanent or near-permanent hydroperiod, shallow water depths (<30 cm), and moderate wetted widths (400–900 m), with management to maintain short vegetation (e.g., grazing, haying), and limited visual obstructions >1.5 m height within 1,200 m. More importantly, this wetland would exist within a landscape matrix where palustrine wetland (particularly open-water slough with emergent vegetation), agricultural land (e.g., alfalfa, wheat/barley, corn), and grassland (e.g., lowland grassland) are abundant ($>30\%$ cover each), and human disturbances and endangerments are limited. Research indicates that wetland availability is particularly limited in the southern Great Plains, and significant, targeted wetland restoration and management efforts in this region could benefit a host of migratory waterbirds in addition to the whooping crane.

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Appendix A. Description of the final dataset and variables used in our analysis examining variation in stopover duration in relation to site characteristics including variable code names as well as the mean, median, range (minimum-maximum), and quartile (1st-3rd) values for continuous variables from pooled data including all 4 imputed databases ($n = 2,420$).

Variable	Description	Mean (median)	Range (quartiles)
Site	Unique single number identification.		
LocID	Identifier specific to a roost/day use site.		
SiteID	Identifier corresponding to stopover site regardless of use point.		
Type	Specifies roost (R1, R2, R3) or day use (DU1, DU2) site.		
Lat	Latitude	41.71 (41.62)	29.33-48.98 (38.45-45.22)
Lon	Longitude	-99.27 (-98.94)	-104.78- -95.83 (-99.87- -98.35)
State	State within the United States of America.		
Marked	Number of marked birds using site.	1.29 (1.0)	1-4 (1.0-1.0)
Meas	Number of marked birds where habitat was measured.	1.14 (1.0)	1-4 (1.0-1.0)
BirdID	Unique identifier for a specific whooping crane. Variable not used for final analyses.		
FirstUse	Julian date of first use.	189.2 (117.0)	55-334 (100.0-307.0)
StayLength	Total stay length rounded to the nearest whole day (i.e. < 12 hrs. = 0).	3.1 (1.0)	0-27 (1.0-3.0)
MedianDate	Median Julian date of a crane's stopover period.	190.7 (118.0)	57-335 (101.0-307.5)
Season	Spring (SPR) or fall (FALL) migration.		
CumSOs	Cumulative number of use locations within the stopover area.	12.4 (5.0)	1-121 (3.0-13.0)
LocationClass	Classifies sites as "wetland", "nonwetland", or "river".		
LandcoverSO	Land cover at immediate stopover location.		
ManagementSO	Management in general area of stopover location.		
DistDist	Distance to nearest disturbance in meters, which is a feature that can make a crane flush (roads, railways, houses, machinery). Capped at 9,600 m as this was the maximum value at which technicians detected a disturbance, endangerment, or obstruction.	1,974 (520)	26-9,600 (246-1,000)
CtEndang	Count of endangerments, which are features that could potentially harm or kill a whooping crane (e.g., major or minor powerline, wind turbine, tower, active hunting blind), noted by stopover crews (0-4).	1.3 (1.0)	0-4 (0.0-2.0)
EndangDistNear	Distance to nearest endangerment in meters. Capped at 9,600 m as this was the maximum value at which technicians detected a disturbance, endangerment, or obstruction.	3,518 (818)	0-9,600 (400-9,600)
ObstAveDist	Average distance in meters to the nearest obstruction in cardinal directions from use point. Also capped at 9,600 m.	318.8 (141.5)	2.0-9,600 (80.3-275.3)
ObstAveHt	Average height in meters of the nearest obstructions in cardinal directions from use point.	3.54 (2.75)	0.0-25.0 (2.0-4.0)
MinObstDist	Nearest obstruction of those located in cardinal directions in meters. Also capped at 9,600 m.	168.7 (60.0)	1-9,600 33.0-106.0

Appendix A. Continued.

Variable	Description	Mean (median)	Range (quartiles)
MaxObstHt	Maximum height of an obstruction located in 1 of the cardinal directions in meters.	5.44 (4.0)	0.0-70.0 (2.0-6.0)
CtForageTypes	Count of unique forage items regardless of abundance as noted by stopover crews (0-5).	2.28 (2.0)	0.0-5.0 (1.0-3.0)
SiltorClay	Percentage of silt or clay (<0.5 mm particle size) present in soil at evaluated location.	59.7 (90.0)	0.0-100.0 (0.0-100.0)
FineSand	Percentage of fine sand (0.5-1.0 mm particle size) present in soil at evaluated location.	26.7 (0.0)	0.0-100.0 (0.0-60.0)
CoarseSand	Percentage of coarse sand (1.0-5.0 mm particle size) present in soil at evaluated location.	12.5 (0.0)	0.0-90.0 (0.0-5.0)
SmallGravel	Percentage of small gravel (5-15 mm particle size) present in soil at evaluated location.	8.4 (0.0)	0.0-40.0 (0.0-15.0)
LargeGravel	Percentage of large gravel (>15 mm particle size) present in soil at evaluated location.	5.9 (0.0)	0.0-60.0 (0.0-5.0)
OrgMatYN	Indicates if organic material was present in sediment or soil (fragments of debris and/or black color).		
WaterPres	Indicates whether water existed and categorical amount within general area surrounding the evaluated location. None = no water present; Small (S) = length of water body <50 m; Medium (M) = length of water body 50-200 m; Large (L) = length of water body >200 m.		
DistH2O	Distance (meters) from evaluated location to nearest water. If in water, distance recorded as 0. If no water present recorded as 5,400 m which is just beyond the max value (5,336 m) documented for distance to water.	258.8 (0.0)	0-5,400 (0.0-0.0)
MaxDepth	Estimated maximum depth (cm) of the entire waterbody. If >1 m, then record as 100 cm. If no water present within 800 m (DistH2O), recorded as "0". If missing data recorded as "NA".	49.6 (39.0)	0.0-100.0 (10.0-100.0)
Turbidity	Clarity of water closest to evaluated point. Categorical: Low = clear; Moderate = murky, transparency reduced; High = very murky. If no water present within 800 m listed as "No Water", missing values listed as "NA".		
DistBank	Distance (meters) to nearest shoreline or riverbank. This is the main shoreline or bank and did not include islands, sandbars. A value of "0" applied to non-wetlands, as the individual is within terrestrial habitat, in this way the variable represents distance into standing water from a terrestrial bank.	72.6 (14.0)	0.0-286.0 (0.0-150.0)
LandcovBank	Dominant land cover of nearest shoreline or riverbank to evaluated point. Coded as "UplandNoBank" for upland sites. "NA" represents missing values.		
BankSlope	Rise (cm) over a 5-m run measured in the field. Several outlying measurements of bank slope from this database exceeded those in the existing literature (Johns et al. 1997, Austin et al 2005). Following an investigation, we determined the slope equation was misapplied for 149 cases from the fall of 2014 to the fall of 2015 (3 migrations). These values were corrected. Whooping cranes used wetlands with shoreline slopes that were roughly equivalent to the topographic slopes at upland feeding sites (Johns et al. 1997). Therefore, all upland sites were assigned the median bank slope value as to have minimal influence on associative analyses and prevent imputation of non-applicable missing values (Manikandan 2011).	6.36 (2.0)	0.0-70.0 (0.8-5.8)

Appendix A. Continued.

Variable	Description	Mean (median)	Range (quartiles)
WetlandClass	Wetland classification as follows: impoundment (includes sandpit), natural temporary, natural permanent, reservoir, river, and upland. Assumed to be a wetland if distance to standing water (DistH20) is "0".		
NatOManWet	Identifies whether the wetland was natural or artificially created.		
WettedWidthCom	Distance (meters) across the contiguous water area perpendicular to wetland length or river reach. Represents data combined from "Wetted Width Channel" and "Wetted Width Wetland."	508.9 (100.0)	0-6,990 (35-311)
CenH2ODepth	Depth of water (cm) at the evaluated location. If use location is recorded as more than 15 m from water assumed to be 0.	13.7 (9.0)	0.0-100.0 (0.0-20.0)
AveVegHt5m	Average height of vegetation (cm) above water/land at the evaluated point and at 5 m in each cardinal direction from the evaluated point.	14.0 (0.0)	0.0-160.0 (0.0-10.0)
Alfalfa	Alfalfa (<i>Medicago sativa</i> , "Ag_Alfalfa" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.019 (0.000)	0.00-0.29 (0.00-0.00)
Aquiculture	Aquiculture ("Ag_Aquiculture" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	<0.001 (0.000)	0.00-0.02 (0.00-0.00)
Canola	Canola (<i>Brassica napus</i> , "Ag_Canola" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.008 (0.000)	0.00-0.33 (0.00-0.00)
Corn	Corn (<i>Zea mays</i> , "Ag_Corn" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.098 (0.033)	0.00-0.83 (0.00-0.16)
Cotton	Cotton (<i>Gossypium</i> spp., "Ag_Cotton" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	<0.001 (0.000)	0.00-0.17 (0.00-0.00)
Fallow	Fallow agricultural land ("Ag_Fallow" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.015 (0.000)	0.00-0.30 (0.00-0.00)
Sorghum	Sorghum (<i>Sorghum</i> spp., "Ag_GrainSorghum_Milo" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.012 (0.000)	0.00-0.34 (0.00-0.00)
Peas	Field/Garden Peas (<i>Pisum sativum</i> , "Ag_Peas" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	<0.001 (0.000)	0.00-0.04 (0.00-0.00)
Soybean	Soybeans (<i>Glycine max</i> , "Ag_Soybean" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.037 (0.000)	0.00-0.42 (0.00-0.06)
Sunflowers	Sunflowers (<i>Helianthus annuus</i> , "Ag_Sunflowers" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.009 (0.000)	0.00-0.43 (0.00-0.00)
Ag_Unknown	Unknown agriculture ("Ag_Unknown" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.028 (0.000)	0.00-0.55 (0.00-0.03)
WheatBarley	Wheat or Barley (<i>Triticeae</i> spp., "Ag_Wheat_Barl" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.119 (0.056)	0.00-0.83 (0.00-0.18)
Ag_Sum	Sum of all "Ag_..." land covers within buffer divided by total buffer size.	0.318 (0.333)	0.00-0.90 (0.13-0.46)
Developed	Area of human development ("DevelopedArea" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.013 (0.000)	0.00-0.35 (0.00-0.00)
FeedLot	Livestock feed lot, ("FeedLot" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.004 (0.000)	0.00-0.11 (0.00-0.00)
Forest	Forest ("Forest" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.119 (0.075)	0.00-0.63 (0.00-0.21)
LowGrass	Lowland prairie/grassland ("LowlandGrassland_Wet" ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.099 (0.041)	0.00-0.80 (0.00-0.17)

Appendix A. Continued.

Variable	Description	Mean (median)	Range (quartiles)
UpGrass	Upland prairie/grassland (“UplandGrassland” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.217 (0.192)	0.00-0.88 (0.09-0.30)
SumGrass	Sum of all “...Grassland” land covers within buffer divided by total buffer size.	0.315 (0.294)	0.00-1.00 (0.19-0.43)
WettedChannel	Wetted river channel (“WettedChannel” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.016 (0.000)	0.00-0.29 (0.00-0.00)
OWLacustrine	Open-water lacustrine wetland (“Open-water Pit/Pond/Lake w/o emergents” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.035 (0.000)	0.00-0.56 (0.00-0.02)
OWCanal	Open-water agricultural canal (“OWCanal” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.001 (0.000)	0.00-0.19 (0.00-0.00)
OWUnspec	Open water unspecified type (“OWPit_Pond_Lake_Unspecified” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.016 (0.000)	0.00-0.41 (0.00-0.00)
OWWemergents	Open water with emergent vegetation (“OWPit_Pond_LakeWemergents” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.093 (0.000)	0.00-1.00 (0.00-0.13)
OWSloughUnspec	Open-water slough unspecified vegetative cover (“OWSlough_Unspecified” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.001 (0.000)	0.00-0.09 (0.00-0.00)
OWSloughWemerg	Open-water slough with emergent vegetation (“OWSloughWemergents” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.026 (0.000)	0.00-0.67 (0.00-0.00)
OWSloughWOemerg	Open-water slough without emergent vegetation (“OWSloughWOemergents” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.008 (0.000)	0.00-0.53 (0.00-0.00)
OWSum	Sum of all “OW_...” land covers within buffer divided by total buffer size.	0.179 (0.118)	0.00-1.00 (0.06-0.25)
SaltFlat	Salt flat (“SaltFlat” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.016 (0.000)	0.00-0.67 (0.00-0.00)
SandGravel	Unvegetated sand and gravel (“Sand_Gravel” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.004 (0.000)	0.00-0.31 (0.00-0.00)
Savanna	Savanna (woodland-prairie interface) (“Savanna” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.003 (0.000)	0.00-0.38 (0.00-0.00)
Shoreline	Unvegetated shoreline (“Shoreline” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.009 (0.000)	0.00-0.40 (0.00-0.00)
Shrub	Shrubland (“Shrub” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase.	0.016 (0.000)	0.00-0.75 (0.00-0.00)
Unknown	Unknown land cover (“Unknown” ArcGIS DB), taken as a proportion of land cover within buffer from geodatabase. Variable not used for final analyses.	0.021 (0.000)	0.00-0.50 (0.00-0.02)
SlpUsePt	Integer pertaining to the down sloping angle of the terrain at the scale of a single pixel assessed via ArcGIS.	0.84 (0.00)	0.0-25.0 (0.0-1.0)

Assessing the hydroregime of an archetypal riverine wet meadow in the central Great Plains using time-lapse imagery

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Abstract. Wet meadows are a declining and increasingly degraded ecosystem type. They contribute numerous ecosystem services, including nutrient cycling, water storage, and filtration, and provision of wildlife habitat, particularly for wetland-dependent species such as the Whooping Crane (*Grus americana*). Conservation and restoration of wet meadows rely on understanding their hydrology but characterization of wet meadow hydroregimes is difficult given their hydrologic complexity, high variability, and distinct regional differences. To address this challenge, we used ground-based time-lapse imagery to assess inundation dynamics of an archetypal wet meadow over a six-year period in the Central Platte River Valley, Nebraska, USA. We analyzed over 6500 images from March 2011 to May 2017 in the open-source java-based image processing software ImageJ. We also obtained data on groundwater, streamflow, precipitation, and evapotranspiration. We assessed the relationship between wet meadow inundation and hydrologic variables using wavelet coherence to look at fluctuations across a time–frequency spectrum and used random forest to identify seasonally specific variables of importance. We found hydroperiod, the duration surface water ponded within the wet meadow, had a mean of 141 d, on average lasting from 10 December to 1 May, but varied annually. Inundation generally peaked in the early spring, on average 10 March, but demonstrated a bimodal distribution, peaking again in late spring during wetter years. While inundation responded rapidly to precipitation events, it was highly related to streamflow, while an elevated groundwater table was necessary for sustained inundation. Overall, our study provided a comprehensive hydrological characterization of a reference wet meadow and demonstrated the utility of time-lapse cameras for high-resolution monitoring and assessment of highly variable wetland systems. Considering the uncertainties surrounding land- and water-use changes, climate change, and the increasing demand for freshwater resources by growing human communities, understanding functional wet meadow hydroregimes and interrelated drivers is essential to inform wet meadow restoration, conservation, and management efforts.

Key words: hydrologic regime; hydrology; image analysis; inundation; Nebraska; Platte River; time lapse; wavelet; wet meadow; wetland.

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INTRODUCTION

Hydrologic variability is a defining characteristic of wet meadows and essential to their maintenance and function (Tiner 2016). As palustrine wetlands structured by wet-dry cycles, wet meadows have dynamic hydroregimes and support a number of rare and threatened species (Nagel and Kolstad 1987, Whiles and Goldowitz 2005, Riggins et al. 2009, Vivian et al. 2013). In the Great Plains of North America, wet meadows generally exist along a hydrological gradient between terrestrial lowland prairies and shallow marshes, which are wetlands with longer duration hydroperiods (a continuous period of inundation; Kantrud et al. 1989, Kirby et al. 2002, Tiner 2016). Sustained inundation or a lack of periodic inundation can result in the ecosystem transitioning to a different stable state (Boswell and Olyphant 2007, Zweig and Kitchens 2009).

Once relatively widespread throughout the Great Plains, wet meadows have been extensively degraded or lost due to land and water-use changes (Laubhan and Fredrickson 1997, Rolfsmeier and Steinauer 2010). In the Central Platte River Valley (CPRV) of Nebraska, estimated wet meadow losses exceed 70% over the last century as a result of reduced river flows, groundwater withdrawals, and conversion to cropland and human development (Sidle et al. 1989). The limited remaining wet meadows face several continued threats including conversion to cropland and hydrological modification as well as growing threats from tree and shrub invasion, invasive species, siltation and fertilization from adjacent cultivation, and climate change (Freeland et al. 1999, Dahl 2000, Galatowitsch et al. 2000, Gage and Cooper 2013, Wright and Wimberly 2013, Joyce et al. 2016). Restoration of wet meadows is challenging, and many restoration efforts are ultimately unsuccessful because of landscape-level alterations to the hydrogeomorphic processes that ultimately sustain them (e.g., increased groundwater depths; Boswell and Olyphant 2007, Riggins et al. 2009). Very few quality sites remain to serve as regionally specific references for restoration efforts, and even fewer have had their hydrological characteristics and dynamics thoroughly described. With continued pressure on freshwater systems globally

(Vörösmarty et al. 2010), there is a need for high-resolution monitoring techniques to assess hydrologic change, particularly in vulnerable and increasingly degraded wetland systems.

Although wet meadow characteristics vary based on geographic location throughout the world, including montane, arid, and prairie landscapes, they share similar defining characteristics (Kantrud et al. 1989, Kindscher et al. 1997, Joyce et al. 2016). Wet meadows have hydric soil features, support wetland vascular plant species, and have temporary and recurrent hydroperiods (Keddy 2010, Gage and Cooper 2013, Tiner 2016). The intermittent cycles of inundation serve as a control over chemical and biological processes and disseminate biotic and abiotic material, creating heterogeneity and influencing species richness, abundance, production, and trophic structure (Currier 1989, Moorhead et al. 1998, Whiles and Goldowitz 2001, Gray et al. 2004, Henszey et al. 2004, Keddy 2010, Greenberg et al. 2015, Tiner 2016).

Wet meadows in the CPRV receive moisture from groundwater, streamflow, precipitation, and overland flooding, and the interplay among these drivers and how they vary seasonally are poorly understood (Hurr 1983, Wesche et al. 1994). Extensive time, money, and resources have been devoted to managing and restoring the Platte River's floodplain and associated habitats, as well as to understanding its interconnected hydrology (Hurr 1983, Wesche et al. 1994, Pfeiffer 1999, Henszey et al. 2004, Meyer et al. 2010). Albeit, due to the complex set of drivers, inherent periodicity, and high variability, wet meadow hydrology in the CPRV is challenging to study, and therefore, our understanding remains limited (Wesche et al. 1994, Riggins et al. 2009).

As wetland dynamics are often temporally heterogeneous, assessing change at higher frequency time intervals is important. In-person measurements and aerial and satellite imagery can be limited by financial resources and the temporal frequency of data collection. In-person measurements are often time-consuming, especially if data collection is conducted in remote areas, and by contrast, satellite imagery is often collected at a lower temporal frequency or image resolution than needed for monitoring highly variable ecological phenomena. Ground-based

cameras can overcome some of these challenges, filling a data-acquisition gap between satellite or aerial imagery and in-person field measurements (Morissette et al. 2009, Brinley Buckley et al. 2017). Increasingly, ground-based cameras have been used to monitor a range of ecosystem and hydrologic processes and dynamics (Parajka et al. 2012, Kramer and Wohl 2014, Gleason et al. 2015, Young et al. 2015, Keys et al. 2016, Brinley Buckley et al. 2017, Leduc et al. 2018). Our primary objective was to assess the hydroregime of an archetypal wet meadow in the CPRV using ground-based digital imagery over a six-year period and to determine the primary drivers of wet meadow inundation and seasonal variation therein. We predicted inundation would exhibit a strong seasonal signal associated with Platte River streamflow. Understanding the complex variability of these systems is necessary to establish a reference baseline, guide management, direct restoration, and consider implications for at-risk and endangered species in a changing landscape.

METHODS

Study site

Mormon Island supports an archetypal wet meadow situated within the CPRV approximately 12 km southwest of Grand Island, Hall County, Nebraska, USA (Fig. 1; 40.799274, -98.416994). The 890-ha island is the largest contiguous parcel of lowland tallgrass prairie and wet meadow habitat remaining in the CPRV (Currier 1989). Historically, much of Mormon Island was too wet for agriculture and, thus, remained in a near-natural state as the surrounding landscape was converted to row-crop agriculture during the last century.

In the late 1970s, Mormon Island was protected for habitat conservation, notably for preservation of Whooping Crane (*Grus americana*) stopover habitat, as well as for the benefit of other migratory waterbirds (VanDerwalker 1982). Wet meadows in the CPRV provide critical stopover and/or breeding habitat in the Central Flyway for a diversity of migratory waterbirds and grassland birds, including the Sandhill Crane (*Antigone canadensis*), Marbled Godwit (*Limosa fedoa*), and Bobolink (*Dolichonyx oryzivorus*) (Lingle and Hay 1982, Skagen and Knopf

1993, Meine and Archibald 1996, Caven et al. 2019c). Wet meadow availability has likely limited the distribution of spring staging Sandhill Cranes in the CPRV (Faanes and LeValley 1993, Caven et al. 2019a) and is generally a preferred habitat for diurnal use by Whooping Cranes (Armbruster 1990, Baasch et al. 2019). In addition, CPRV wet meadows support a wide range of biodiversity, including anurans like the boreal chorus frogs (*Pseudacris maculata*; Geluso and Harner 2013, Brinley Buckley et al. 2021), regionally endemic macroinvertebrates such as the Platte River caddisfly (*Ironoquia plattensis*; Whiles et al. 1999, Geluso et al. 2011, Vivian et al. 2013), and historically the federally threatened western prairie fringed orchid (*Platanthera praeclara*; Currier 1982).

Mormon Island is characterized by distinctive and relatively linear landscape features that vary in elevation, often described as ridge and swale topography (Hurr 1983, O'Brien and Currier 1987, Currier 1989, 1995, Henszey et al. 2004). Hydrologically connected to groundwater and periodically retaining surface water, swales within the landscape have concomitantly been referred to as "sloughs" in the region (Whiles et al. 1999, Vivian et al. 2013). However, these depressional and linear topographical landforms do not directly relate to a particular hydrological or vegetation-based wetland classification (Kanttrud et al. 1989, Keddy 2010, Tiner 2016) and may support wet meadow, shallow marsh, or even deep marsh vegetative communities depending on their average annual hydroperiod (Kanttrud et al. 1989, Davis et al. 2006, Meyer and Whiles 2008, Tiner 2016). Therefore, when contextualizing research in the CPRV, it is important to note that the term "slough" is occasionally used to describe linear wet meadow features in the regional scientific literature, but the term also can be used to describe topographically similar wetlands with more permanent hydroperiods. Barney series soils composed of deep, poorly drained loams on highly permeable alluvial deposits of sand and gravel predominate in Mormon Island's wet meadows (USDA-NRCS 2004). Dominant graminoids in Mormon Island's wet meadows include woolly sedge (*C. pellita*), common threesquare (*Schoenoplectus pungens*), and prairie cordgrass (*Spartina pectinata*). Common forbs (dicots) include common sneezeweed

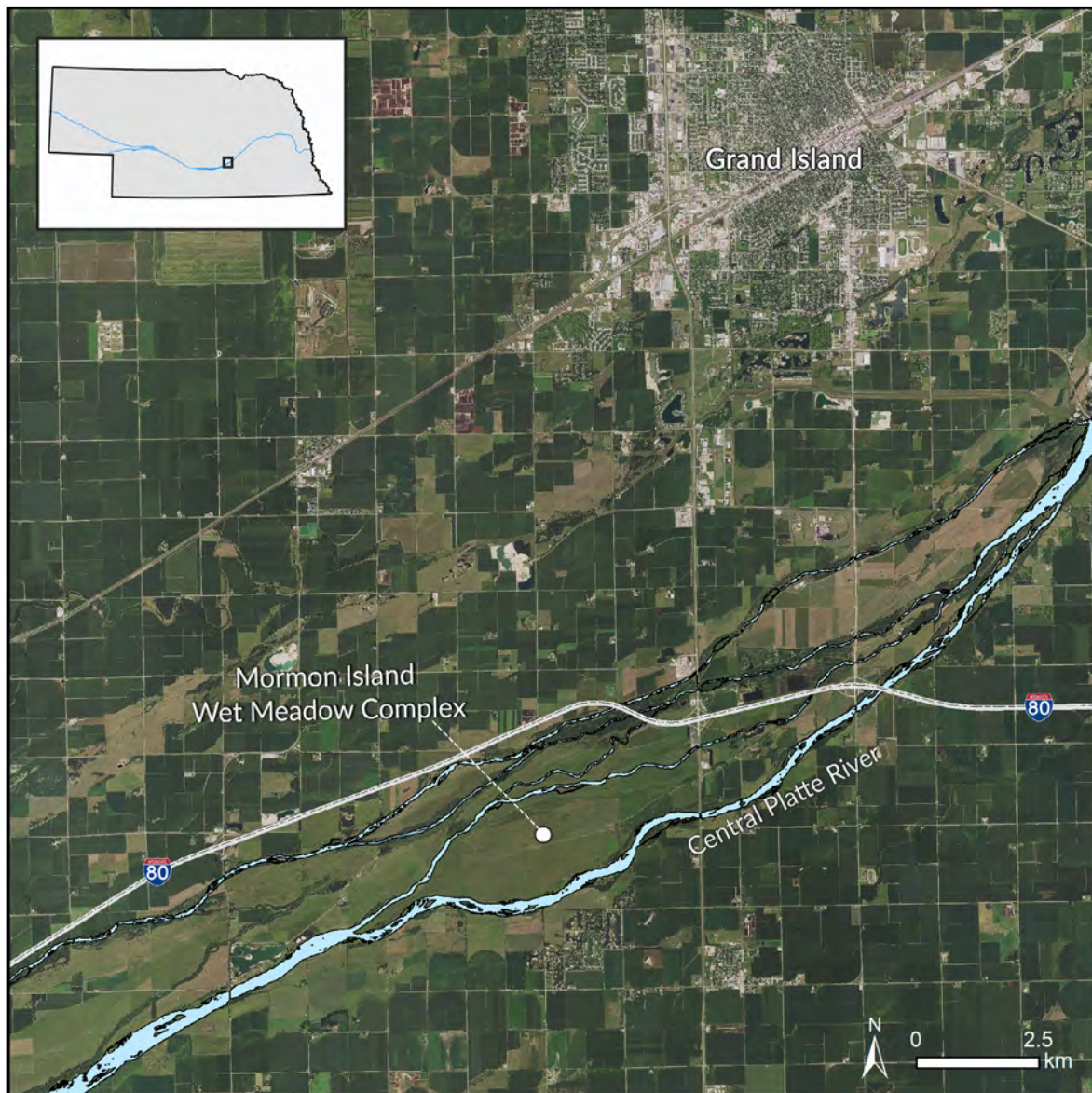


Fig. 1. Aerial view of Mormon Island wet meadow complex located along the Platte River south of Grand Island, Nebraska, USA (40.799, -98.416). Inset (top left) shows study location along the Central Platte River within the state of Nebraska. Landsat-7 image courtesy of the U.S. Geological Survey.

(*Helenium autumnale*), prairie ironweed (*Vernonia fasciculata*), and lanceleaf frog fruit (*Phyla lanceolata*) (Nagel and Kolstad 1987).

Hydrologic variables

Surface weather data were obtained from the High Plains Regional Climate Center. Daily totals of precipitation (rainfall) and snowfall were from

the Grand Island Central Nebraska Regional Airport Weather Station (40.9611, -98.3136; climo.d.unl.edu), and evapotranspiration was collected near Alda, Nebraska (station ID A253409; 40.53, -98.31). Both stations are less than 20 km from Mormon Island. We obtained daily streamflow records from the US Geological Survey National Water Information System for gage 06770500 at

Grand Island, Nebraska, approximately 17.7 km (11 mi) downstream from the camera and well location. Groundwater data were monitored approximately 608 m south from the middle channel of the river and approximately 1038 m north from the south channel of the Platte at an elevation of 576.13 m above mean sea level (m asl; 40.80191, -98.40873). The well was instrumented to measure groundwater levels to an elevation of 575.12 m asl (approximately 1 m below surface) using a Levellogger pressure transducer (Solinst LT Edge Model 3001 M10, Ontario, California, USA). Groundwater measurements were compensated for changes in atmospheric pressure using a barologger (Solinst Barologger Edge Model 3001, California, USA) installed approximately 4.5 km west of the well site.

We monitored water inundation using a digital time-lapse camera at one location within a wet meadow swale in the center of Mormon Island. The camera was located 100 m east of the groundwater well within the same swale formation. The study site was rarely connected to riverine surface water, as circuitous connections between the majority of wetland habitats on Mormon Island and the middle channel of the Platte River occur only during substantial and sustained peak flow events ($>425 \text{ m}^3/\text{s}$ or $>15,000 \text{ ft}^3/\text{s}$; June 2015) as a result of overbank flooding. The camera was installed as part of the Platte Basin Timelapse project, a multimedia endeavor cataloging a watershed (plattebasin-timelapse.com; for camera configurations, see supplemental information). The camera took one photograph every hour of daylight. The immediate frame of view was approximately $26,300 \text{ m}^2$ (2.6 ha) of wet meadow habitat, with an average elevation of 576.88 m asl, slightly above the south channel's mean bed elevation (576.77 m asl) but below the middle channel's mean bed elevation (577.63 m asl) perpendicular to our study site. The resulting image data set consisted of three photos a day, taken between the hours of 10:00 and 14:00 to standardize for shadows and sun position from 17 March 2011 to 3 May 2017. Images with inconsistencies within the frame of view (e.g., rain on the lens, cows in view) were replaced by the next sequential image to complete a set of three per day.

Images were classified using an original macro script and automated batch image analysis in the

Java-based open-access program Fiji (Schindelin et al. 2012). A region of interest (ROI) within the image was selected that was comprised of a wet meadow swale that excluded all sky, horizon, and additional landscape to reduce variability (Fig. 2). The colorspace of the ROI was then transformed from red-green-blue (RGB) to hue-saturation-value (HSV) to overcome potential limitations for classifying water (Pekel et al. 2014). Classification consisted of converting the ROI to binary (water, not water) using automated thresholding, calculated as $\text{threshold} = (\text{average background} + \text{average objects})/2$. We manually traced visible inundation for periods of dense vegetation growth that obstructed the image frame of view. Tracing was conducted through inference of visible areas and referencing of sequential images. The manually traced masks of water inundation were then measured in ImageJ. An inundation value was calculated as the percent area classified as water within the ROI. Resulting masks of inundated area were visually inspected and manually compared to the original image for accuracy. If a mask was deemed inaccurate, the original image was classified using heads-up digitizing by manually tracing water inundation. We conducted an accuracy assessment using a random number generator to draw five random numbers from 1 to 365, corresponding to days of year (30 January, 7 February, 4 March, 11 April, and 17 May) for a total of 30 images. If an image was unavailable or obstructed (i.e., snow), the closest alternative date was selected. The images were then heads-up digitized by manually tracing visible water inundation with the ROI and measured in ImageJ. Regression analysis was used to compare the results of the heads-up classification with the automated batch classification method.

Analysis

To characterize the wet meadow hydroregime, we calculated a number of metrics to describe the hydroperiod, timing, and frequency of ponding and drying. These metrics were calculated on wet meadow inundation data from 11 March 2011 to 3 May 2017. All other statistical analyses were conducted on a truncated data set, from 11 November 2011 to 3 May 2017, as the groundwater well was not instrumented until eight months after the time-lapse camera. We used a series of

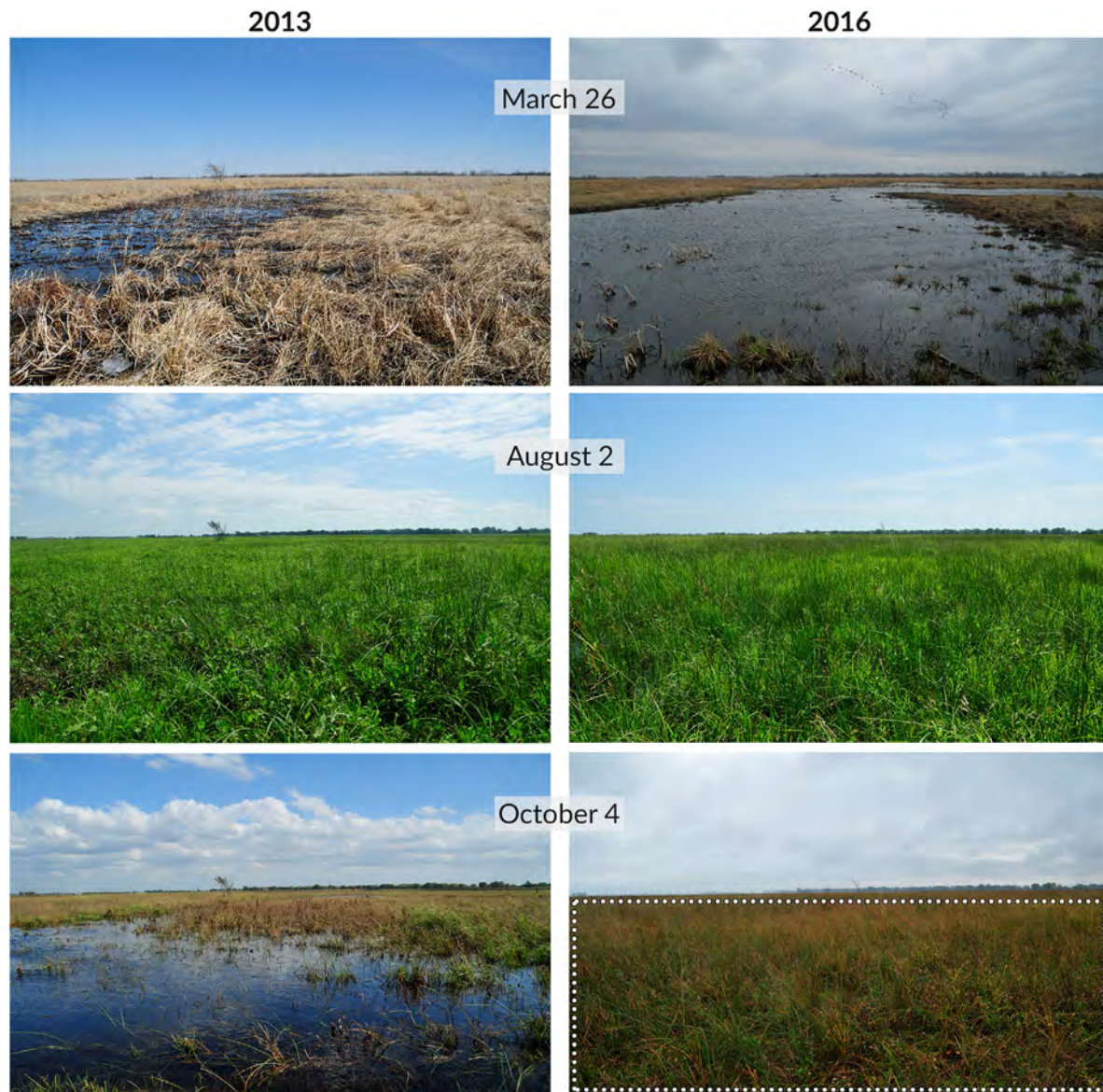


Fig. 2. Time-lapse images showing water inundation at Mormon Island wet meadow in 2013 (left) and 2016 (right) for three dates. The region of interest (ROI) used for image analysis is shown in the bottom right image. Images copyright Michael Forsberg/Platte Basin Time lapse.

statistical approaches to further characterize the wet meadow hydroregime and understand associations between inundation and hydrologic variables, including streamflow, precipitation, groundwater, snowfall, and evapotranspiration. All analyses were conducted using R 3.5.0 (R Core Team 2018), and for days with missing images, inundation data were imputed using the R package *imputeTS* (Moritz 2016).

To evaluate how hydrologic variables related to inundation, we designated thresholds of wet meadow inundation and calculated the mean of hydrologic variables at these levels. Thresholds of water inundation (WI) were calculated as quartile 1 (Q1; WI = 0%), quartile 2 (Q2; WI > 3.62%), quartile 3 (Q3; WI > 16.6%), and when inundation was greater than the 99th percentile (99th, WI > 39%). The mean value for streamflow,

groundwater, and precipitation were calculated for each of the four thresholds.

Continuous wavelet transform (CWT) was used to identify periodicities in wet meadow inundation, as well as hydrologic variables, and to visualize change over time. CWT detects signals in time-series data relating to ecological processes (Cazelles et al. 2008) and handles non-stationarity and transient properties often present in hydrologic data, while evaluating signals in both the time and frequency domains (Torrence and Compo 1998, Grinsted et al. 2004). The analysis was conducted using the Morlet wavelet in the biwavelet R package (Grinsted et al. 2004). Within the wavelet spectra, areas of statistical significance ($P < 0.05$) were delineated by a black contour outline, and wavelet power, the energy of the signal as a function of time and frequency, was indicated by color, ranging from areas of high power illustrated in red to low power in blue. Areas within the visualized spectrum less reliable to interpretation due to edge effect, an artifact of using CWT, were delineated by a white line and faded color. To assess how hydrologic variables co-varied in frequency and over time, we used wavelet coherence, a measure similar to correlation coefficients (Grinsted et al. 2004). Arrow directionality indicated the phase relationship of the two series; right-facing arrows were “in-phase”, meaning that the time-series values varied together, left-facing were “out-of-phase”, suggesting they were inversely related, down-facing arrows indicated Y lags X at 90° , and up-facing arrows indicated X lags Y at 90° .

To account for seasonal variability in hydrologic processes and interactions, as well as to understand associations of wet meadow inundation with hydrologic variables at differing times of the year, we delineated six *a priori* seasonal periods defined by climatic averages and regional irrigation schedules (see supplemental information for detailed methods). For each seasonal period (early spring, late spring, summer, early fall, late fall, winter), we calculated summary statistics and identified significant time lags and associations between inundation and hydrologic variables using cross-correlation.

To examine the importance of and predict how wet meadow inundation responded to hydrologic factors during these seasonal time periods, we used Random Forest (RF) regression, a

machine-learning algorithm based on an ensemble of decision trees. RF is increasingly used to analyze complex data sets, as it is non-parametric, includes a built-in generalization error (out-of-bag error rate; OOB), and uses two methods of randomization to increase predictive accuracy and overcome over-fitting (Breiman 2001, Cutler et al. 2012). We used the randomForestSRC package in R (Ishwaran and Kogalur 2018), generating 1000 trees, with three variables at each split, and a minimum node size of five. We included year, day of year, stream-flow, groundwater, precipitation, snowfall, and evapotranspiration in each seasonally specific model and assessed the contribution of each variable to the models using permutation-based metrics of variable importance (VIMP). VIMP scores rank covariates in terms of the mean decrease in accuracy observed when a particular variable was absent from models, where variables of top importance have higher scores and negative values decrease model accuracy. Partial dependence plots were constructed for the three hydrological variables with the highest VIMP scores using the ggRandomForests package to observe the predicted effect of a variable on water inundation given all other variables are held at their mean (Ehrlinger 2015).

RESULTS

We analyzed 6723 images from 17 March 2011 to 3 May 2017 to assess water inundation. Image analysis resulted in 91% retainment of images using batch-automated classification; 207 resulting masks were identified as inaccurate and corrected where applicable. Inaccuracy was most often due to snow accumulation in the winter or high vegetation growth in the summer, particularly in 2015 when extensive flooding occurred at near peak vegetation height. The accuracy assessment evaluating automated batch classification compared to heads-up classification resulted in an R^2 of 0.97 with a mean error of 0.55% and error range of 0 to 4.84%.

Time-lapse images recorded seasonal and cyclical hydrologic change in the wet meadow. For example, images showed limited water inundation in the wet meadow in the dry spring of 2013 (Fig. 2) and cattle wading in open water during the wet summer of 2015. Broadly,

inundation began in late fall (~November), generally exhibited an annual bimodal peak in early and then late spring, before drying in early summer (Fig. 3). The CPRV experienced periods of extreme drought as well as wetter than average periods during our study. From Summer 2012 to Summer 2013, Hall County, Nebraska experienced extreme to exceptional drought, and contrastingly, 2015 and 2016 were generally high-water years (USGS Stream gage 06770500; US Drought Monitor, <https://www.drought.gov/drought/> <accessed March 2018>). Flood events (Platte River gage height >2 m) occurred in late September of 2013, February, May, and June of 2015, and January of 2016.

Hydroregime metrics

The high temporal frequency of the time-lapse images allowed us to characterize the wet meadow hydroregime (Figs. 3a, 4, and Appendix S1: Fig. S1). Hydroperiod had a mean duration of 141 d and varied from 35 d (2013) to 224 d (2015) (Table 1). On average, the wet meadow hydroperiod began on mean day of the year 344 (10 December) and ended on mean day of year 121 (1 May) (Table 1); however, the hydroperiod began as early as 23 October (2016) and as late as 28 February (2013). For wet years (2015–2017), the hydroperiod began earlier, averaging day of the year 309 (5 November), while for dry years (2012, 2013), it began later, averaging day of year 39 (9 February). Within the hydroperiod, water inundation reached a maximum extent on mean day of the year 69 (10 March) (Table 1), with the earliest peak during the study on 24 February (2015) and the latest peak on 29 March (2017). For the duration of the study (2241 d), the wet meadow was dry 45% of the time (1012 d), while 11% of the days showed trace amounts of inundation (238 d, <5% of the ROI classified as water). This varied by year, where in 2011 the wet meadow was dry 75% of the time (217 d of 290 beginning 17 March 2011), and comparatively, it was dry 23% of the time in 2015 (Table 1; Appendix S1: Fig. S1). Groundwater elevation ranged from 575.12 to 576.13 m asl (3.3–0 ft below surface; Table 2). However, from May to December 2012, the groundwater table declined below levels measurable by the pressure transducer (575.12 m asl). Streamflow varied from a minimum of approximately 0 m³/s to a

maximum of 453.0 m³/s, daily total precipitation from 0 to 83.82 mm, and snowfall from 0 to 254 mm.

Inundation thresholds

Differing thresholds of wet meadow water levels were calculated as Q1 (WI = 0; no ponding water visible), Q2 (WI > 3.62; some water inundation present), Q3 (WI > 16.6; high-water inundation), 99th (WI > 39; extensive water inundation) (Fig. 5). For Q1, mean groundwater level was 0.60 m belowground surface (1.97 ft or 575.52 masl) and 0.12 m (0.40 ft or 576.0 masl) for the 99th percentile. Mean streamflow was 29.49 m³/s (1041.33 ft³/s) for Q1 and 211.48 m³/s (7468 ft³/s) for the 99th percentile. Mean precipitation was 1.26 mm for Q1 and 16.93 mm for the 99th percentile.

Wavelet and wavelet coherence

Wavelet transform revealed a statistically significant ($P < 0.05$) annual periodicity of water inundation ($\lambda = \sim 365$ d) from 2014 to 2017 (Fig. 6a), while no annual periodicity was evident in low-water years (2012–2013). Significant periods at $\lambda = 4$ –32 d occurred during the spring of high-water years (2015–2017), while shorter periods at $\lambda = 4$ –16 d were significant in 2013 and 2014. Groundwater exhibited significant annual periodicity from 2012 to 2013 and at shorter periodicities ($\lambda = 2$ –64 d) in the summers of 2013–2016 (Fig. 6b). Streamflow periodicity was significant at $\lambda = 4$ –64 (d) in 2013–2015 and at $\lambda = 180$ d in 2015 and 2016 (Fig. 6c). Significant annual periodicity was evident from 2012 to 2017 for precipitation, evapotranspiration, and snowfall within the wavelet spectra (Fig. 6d–f).

Wavelet coherence analysis between water inundation and hydrologic variables is depicted in Fig. 7. Coherence between water inundation and groundwater varied, but higher power levels were predominately focused in the 2-d to 30-d periodicities (Fig. 7a). Coherent oscillations of groundwater and inundation occurred at similar times of high-water events as streamflow and inundation, with slightly differing frequencies and less power, for example summer 2014 and spring 2016. A coherent annual periodicity was not observed until 2015, where the strength of the in-phase relationship between inundation and groundwater was moderate. Coherence

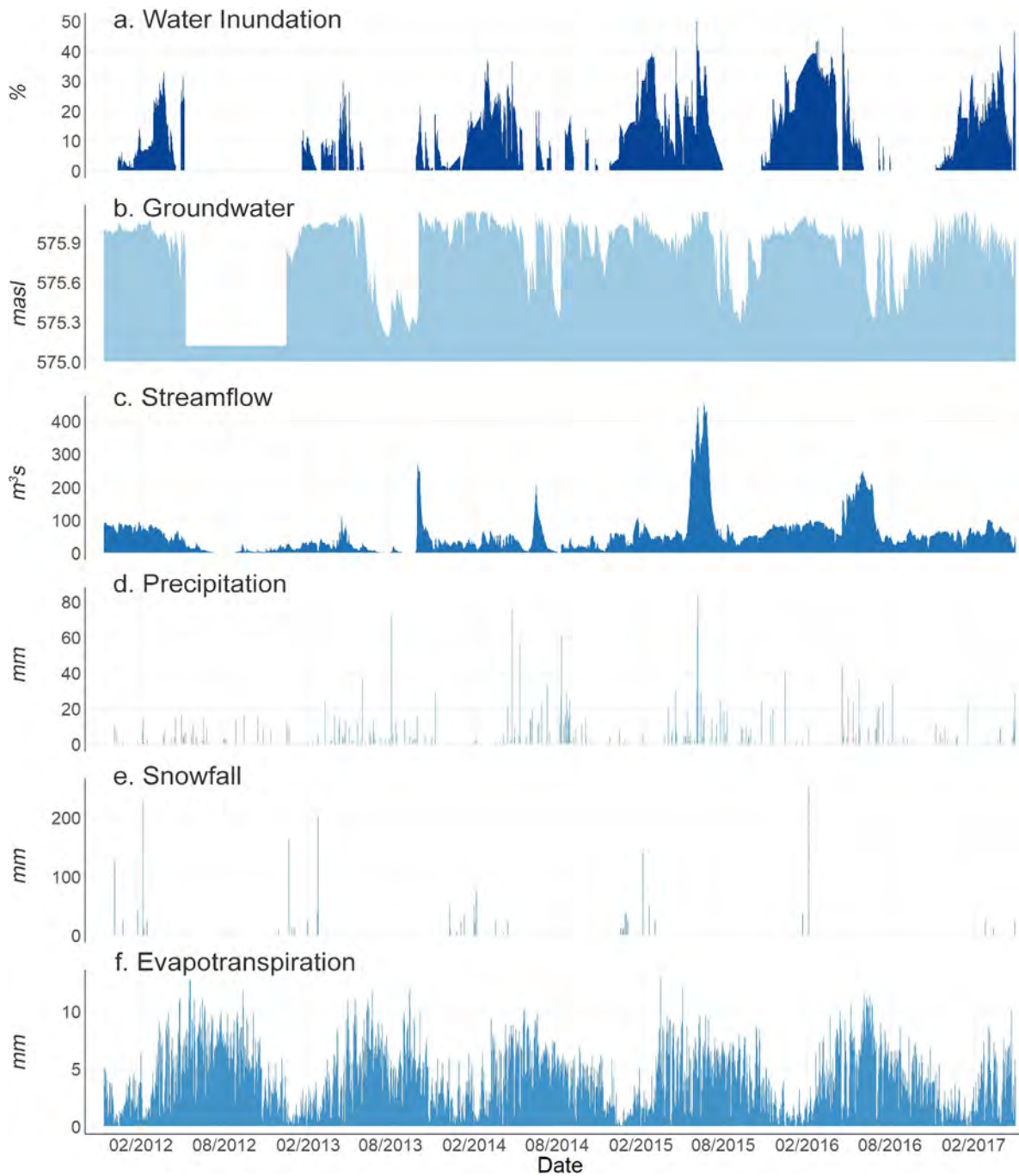


Fig. 3. Hydrologic variables at Mormon Island wet meadow from November 2011 to May 2017. Water inundation in meadow (a) was derived from classification of time-lapse imagery. Groundwater (b) was monitored from a well in the same swale feature at the time-lapse camera. Streamflow (c) was obtained from a USGS streamgage 17.7 km (11 mi) downstream. Precipitation as rainfall (d) and snowfall (e) was obtained from CLIMOD, and evapotranspiration (f) from the High Plains Regional Climate Center.

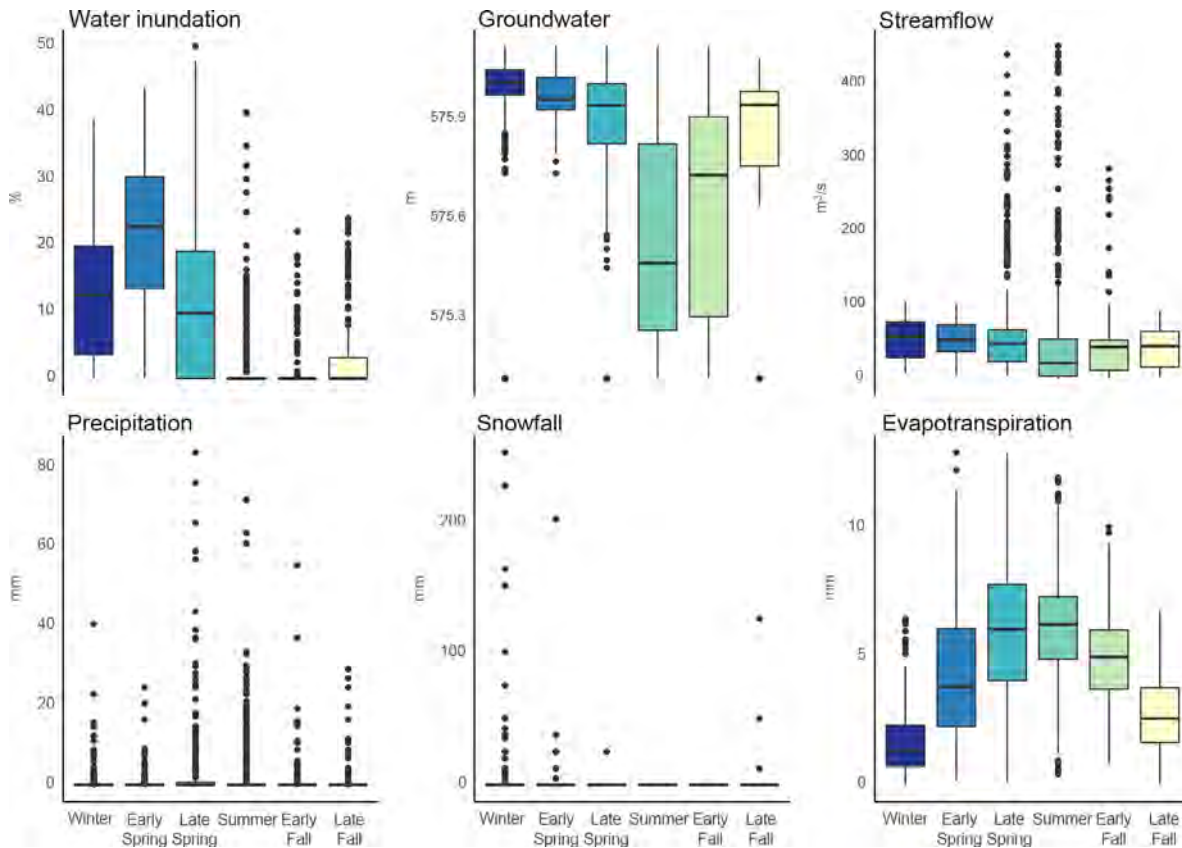


Fig. 4. Boxplot showing the seasonal distribution of water inundation, groundwater elevation, streamflow, precipitation as rainfall, snowfall, and evapotranspiration over six years (2012–2017).

between water inundation and streamflow varied in scale from 1-d to 1-year periods (Fig. 7b). In normal to wet years (2014–2017), inundation and streamflow exhibited coherence at periodicities of one year, where streamflow lagged inundation indicated by arrow directionality. In 2013, streamflow and inundation coherence for periods ranging from 16 to 64 d were in-phase for most of the low-water year. In-phase coherence was evident at 16-d periods during high streamflow events in fall of 2013, summer of 2014, summer of 2015, and spring of 2016. Coherence between water inundation and precipitation (Fig. 7c) was significant at annual periodicities, where water inundation led precipitation. In addition, high-power periods of coherence varied in scale from 1 d to 3 months, with inundation often lagging precipitation. This was evident at periods of 2–16 d from May to August, with exceptions in 2012, which had minimal water,

and 2015, which exceeded average, and was observed during this high-water time at coherent periodicities of 16–30 d. Significant coherence at annual periodicities was observed between evapotranspiration and inundation, with fluctuations in evapotranspiration lagging water inundation (Fig. 7d). Inundation and evapotranspiration were often out of phase for periodicities shorter than a year. Overall, inundation and snowfall showed low coherence power, but were significant at annual periodicities where inundation lagged snowfall (Fig. 7e).

Seasonal statistics and correlations

Seasonal variability was evident in all hydrologic variables (Table 2, Figs. 3, 4). Water inundation, on average, was highest in the early spring (mean = 22%), followed by winter (mean = 14%) and late spring (mean = 12%) (Table 2, Fig. 4). Comparatively, groundwater elevation was

Table 1. Characterization of wet meadow hydroregime from 2011 to 2017 identifying key days of the year (DOY) for hydroperiod (HP) and dry period (DP), including 1-start (first day of year of period), z-end (last day of year of period), and ext-duration (the number of days of period).

Characterization	2011	2012	2013	2014	2015	2016	2017
HP ₁ (DOY)	–	346	58	3	324	296	309
		12 December	28 February	3 January	20 November	23 October	5 November
HP _z (DOY)	–	107	93	130	183	99	115
		17 April	3 April	10 May	2 July	9 April	25 April
HP _{ext} (days)	–	126	35	127	224	165	171
HP _{max} (DOY)	–	82	72	61	55	56	90
		20 March	12 March	1 March	24 February	25 February	29 March
DP ₁ (DOY)	178	126	154	200	211	214	–
	25 June	5 May	3 June	19 July	30 July	2 August	
DP _z (DOY)	345	365	267	229	295	311	–
	11 December	31 December	24 September	17 August	22 October	7 November	
DP _{ext} (days)	167	239	113	29	84	97	–
Dry	0.75	0.69	0.46	0.36	0.23	0.43	–
Wet	0.25	0.31	0.54	0.64	0.77	0.57	–

Notes: Dry is the percentage of days in the year the wet meadow did not have visibly ponding water, while wet is the percentage of days that the wet meadow was inundated. For 2011, the time-lapse camera was not installed until 17 March, when inundation had already begun, and therefore, the hydroperiod was not calculated. Data for 2017 are until May and include the full hydroperiod for this year; however, the data set does not cover the extent of the dry period and therefore this was not included.

Table 2. Range (minimum and maximum values) and mean (with standard error of the mean) of water inundation (WI), groundwater elevation (GW), precipitation as rainfall (Precip), snowfall, streamflow, and evapotranspiration (ET) during six seasonal periods.

Seasonal period	Statistic	WI (%)	GW (m asl)	Precip (mm)	Snowfall (mm)	Streamflow (m ³ /s)	ET (mm)
Early spring (N = 269)	Range	0–44	575.74–576.13	0–24.6	0–203.2	4.0–102.2	0.2–13.0
	Mean	22 (±0.7)	575.97 (±0.00)	0.5 (±0.2)	1.3 (±0.8)	55.2 (±1.4)	4.3 (±0.2)
Late spring (N = 334)	Range	0–50	575.12–576.13	0–83.8	0–25.4	4.0–441.7	0.1–12.9
	Mean	12 (±0.6)	575.86 (±0.01)	3.6 (±0.6)	0.2 (±0.1)	74.5 (±4.4)	5.8 (±0.2)
Summer (N = 495)	Range	0–40	575.12–576.13	0–71.9	0	0.0–453.0	0.4–12.0
	Mean	3 (±0.3)	575.54 (±0.01)	2.4 (±0.3)	0	54.1 (±4.0)	6.17 (±0.1)
Early fall (N = 185)	Range	0–22	575.12–576.13	0–55.4	0	0.4–286.0	0.8–10.0
	Mean	2 (±0.3)	575.64 (±0.02)	1.4 (±0.4)	0	44.3 (±3.7)	4.9 (±0.1)
Late fall (N = 260)	Range	0–24	575.12–576.09	0–29.2	0–127.0	1.2–92.0	0.03–6.8
	Mean	3 (±0.3)	575.79 (±0.02)	0.8 (±0.2)	0.7 (±0.5)	42.7 (±1.7)	2.8 (±0.1)
Winter (N = 458)	Range	0–39	575.12–576.13	0–40.6	0–254.0	7.1–105.3	0–6.5
	Mean	14 (±0.5)	575.99 (±0.00)	0.5 (±0.1)	3.6 (±0.9)	53.4 (±1.2)	1.7 (±0.06)
Total (N = 2001)	Range	0–50	575.12–576.13	0–83.8	0–254.0	0–453.0	0–12.9
	Mean	9.2	575.80 (±0.01)	1.6 (±0.1)	1.1 (±0.3)	55.1 (±1.4)	4.3 (±0.06)

highest in winter (mean = 575.99 m asl) followed by early spring (mean = 575.97 m). Platte River streamflow was highest in late spring (mean = 74.5 m³/s) followed by early spring (mean = 55.2 m³/s). Precipitation was highest in late spring (mean = 3.6 mm) followed by summer (mean = 2.4 mm), while snowfall was highest in winter (mean = 3.6 mm) and then early spring (mean =

1.3 mm). Correlations among hydrologic variables and wet meadow inundation varied among seasonal phases. Here, we report significant relationships ($P < 0.05$), including time lags, between inundation and streamflow, groundwater, precipitation, and evapotranspiration by seasonal period (Table 3). Of note, for all seasonal periods, no significant associations were

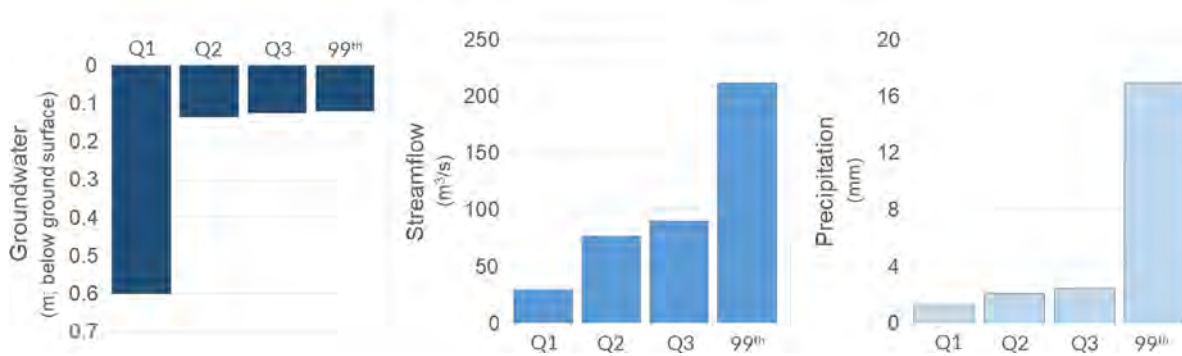


Fig. 5. Mean values of hydrologic variables (groundwater, streamflow, precipitation as rainfall) for water inundation (WI) thresholds. Q1 = quartile 1 (WI = 0), Q2 = quartile 2 (WI > 3.62), Q3 = quartile 3 (WI > 16.6), 99th = values greater than the 99th percentile (WI > 39).

found between snowfall and inundation. In early spring, water inundation was highly correlated with streamflow with a time lag of one day ($r = 0.6$), that is, one day after Platte River discharge increased the wet meadow inundation increased. During this seasonal phase, inundation was not significantly associated with any other variables (Table 3). In late spring, water inundation was moderately correlated with groundwater ($r = 0.46$), streamflow ($r = 0.33$), and precipitation ($r = 0.34$) and negatively correlated with evapotranspiration ($r = -0.39$), all with no time lag. In summer, inundation was highly correlated with streamflow ($r = 0.79$) and groundwater ($r = 0.62$), as well as to a lesser degree but significantly with precipitation ($r = 0.19$), again with no time lags (Table 3). In early fall, both streamflow ($r = 0.68$) and precipitation ($r = 0.33$) were correlated with inundation at a lag of one day, where streamflow and precipitation preceded water inundation. In addition, inundation was correlated with groundwater with a lag of four days ($r = 0.42$), where groundwater lagged water inundation. In late fall, inundation was correlated with streamflow ($r = 0.43$), groundwater ($r = 0.33$), and precipitation ($r = 0.22$) and negatively correlated with evapotranspiration ($r = -0.21$) with no time lags. During the winter, water inundation was moderately correlated with groundwater ($r = 0.34$), and streamflow lagged water inundation with a delay of one day ($r = 0.5$). Also of note, during the late fall period groundwater and streamflow showed the highest significant correlation ($r = 0.63$) (Table 3).

Random forest

RF varied seasonally in their error rate and ability to predict water inundation. A mean of 82.6% variance was explained across all models, and error rates ranged from 3.2 in late fall to 44.1 in late spring (Table 4). The high error rate for late spring is likely attributed to high variability in water inundation, as well as other hydrologic variables, during this period; water inundation, precipitation, and evapotranspiration exhibited the highest range, with the range of streamflow in late spring second highest to summer (Table 4). This was further reflected by the VIMP metrics in late spring, where six parameters were in double-digit significance (Table 4).

For all seasonal periods, streamflow was one of the top two variables of importance (Table 4). Similarly, groundwater was an important variable in all seasons except winter. Year was important for model accuracy in winter, spring, and late fall; however, it was less important in the summer and early fall, indicating water inundation exhibited less annual variability during these seasons.

Partial dependence plots from RF models showed a near-linear relationship between streamflow and water inundation in the winter, early spring, summer, and late fall, and a polynomial response in late spring and early fall (Fig. 8). The seasonal difference in late spring and early fall corresponded to the groundwater exceeding streamflow in measures of variable importance. Although evapotranspiration was not ranked in the top three important variables

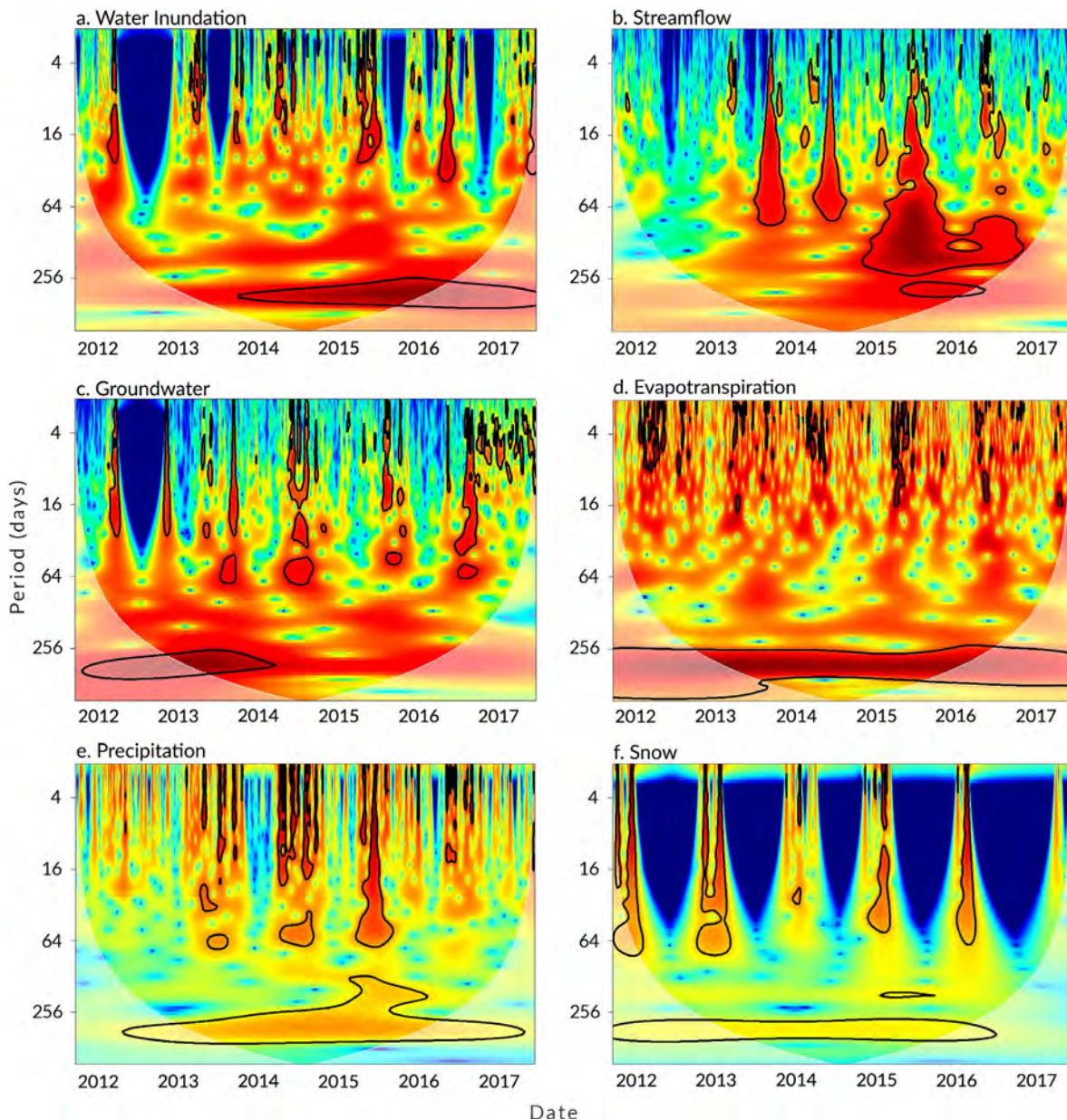


Fig. 6. Wavelet spectrum of water inundation (a), Platte River streamflow (b), groundwater (c), evapotranspiration (d), precipitation as rainfall (e), and snowfall (f) from 2012 to 2017. The black contour line indicates significant ($P < 0.05$) areas, and the gray shaded cone denotes areas influenced by edge effects. Power levels are indicated by color, with areas of high power shown in red and areas with less to no power in blue.

for any seasonal period, during the early and late spring it contributed more to the accuracy of the model, and its inverse relationship was nearly linear, with the strongest effect predicted in late spring (Fig. 8).

The RF model indicated water inundation was not predicted to respond to groundwater until levels are above 575.75 m asl (Fig. 8). This was especially evident in the winter, where groundwater remained relatively high. The influence of

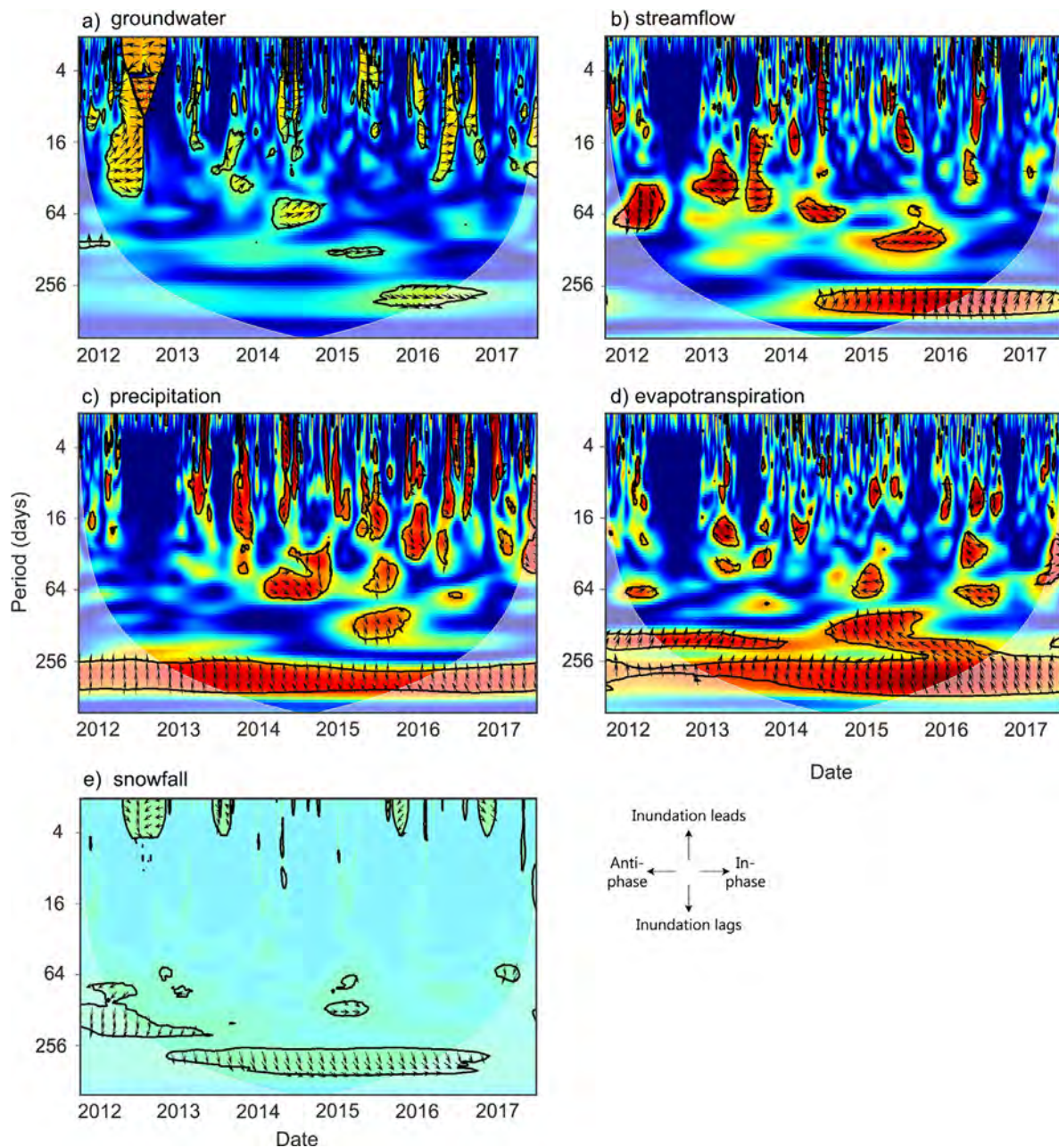


Fig. 7. Wavelet coherence between wet meadow water inundation and hydrologic variables (groundwater [a], streamflow [b], precipitation as rainfall [c], evapotranspiration [d], and snowfall [e]). The black contour line indicates areas of significant ($P < 0.05$) coherence, and the gray shaded cone denotes areas influenced by edge effects. Power levels are indicated by color, with areas of high power shown in red and areas with less to no power in blue. Arrows indicate how the wavelet spectra of water inundation and hydrologic variables relate. Right pointing arrows (in-phase) indicate they are synchronous, left arrows (out of phase) denote an inverse relationship, arrows pointing up indicate the hydrologic variable lags water inundation, and arrows pointing down denote water inundation precedes the hydrologic variable.

Table 3. Cross-correlation analysis with time lags of water inundation and hydrologic variables.

Seasonal period	WI-GW		WI-CMS		WI-PRCP		WI-ET		GW-CMS	
	<i>r</i>	<i>k</i>	<i>r</i>	<i>k</i>	<i>r</i>	<i>k</i>	<i>r</i>	<i>k</i>	<i>r</i>	<i>k</i>
Winter	0.34*	0	0.5*	−1	0.08 ^{NS}	0	−0.05 ^{NS}	0	0.30*	0
Early spring	−0.09 ^{NS}	0	0.6*	1	0.0 ^{NS}	0	−0.11 ^{NS}	0	−0.3*	−1
Late spring	0.46*	0	0.33*	0	0.34*	0	−0.39*	0	0.33*	0
Summer	0.62*	0	0.79*	0	0.19*	0	−0.07 ^{NS}	0	0.52*	0
Early fall	0.42*	−4	0.68*	1	0.33*	1	0.13 ^{NS}	0	0.56*	−4
Late fall	0.33*	0	0.43*	0	0.22*	0	−0.21*	0	0.63*	0

Notes: *r* denotes cross-correlation coefficient; *k* denotes time lag in days, where positive values indicate water inundation lagged hydrologic variables, and negative lags indicate water inundation preceded variables; * denotes significance at $P < 0.05$; NS marks not significant variables; WI, water inundation; GW, groundwater; CMS, streamflow; and PRCP, precipitation as rainfall.

Table 4. Results of random forest regression modeling water inundation over six seasonal periods showing the variable importance scores (VIMP).

Winter		Early spring		Late spring		Summer		Early fall		Late fall	
Variable	VIMP	Variable	VIMP	Variable	VIMP	Variable	VIMP	Variable	VIMP	Variable	VIMP
Year	141.0	Year	108.9	GW	44.0	CMS	35.1	GW	11.2	Year	29.4
CMS	44.4	CMS	52.1	CMS	41.9	GW	33.3	CMS	8.3	CMS	29.3
DOY	30.4	GW	37.2	Year	38.3	DOY	7.6	DOY	2.6	GW	12.0
GW	23.1	DOY	19.6	DOY	32.1	Year	6.3	Year	2.4	DOY	2.3
ET	3.1	ET	9.8	Prcp	12.8	ET	0.3	Prcp	0.0	ET	1.0
SNW	0.0	Prcp	0.4	ET	10.0	Prcp	0.0	SNW	0.0	Prcp	0.4
Prcp	0.0	SNW	0.0	SNW	0.1	SNW	0.0	ET	0.0	SNW	0.0

Notes: The included variables were year, streamflow (CMS), day of year (DOY), groundwater (GW), evapotranspiration (ET), snowfall (SNW), and precipitation as rainfall (PRCP). Explained variance and error rate, respectively, are as follows: winter, 90.6, 12.6; early spring, 86.7, 15.8; late spring, 63.6, 44.1; summer, 90.7, 5.0; early fall, 74.5, 4.5; late fall, 89.1, 3.2.

groundwater on water inundation stabilized at approximately 575.95 m asl, likely due to soils reaching full saturation. Water inundation at a level of 10% was associated with streamflow between 25 and 30 m³/s in winter, early spring, and late spring (883–1059 ft³/s; Fig. 8). However, 10% water inundation was associated with much higher streamflow in the summer (~220 m³/s or 7769 ft³/s), as well as in the early and late fall periods (both ~110 m³/s and 3885 ft³/s; Fig. 8).

Observations of streamflow–groundwater–inundation relationships

Interactions among wet meadow inundation, groundwater, and streamflow are highlighted in the following five events that occurred during our study. In 2013, streamflow increased from 14.52 m³/s (513 ft³/s) on 15 January to 31.71 m³/s (1120 ft³/s) on 20 January, which raised groundwater by 0.09 m (0.29 ft) and increased water inundation from zero to 14% within three days.

On 25 September 2013, four days of high flows peaking at 262.16 m³/s (9258 ft³/s) raised the groundwater table 0.69 m (2.25 ft) with a six-day lag and increased water inundation by 17% following a five to ten-day lag. In 2014, on 15 February, streamflow increased from 25.03 m³/s (884 ft³/s) to 64.56 m³/s (2279 ft³/s), which increased inundation in the wet meadow by 20% within two days. Groundwater was and remained fully saturated for approximately seven days subsequent to increased streamflow. On 13 January 2015, streamflow increased from 24.95 m³/s (881 ft³/s) to 105.34 m³/s (3720 ft³/s), increasing groundwater by 0.25 m (0.82 ft). Water inundation increased from 15% on 19 January to 34% on 24 January, responding to streamflow at a lag of six days. Finally, following 4.37 cm (1.72 in) of precipitation on 17 April 2016, we observed a 107.6 m³/s (3800 ft³/s) increase in streamflow, a 0.33 m (1.08 ft) rise in groundwater, and 47% increase in water inundation within one day.

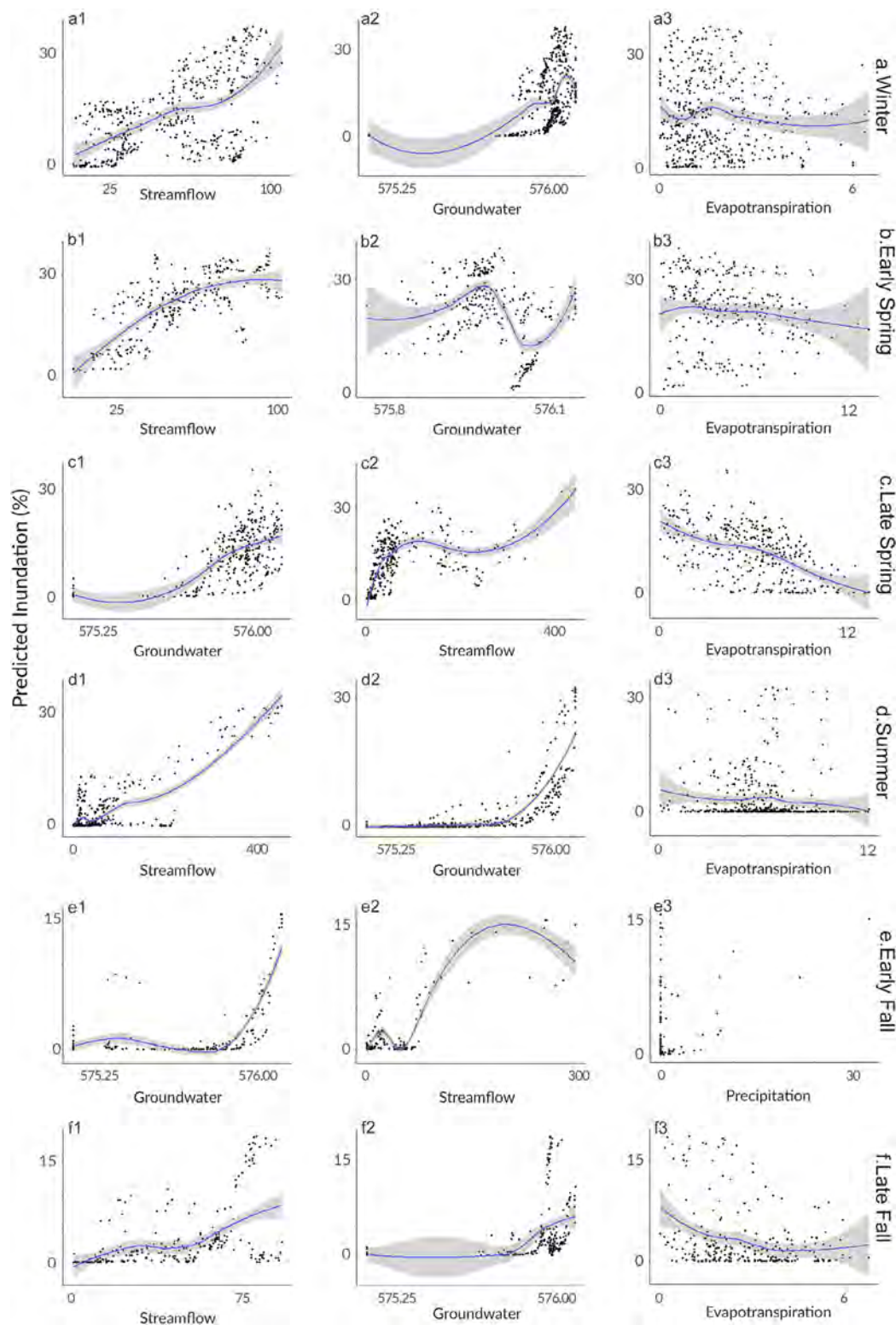


Fig. 8. Partial dependence plots from random forest models illustrating the predicted effect of hydrologic

(Fig. 8. *Continued*)

variables on wet meadow water inundation given all other variables are held at their mean. The plots shown are the three hydrologic variables with the highest variable of importance (VIMP) score for six seasonal periods (winter [a1–3], early spring [b1–3], late spring [c1–3], summer [d1–3], early fall [e1–3], and late fall [f1–3]).

These examples illustrate the dynamic response of wet meadow inundation to interconnected changes in streamflow, precipitation, and groundwater levels at varying times of the year.

DISCUSSION

Hydrologic variability of wetlands facilitates the interaction between aquatic and terrestrial systems, driving ecosystem processes and ecological functions as well as influencing biodiversity (Mitsch and Gosselink 2000). Analysis of time-lapse imagery allowed us to monitor and characterize the hydroregime of an archetypal wet meadow site, a vanishing and increasingly altered habitat type in the CPRV. Our findings revealed high temporal variability and a hydrologically connected riparian ecosystem.

Sustained wet meadow inundation typically began in November, likely as a result of increasing streamflow, rising groundwater levels, stochastic snowfall, and/or less permeable frozen soils typical of that time of year (Fig. 3). However, sustained ponding was delayed by approximately six weeks in dry years (2012 and 2013) as a result of limited increases in these hydrologic drivers. Inundation peaked in early March and again in May, likely in response to precipitation events and a fully saturated water table (Fig. 3). In June, inundation began to rapidly decline with minimal inundation through October; however, stochastic inundation events were present during the summer in response to precipitation. These findings parallel seasonal groundwater patterns observed by Wesche et al. (1994). We found groundwater began to rise generally in late September, earlier than identified by Wesche et al. (1994), and preceded the start of inundation (Fig. 3, 4). Past research indicated that median groundwater levels at Mormon Island ranged from 0.06 to 0.98 m (0.2 to 3.2 ft) belowground from February to April and 0.55 to 1.29 m (1.8 to 4.2 ft) belowground from June to September from 1989 to 1992 (Henszey and Wesche 1993, Wesche et al. 1994, Henszey et al. 2004). Our

findings were within the shallower end of this range, with median groundwater elevation at 0.15 m (0.48 ft) below surface for February to April and at 0.63 m (2.08 ft) below surface from June to September. However, it was notable that average Platte discharge was 25.3 m³/s from 1990 to 1992 during studies by Henszey and Wesche (1993) and Wesche et al. (1994). By contrast, we observed a mean streamflow of 55.1 m³/s during our study, similar to Chen (2007) who noted average streamflow at 54.3 m³/s from 1983 to 2003. Although influenced by differences in study time periods, our observations aligned with the findings of Chen (2007) and Henszey and Wesche (1993), indicative of the high connectivity among streamflow, groundwater, and overall hydrologic dynamics, albeit, with limitations in inference given the study was restricted to one site.

Hydrologic signals and correlations at various scales and frequencies indicated inundation was associated with streamflow, and to a lesser extent groundwater, suggesting these may be dominant hydrologic drivers of inundation. In addition, we observed a rapid response of inundation to precipitation events, primarily in the summer. During the study, inundation exhibited greater association with streamflow than groundwater (Fig. 7), with streamflow correlated with inundation at a greater range of frequencies, as well as a consistent annual periodicity starting in 2014 (Fig. 7). Inundation and groundwater exhibited an association during times of hydrologic decline or variability at shorter frequencies (1–16 d; Fig. 7), as well as an association in late spring and summer. This may reflect the lower probability and decreased permanence of inundation in conditions when groundwater is low.

Wet meadow inundation responded to hydrologic drivers with distinctive seasonal regimes. Groundwater was a more important variable in early fall, streamflow in early spring and summer, and both were important drivers in late spring. Evapotranspiration was not an important predictor of wet meadow inundation until late

spring (Fig. 8), which was a similar finding to Henszey and Wesche (1993). The late spring random forest model accounted for the lowest explained variance and highest error rate of all seasonal models, indicating other factors may be influencing inundation during this time period. The significant variations in ambient temperature common to this period could have an impact on biological processes, such as plant growth (Beeson 2006, Hatfield and Prueger 2015), in turn influencing inundation levels (Sánchez-Carrillo et al. 2004). This period likely demonstrates the most complex ecohydrological drivers of inundation, as many environmental attributes, including temperature, plant growth, streamflow, and groundwater, are in flux during this time. During drier late springs, summers, and occasionally early falls, the wet meadow experienced periods of episaturation, as large rain events created temporary spikes in inundation before percolating downward into unsaturated soils (Fig. 7, Tables 3 and 4). For instance, episaturation events that contribute to shallow groundwater replenishment occurred with regularity in the early fall when significant lag times (4 d) were observed between water inundation and subsequent increases in groundwater elevation as groundwater levels were typically low at this time of year as a result of high rates of evapotranspiration and ground water pumping (Table 3, Kranz et al. 2008). Wesche et al. (1994) found that thunderstorms in the summer resulted in peaks in daily groundwater levels, and if no additional precipitation events occurred, the groundwater table returned to previous levels within two weeks. We found water was retained on the landscape an average of nine days after a single precipitation event, but varied seasonally and in relation to groundwater levels. Stochastic precipitation events were coherent with groundwater with high power across 1- to 16-d periods in the summer of 2013, 2014, and 2016 (Fig. 7), but coherence was not observed in years with minimal precipitation (2012; Fig. 3) or summers with high-water levels (2015; Fig. 7). Sustained inundation was likely driven by endosaturation resulting from a complex relationship between streamflow and groundwater throughout the year and was highlighted by the large flows associated with 10% inundation from summer through late fall (Fig. 8).

In addition to seasonally disparate associations, our findings suggest that differing hydrologic drivers may govern the amount as well as duration of water inundation. A lack of inundation within the wet meadow is likely a response to a low groundwater table (Fig. 5). Contrastingly, high-water inundation may be attributed to high streamflow in addition to large precipitation events (Fig. 5). Mean groundwater level varied less than 0.01 m (0.6 in) between Q2, Q3, and 99%. In comparison, the difference in mean streamflow for Q1 and Q2 was 46.9 m³/s (1656 ft³/s) and for Q2 and 99th was 182 m³/s (6426 ft³/s), demonstrating the importance of high streamflow events that initiate wet meadow inundation. However, groundwater levels above a certain threshold, an estimated 575.75 m asl (~0.48 m belowground surface) in our exemplar system, set the stage for sustained periods of inundation. In this way, groundwater level likely has a significant influence on the temporal duration of inundation but plays a smaller role in moderating the extent of wet meadow inundation.

During the study period, increases in streamflow preceded both water inundation increases as well as groundwater level increases, with the exception of inundation in winter (Table 3). This aligned with the findings of the Platte River Environmental Impact Statement Team Technical Report (Bureau of Reclamation 2001), which found that groundwater rises lag behind river rises unless there is impact from an additional factor such as precipitation. The report suggests 170–283 m³/s (6000–10,000 ft³/s) sustained over three days would raise groundwater elevation by approximately 3.81 cm (1.5 in) within 152.4 m (500 ft) from the river. Our results reinforce this finding from a distance of approximately 800 m (2625 ft) from the nearest river channel, discerning a delayed response of inundation and groundwater to changes in streamflow, on average approximately five days for inundation to respond, and a rapid response to precipitation, usually within the day. Furthermore, it may suggest that lag time through the hydrogeological system increases as connectivity via saturated soils decreases. However, the sustained impact would likely differ seasonally and be an aggregated result of groundwater elevation, streamflow amount and duration, and precipitation.

Hydroperiod is a defining characteristic of wetlands, contributing to our understanding and classification of wetland type (Kantrud et al. 1989, Tiner 2016). We found the wet meadow site generally had a shorter hydroperiod (Table 1) than the slough wetland hydroperiods (5–12 months) reported by Whiles and Goldowitz (2005), but demonstrated a similar range (6 months) reported by Meyer and Whiles (2008). We found that water was present in the archetypal wet meadow a mean of 51% of the time and ranged from 25% to 77%, indicative of wetland hydrology bordering between ephemeral and intermittent (Whiles and Goldowitz 2001), and findings suggest that the biological productivity of our study site may vary greatly between dry and wet years. As wet meadows are generally seasonally inundated with more ephemeral hydrology, our results indicate our site may have been on the wetter end of the wet meadow classification continuum (Currier 1989, Kantrud et al. 1989, Euliss et al. 2004, Henszey et al. 2004, Tiner 2016).

The drivers of wet meadow inundation range from relatively singular to highly complex. For instance, wet meadows often exist within an ephemeral zone surrounding a more permanent wetland such as in the Prairie Pothole region of South Dakota, USA (Kantrud et al. 1989). Similarly, wet meadows exist topographically above and generally inland of shallow marshes surrounding the outer edges of the Great Lakes, as they are periodically but less frequently inundated by water level fluctuations (Wilcox et al. 2018). By contrast, wet meadows can represent significant expanses of herbaceous wetland similar to grasslands that are supported by shallow springs linked to perched aquifers in lower elevation arid regions (Lord et al. 2011, Cooper et al. 2012, Caven 2014) and spring glacial melt in high mountain landscapes (Rocchio 2006, Tiner 2016). Inundation at our wet meadow study site resulted from a relatively diverse set of drivers, and the seasonally variable linkages between river discharge, groundwater, and precipitation, and the associated time lags, suggest the ecosystem is relatively distinct and reasonably complex. Despite geographic variation in the drivers of wet meadow inundation, there is considerable overlap regarding functional characteristics reflected by our study site. For

instance, many wet meadows in the United States are similarly dominated by *Carex* spp. and sustained by relatively shallow groundwater (generally < 1.0 m depth; Sanderson and Cooper 2008, Lord et al. 2011). Additionally, inundation tends to occur temporarily and seasonally but persist long enough (>2 weeks) for the development of hydric soil features (Rocchio 2006, Schook et al. 2019). As in the CPRV, the regulation of rivers and lakes has resulted in the stabilization and reduction of water levels, promoting the decline of wet meadows globally (Tiner 2016, Wilcox et al. 2018). It is important that water resources are managed to maintain hydrologic variation at a landscape scale to maintain the current extent of wet meadow, a limited yet important habitat for several plant and wildlife species (Jiang et al. 2018, Wilcox et al. 2018, Yang et al. 2020).

Wet meadows have been reduced in the CPRV to 5% of their historic area (Currier et al. 1985, Sidle et al. 1989). A myriad of hydrologic, climatic, and anthropic changes (Johnson et al. 2012, Fassnacht et al. 2018, Pauley et al. 2018, Caven et al. 2019b) have resulted in encroachment of woody vegetation and channel incisions that threaten to lower the shallow groundwater table (Williams 1978, Currier 1982, Eschner et al. 1983, Randle and Samad 2003). In turn, this has resulted in the drying of some wet meadow systems, causing a change in stable state to lowland prairie ecosystems, thus rendering the previous wet meadows drier and more viable for agricultural row-crop conversion (Sidle and Faanes 1997). This necessitates the need for baseline data as well as understanding connected hydrologic drivers of remaining wet meadow systems to gauge shifts in conditions, monitor impacts, and restore wet meadow habitat. Our study laid a foundation to apply image-analysis techniques for high-resolution monitoring in addition to providing detailed reference data on a representative wet meadow site. Moreover, the use of time-lapse imagery offered tangible and visual evidence of change that can dually provide a powerful approach for communication and education (see Video S1: time lapse and data graphic of wet meadow inundation). Our results, in tandem with prior research (Henszey and Wesche 1993, Chen 2007), show an interconnected relationship between streamflow, groundwater, and

wet meadow inundation. However, as our study was conducted at one location, we recognize inference is limited, and further investigation, including spatial replicates, would be ideal.

CONCLUSIONS

Characterization of the hydroregime of an archetypal wet meadow site in the CPRV of Nebraska through analysis of time-lapse imagery revealed high temporal variability, seasonal patterns, and dynamism of a hydrologically connected system. The hydroperiod of the Mormon Island wet meadow complex averaged 141 d and spanned from 10 December to 1 May, on average. Inundation peaked in early spring (mean 10 March), but demonstrated a bimodal distribution, particularly in wet years, peaking again at variable dates in late spring (~early May). Inundation was strongly related to streamflow throughout all seasons. However, the temporal duration of inundation was influenced significantly by groundwater levels. Our models suggested that water inundation did not respond to groundwater below a threshold of 575.75 m asl, and the influence of groundwater elevation on water inundation stabilized at approximately 575.95 m asl, likely due to soils reaching full saturation. Maintaining wet meadow inundation levels is necessary to promote wetland function and support numerous species, with early spring and late spring of notable ecological importance in the CPRV. Our models predicted 17% inundation, the current seasonal mean and approximate third quartile metric, at Platte River streamflow above 35 m³/s (1240 ft³/s) in early spring and 70 m³/s (~2470 ft³/s) in late spring, with groundwater levels at seasonal means of 575.97 m asl and 575.86 m asl, respectively. However, Mormon Island is one of the wettest sites in the CPRV and higher flows are likely necessary to promote the same level of inundation at other wet meadows in the CPRV (Wesche et al. 1994). Hydrologic variables demonstrated dynamic temporal relationships at a range of frequencies. Understanding the hydrologic character, variation, and drivers of wet meadow hydroregime is integral to establishing sound water conservation measures that will protect the ecological structure and function of wet meadow systems.

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