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WHOOING 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

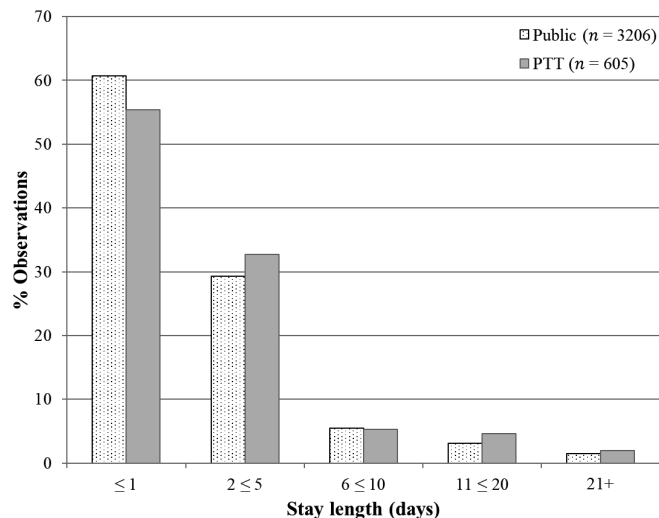


Figure 1. Stopover stay lengths from the USFWS public sightings database (Public; 1942-2018) and field crew assessed stopovers of whooping cranes from the Aransas-Wood Buffalo population tracked by platform transmitting terminals (PTT; 2012-2015).

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

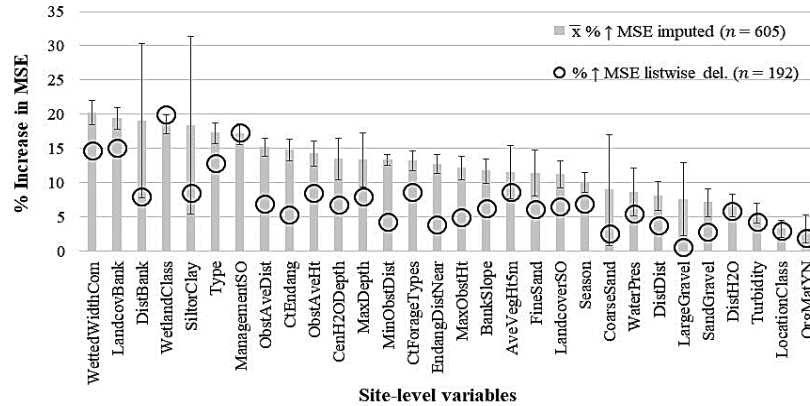


Figure 2. Importance estimates for site-level variables predicting whooping crane stopover duration measured as the increase in the mean squared error (MSE) when a variable is removed from the model with results averaged across 4 analyses using separate databases with imputed values (\bar{x} % ↑ MSE 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.

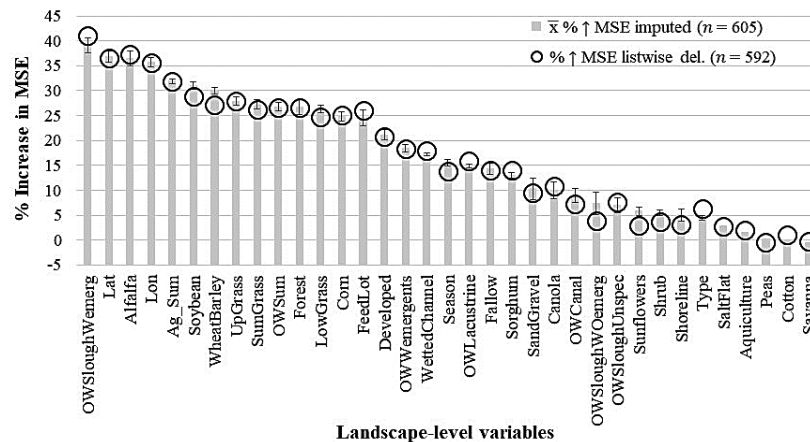


Figure 3. Importance estimates for landscape-level variables predicting whooping crane stopover duration measured as the increase in the mean squared error (MSE) when a variable is removed from the model with results averaged across 4 analyses using separate databases with imputed values (\bar{x} % ↑ 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

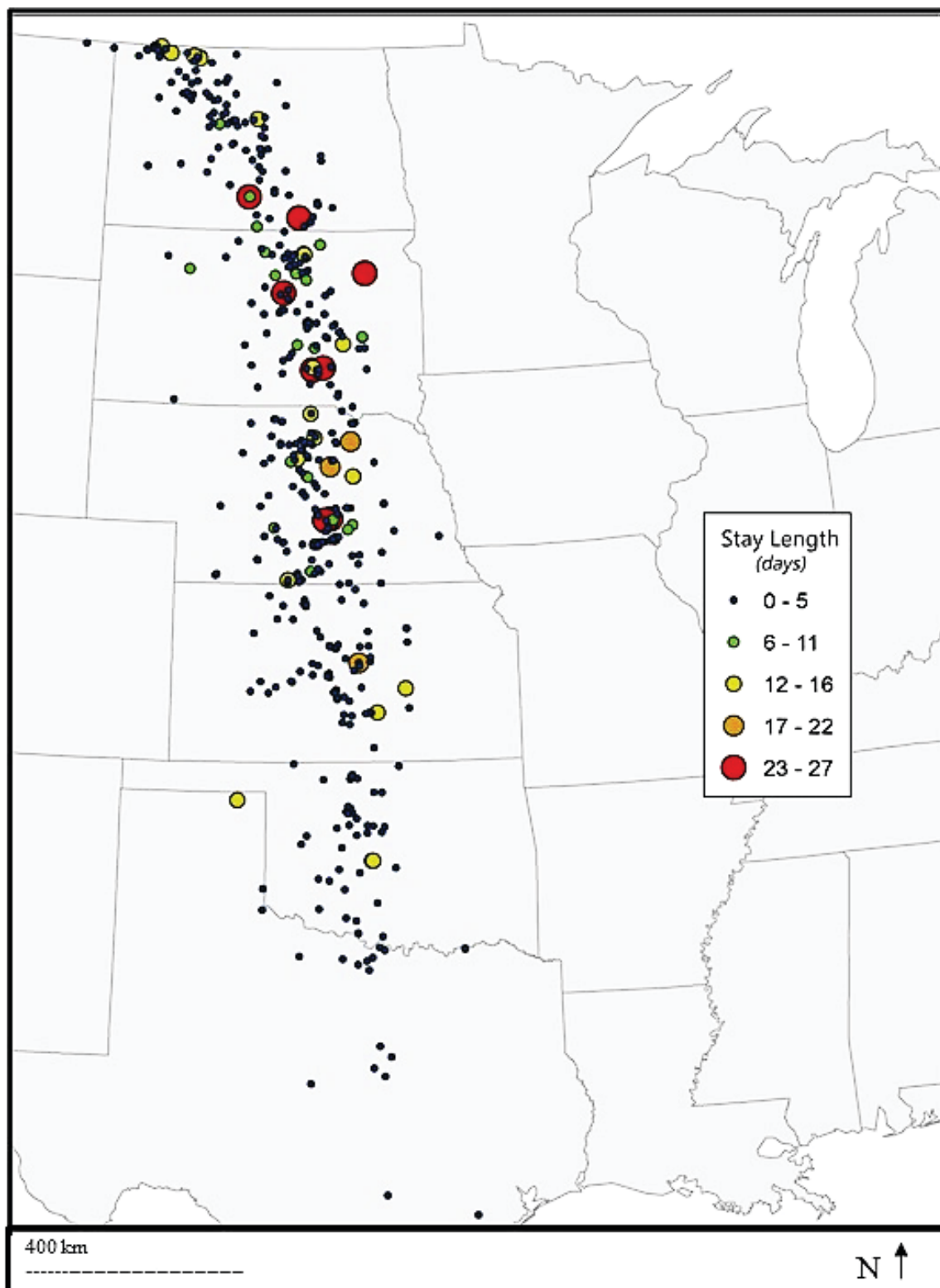


Figure 4. The distribution and associated stay lengths of PTT-tracked whooping cranes at stopover sites assessed by field crews from 2012 to 2015 throughout the Great Plains of the United States.

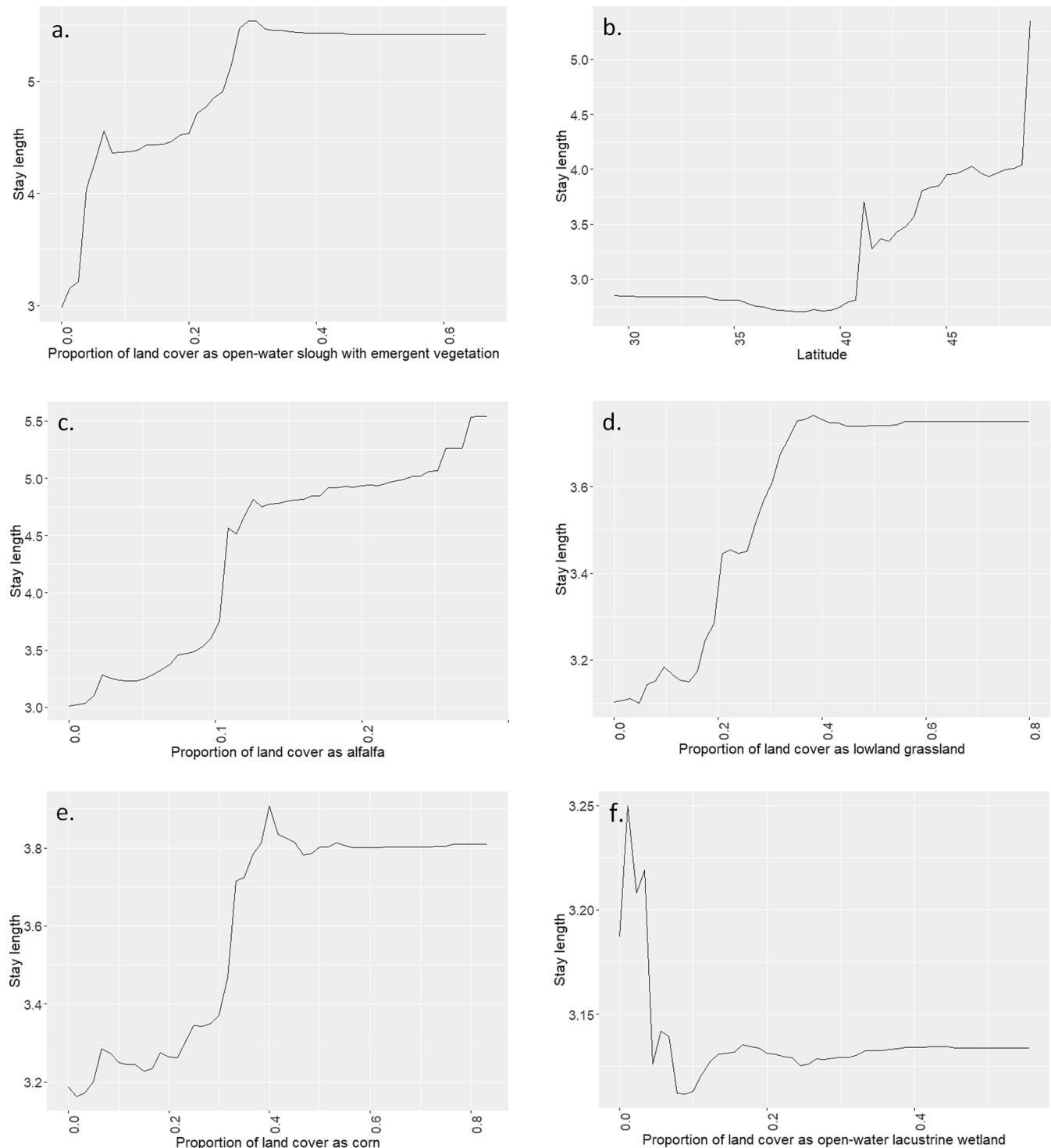
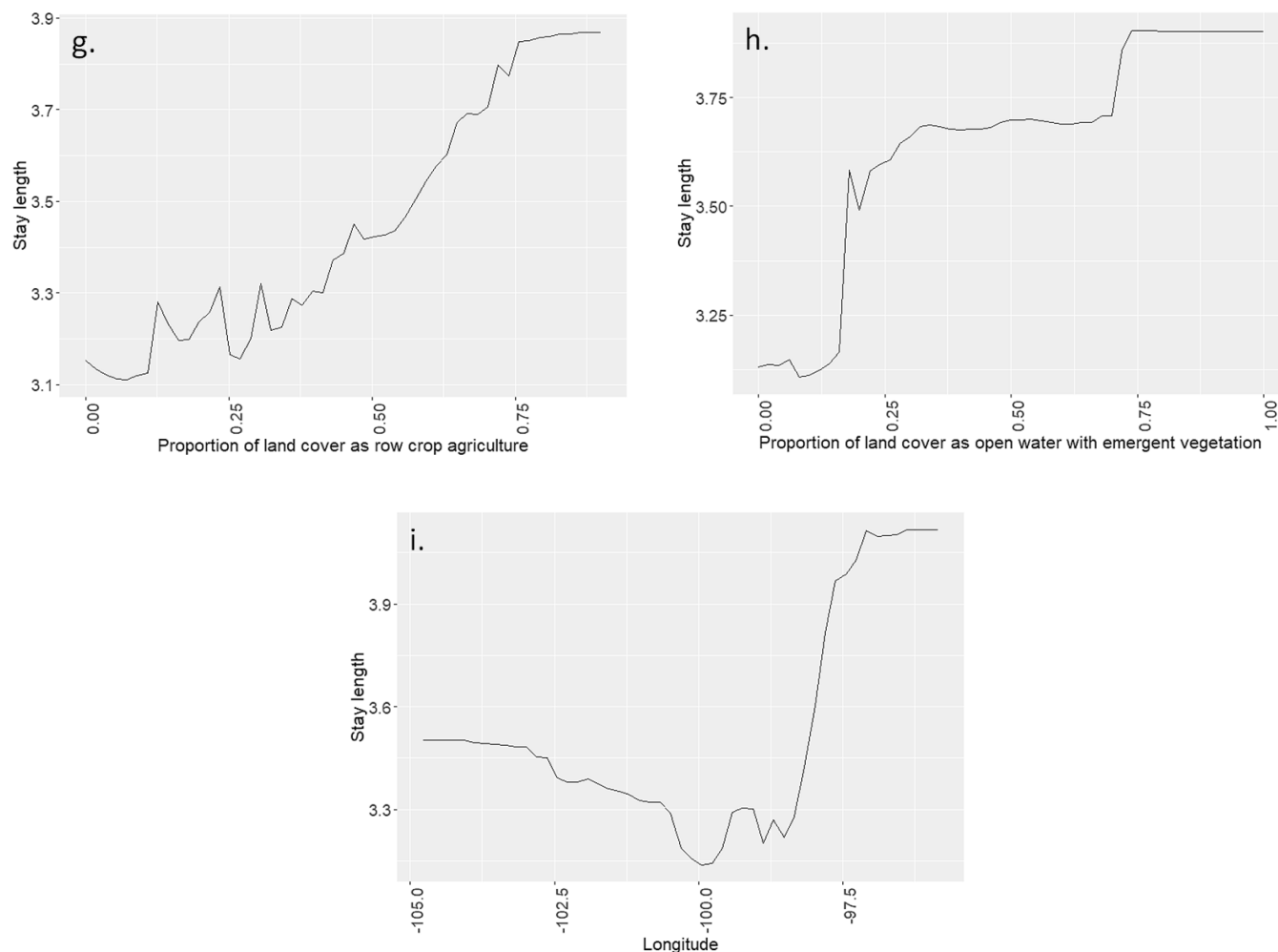


Figure 5. Partial dependence plots describing predicted stopover stay length of whooping cranes (WHCR) (y-axis) in relation to top and selected continuous landscape-level predictor variables, including the proportion of land cover within stopover buffers (x-axis) as (a) open-water slough with emergent 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

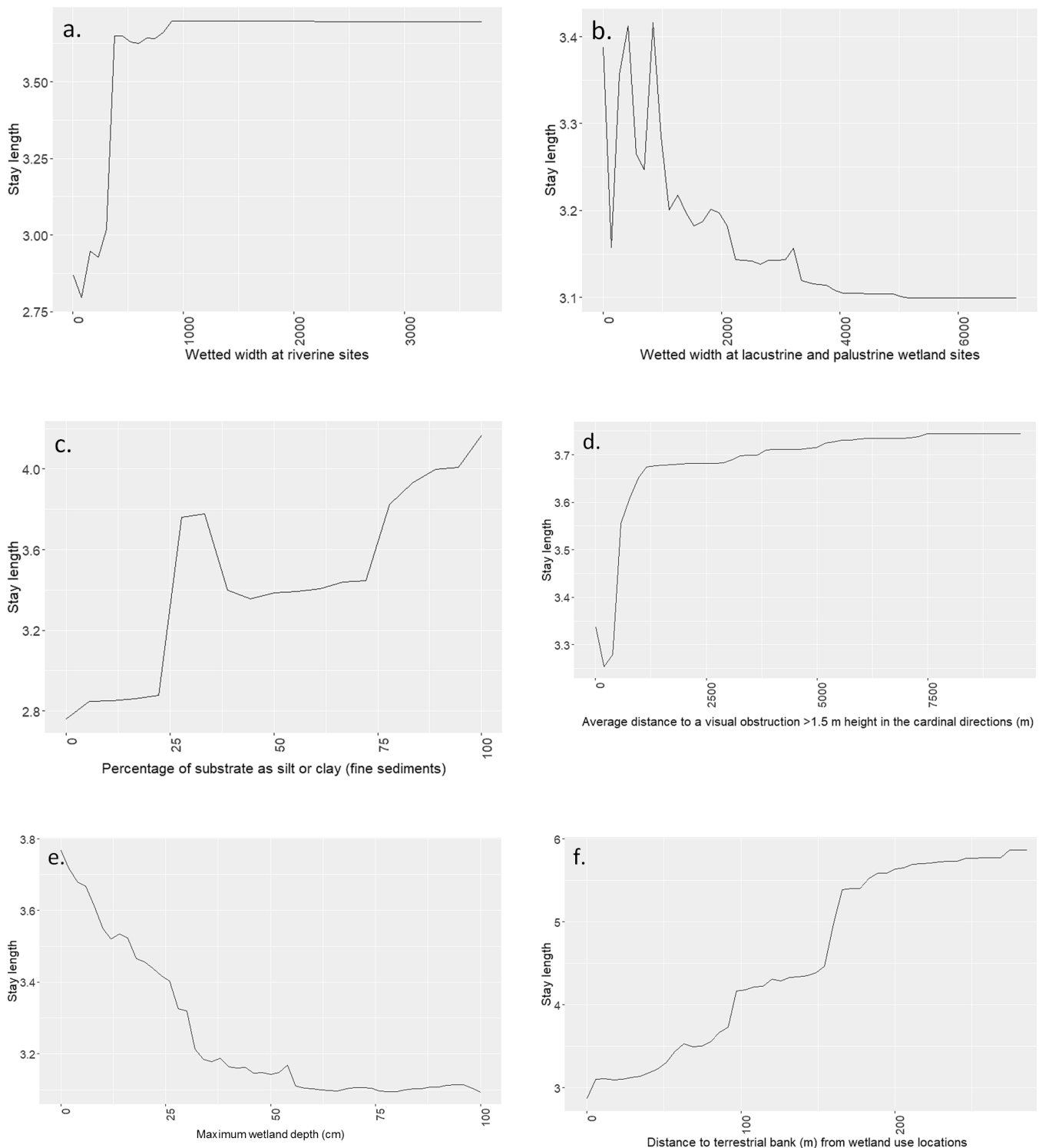


Figure 6. Partial Dependence plots describing predicted stopover stay length of whooping cranes (WHCR) (y-axis) in relation to top and selected continuous site-level predictor variables (x-axis), including (a) wetted width at riverine sites (WettedWidthCom), (b) wetted width at palustrine and lacustrine 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.

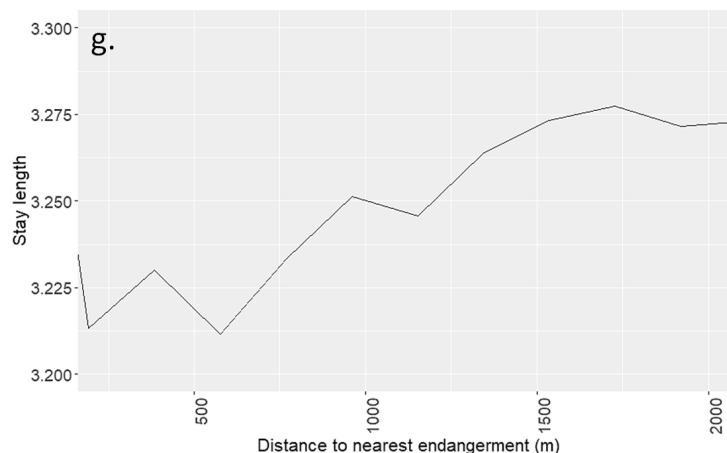


Figure 6. Continued.

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,

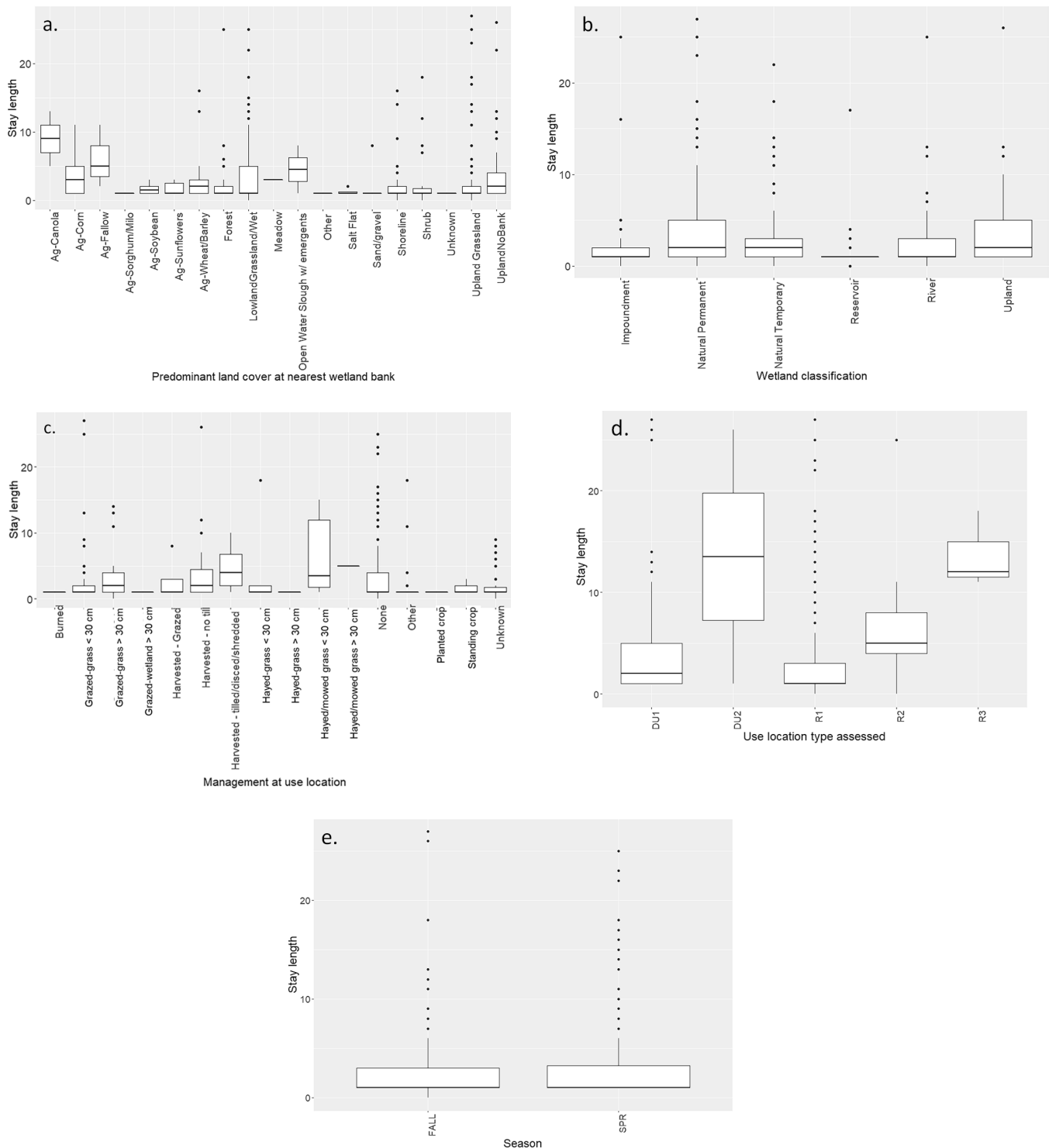


Figure 7. Box plots using data from imputed databases describing variation in stopover stay length of whooping cranes (WHCR) (y-axis) in relation to top and selected categorical site-level predictor variables including (a) land cover at the nearest terrestrial bank of a wetland (LandcovBank), (b) wetland 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) |