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Research Paper

Whooping Crane (*Grus americana*) use patterns in relation to an ecotope 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 ecotope-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. Ecotope 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'écotope 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'écotope, 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: *ecotope; Grus americana; habitat selection; landcover classification; Whooping Crane*

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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, Rolfsmeier 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.

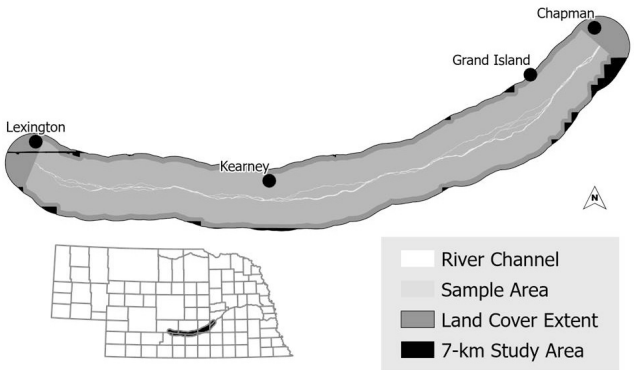
We used multiple fine-scale geospatial data sources to reassess Whooping Crane occurrence in the CPRV at the ecotope level. We also examined landscape features associated with diurnal terrestrial occurrence at multiple spatial scales to determine which was most predictive of Whooping Crane occurrence (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-NCRS (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 ecotope 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 Brie 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 ecotope, 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	
Brei and Bishop 2008	*Our Classifications*
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 ecotope 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 ecotope, 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 ($y \sim 1 + (1|\text{Landcover Class}) + (1|\text{Categorical Population})$) 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.

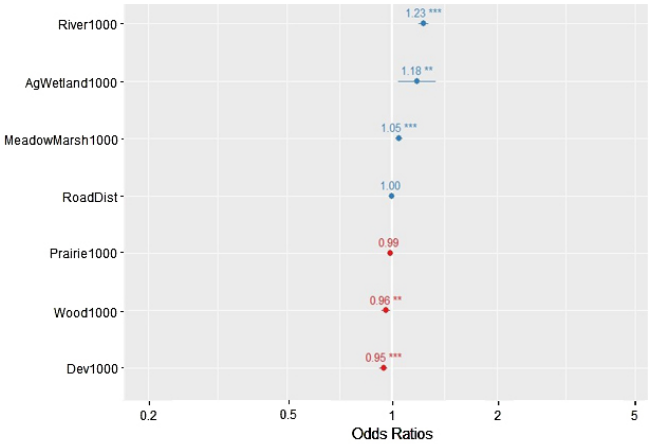
RESULTS

Ecotope-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 ecotope 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 ecotope 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 Δ AICc ≤ 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.

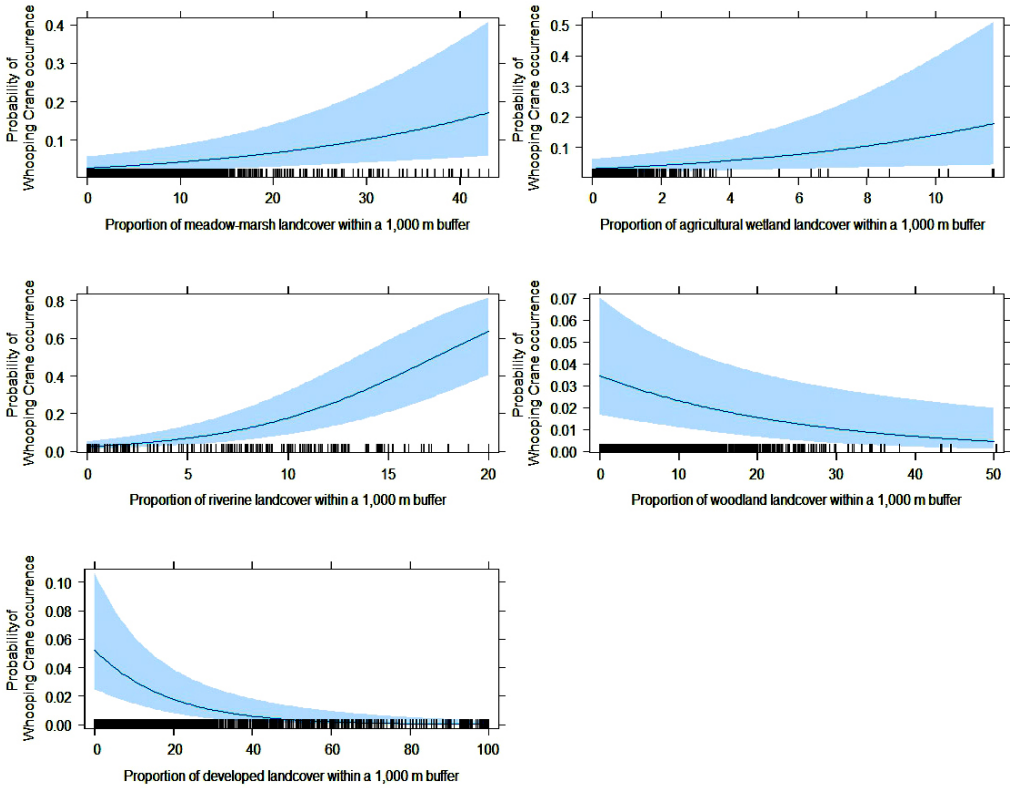
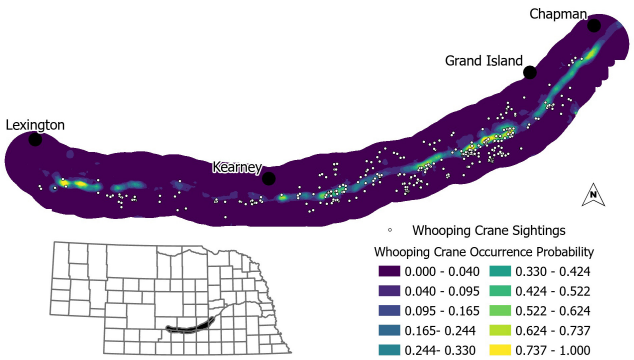


Fig. 4. Heat map depicting areas within the Central Platte River Valley most likely to be occupied by Whooping Cranes (*Grus Americana*) based on the top model from our analysis including terrestrial Whooping Crane locations (white circles) documented between 1995 and 2015 that were included in our study.



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 to 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