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NEST DISTRIBUTION OF FOUR PRIORITY RAPTOR SPECIES IN COLORADO

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ABSTRACT.—Raptors face threats such as habitat modification, climate change, and environmental pollutants in many parts of the western USA, where rapid human population growth exacerbates such pressures. However, information about distribution of raptor nests at broad spatial scales that could inform conservation efforts is lacking. To provide a contemporary estimate of nest distribution of four raptor species of special conservation concern (Bald Eagle [*Haliaeetus leucocephalus*], Ferruginous Hawk [*Buteo regalis*], Golden Eagle [*Aquila chrysaetos*], and Prairie Falcon [*Falco mexicanus*]) throughout Colorado, we used a statewide database of raptor nesting locations to inform species distribution models for monitoring and management efforts. We used generalized linear models to identify the relationship between nest locations and explanatory covariates relating to land cover, temperature, topography, and prey distribution. We investigated the effect of different methods for selecting the sample of locations available to raptors, comparing four selection frames: sampling from the observed locations of the target-group (i.e., other raptor nests), sampling from within a spatial buffer around observed locations, sampling from outside of the same buffer, or complete random sampling of the background locations without respect to observations. Out-of-sample validation techniques indicated strong predictive accuracy of our models. Each raptor species was best represented by a different one of the four approaches to sample available locations, refuting our expectation that models accounting for bias would perform better than those that did not. Our findings were consistent with generally understood habitat associations of these species. These models can be used to identify hot spots with high relative probability of use by breeding raptors and to inform future monitoring practices that use a standardized, stratified sampling design.

KEY WORDS: *breeding*; *Colorado*; *habitat selection*; *nesting habitat*; *raptor*; *spatial distribution*; *species distribution modeling*.

DISTRIBUCIÓN DE NIDOS DE CUATRO ESPECIES DE RAPACES PRIORITARIAS EN COLORADO, ESTADOS UNIDOS

RESUMEN.—Las aves rapaces enfrentan amenazas tales como la modificación del hábitat, el cambio climático y los contaminantes ambientales en muchas partes del oeste de los Estados Unidos, donde el rápido crecimiento de la población humana exacerba tales presiones. Sin embargo, se carece de información sobre la distribución de los nidos de rapaces a escalas espaciales amplias que pueda informar los esfuerzos de conservación. Con el fin de brindar una estimación actual de la distribución de los nidos de cuatro especies de aves rapaces de especial interés para la conservación (*Haliaeetus leucocephalus*, *Buteo regalis*, *Aquila chrysaetos* y *Falco mexicanus*) en Colorado, utilizamos una base de datos estatal de lugares de anidación de rapaces para generar modelos de distribución de especies, necesarios para los esfuerzos dedicados a su seguimiento y manejo. Utilizamos modelos lineales generalizados para identificar la relación entre la ubicación de los nidos y las covariables explicativas relacionadas con la cobertura terrestre, la temperatura, la topografía y la distribución de presas. Investigamos el efecto de diferentes métodos de selección de muestras de ubicaciones disponibles para las aves rapaces, comparando cuatro marcos de selección: muestreo de las ubicaciones observadas del grupo objetivo (i.e., otros nidos de aves rapaces), muestreo desde dentro de una zona de influencia alrededor de las ubicaciones observadas, muestreo desde fuera del mismo búfer, o muestreo aleatorio completo de las ubicaciones de referencia sin tener en cuenta las observaciones. Las técnicas de validación fuera de la muestra indicaron una gran precisión predictiva de nuestros modelos. Cada especie de rapaz estuvo mejor representada por uno de los cuatro enfoques de muestreo de las ubicaciones disponibles, refutando nuestra expectativa de que los modelos que tuvieron en cuenta el sesgo funcionarían mejor que

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los que no lo hicieron. Nuestros hallazgos fueron consistentes con las asociaciones de hábitat generalmente consideradas para estas especies. Estos modelos pueden usarse para identificar zonas con alta probabilidad relativa de uso por parte de aves rapaces reproductoras y para informar las prácticas de seguimiento futuras que utilizan un diseño de muestreo estandarizado y estratificado.

[Traducción del equipo editorial]

INTRODUCTION

Raptors are charismatic species generating widespread interest among the public and attention related to land use issues among management agencies. Golden Eagles (*Aquila chrysaetos*) are classified as a Tier 1 Species of Greatest Conservation Need in Colorado and are considered a priority species by multiple states and federal agencies. Bald Eagles (*Haliaeetus leucocephalus*), Prairie Falcons (*Falco mexicanus*), and Ferruginous Hawks (*Buteo regalis*) are on the Tier 2 list in Colorado and are species of Special Concern throughout much of the western United States. Bald Eagles in particular are a species of management concern due to the recent attention to nest "take," contention over regulations, and eagles' tendency to nest in areas with rapidly accelerating development (Migratory Bird Treaty Act, 16 U.S.C. 703-712; Bald and Golden Eagle Protection Act, 16 U.S.C. 668-668c; US Fish and Wildlife Service 2016). Colorado Parks and Wildlife (CPW) frequently provides consultation on these four species in relation to oil and gas development (consultation mandated by Colorado Senate Bill 19-181) and other land use issues.

To aid in conservation of the four target species (Golden Eagles, Bald Eagles, Prairie Falcons, and Ferruginous Hawks), tools are needed to inform understanding of habitat-use patterns. Generating these tools requires intensive monitoring and data collection. Habitat use and associated processes can be estimated using behavioral and historical patterns to inform computational modeling techniques (Keating and Cherry 2004, Fieberg et al. 2010). This often involves a review of the literature and/or expert elicitation, coupled with some form of a logistic regression using location data and environmental information to describe patterns of habitat use (e.g., Johnson et al. 2004, Northrup et al. 2013, Rice et al. 2013). We employ this strategy to assemble a set of candidate features thought to be useful predictors of raptor nesting habitat use at the scale of the state of Colorado, USA, and then to evaluate models of nesting habitat use for predicting nesting habitat patterns more broadly.

CPW has a statewide raptor nest database (henceforth, CPW database) that currently contains >30,000 nest records of 30 species since 1975. Most of the nest data have been collected opportunistically and known nest sites are resurveyed at a higher rate than new areas are surveyed. CPW defines a nest site as "occupied" if there are signs of reproduction, such as a pair of adults present at the site during the nesting season (as in Steenhof et al. 2017). Although some sites are visited once every 5 yr (and some annually), many have not been visited on a 5-yr cycle. More detailed information (e.g., biweekly observations) was available for a subset of nests in individual project databases, but those detailed data were often summarized prior to entry into the statewide database. Thus, the overarching goal of the raptor nest database has been to document nesting locations for agency land use consultations, but levels of effort and emphases of data collection have varied over space and time. Accounting for variable effort in data collection is especially important in the context of existential threats such as habitat modification and related anthropogenic disturbance (through development near nests), climate change, and environmental pollution. Raptors in Colorado, USA, are under pressure from all of these threats, especially in and around growing human populations along the Front Range of the Rocky Mountains in Colorado, USA.

Distribution models have been developed for raptors at a variety of scales and using various data sources (Sanchez-Zapata and Calvo 1999, Bustamonte and Seoane 2004, Sergio et al. 2004, López-López et al. 2007, McConnell et al. 2008, Booms et al. 2010). These and other previous studies predominantly rely on telemetry data from radio or satellite transmitters. In contrast, the CPW database consists of opportunistic records of nest locations and nesting activities and therefore is subject to observation bias related to variable survey effort and opportunistically encountered nests (Lele and Keim 2006, Lele 2009, Avgar et al. 2017). Ignoring this observation bias can yield misleading results and suggest inappropriate conservation and management practices.

One way to account for these potential biases, while still taking advantage of a large dataset collected statewide over more than four decades, is to put "used" nesting locations in their proper context of "available" locations. Available locations are those that are sampled from the background—the subset of non-used pixels across the state of Colorado—in contrast to locations where occupied nests were observed. We tested four different methods for selecting available locations that: (1) accounted for observation bias by sampling available locations for each species from the set of other raptor species' use locations (the target-group approach advocated by Phillips et al. 2009); (2) accounted for observation bias by sampling available locations near use locations (within-buffer sampling, as in Dunk et al. 2019); (3) ignored observation bias by sampling available locations in areas that maximize the likelihood of their being representative of true absences (outside-buffer sampling as in Olivier and Wotherspoon 2006); and (4) did not account for observation bias at all (complete random sampling from the background locations, comprising all 1 km^2 pixels across Colorado). We anticipated that models fully accounting for observation bias would outperform all others. We also expected that differences would be most stark for species with lower sample sizes of used nest locations, as there would be greater divergence among methods relative to the degree of spatial heterogeneity represented by the available sample.

Our objectives were to (1) identify which variables predicted nest locations for breeding populations of the four target raptor species, (2) map areas with high-to-low relative probability of use for mitigation planning and statewide species assessment, and (3) evaluate how best to account for observation bias in the CPW database by sampling available locations according to four selection frames. We generated distribution models for each species to evaluate the importance of ecological and anthropogenic covariates that were predicted to influence habitat use. The resulting maps, which were based on the best-performing selection frame for available locations, can be used to identify priority areas for future surveys and to target areas for conservation and management actions. Finally, we discuss limitations inherent to these types of monitoring data, suggest how the results can be used to inform conservation actions, and make recommendations for future surveys that can be consistently applied across broad regions.

METHODS

Study Area. Our study encompassed the entire state of Colorado, USA, which contains highly variable topography (High Plains to Rocky Mountains) and land cover types, with correspondingly diverse raptor nesting habitats. Colorado includes portions of the Northern Rockies, Southern Rockies/Colorado Plateau, and Shortgrass Prairie Bird Conservation Regions (Bird Studies Canada and North American Bird Conservation Initiative [NABCI] 2014).

Nest Data. The CPW raptor-nesting database comprised 36,388 recorded nest observations from throughout Colorado, 15,445 of which were from 2010–2020. Nests in the database were grouped if multiple alternative nest structures existed within a nesting territory. Where alternative nests existed, we included only the most recently occupied location in our sample. Similarly, nest locations that were occupied for multiple years were counted only once in our sample. We eliminated the few records that had missing dates or undetermined species-nest associations, leaving 3195 unique observations, 723 for the target species: 194 for Bald Eagles, 106 for Ferruginous Hawks, 344 for Golden Eagles, and 79 for Prairie Falcons.

We solicited opinions of CPW state avian researchers, species coordinators, land use coordinators, and raptor biologists to evaluate the candidate list of variables, which differed based on the biology of each target species. Many of these variables were also used in the construction of a Golden Eagle nesting habitat suitability model for the Wyoming Basin (for the Western Golden Eagle Team; Tack and Fedy 2015, Dunk et al. 2019). Based on these sources and a literature review, we identified environmental variables with associated landscape layers that we expected to influence nest distribution for each of our target species (Table 1).

Bald Eagles usually nest in trees, and often nest near water (Yates 1989, Watson 2002), so we included mixed forest, cottonwood (*Populus* spp.), and riparian-riverine land cover types, and linear distance to water features in our Bald Eagle distribution model. Ferruginous Hawks primarily use open grassland and shrubland, and avoid forest interiors (Wakeley 1978, McAnnis 1990, McConnell et al. 2008, Ng et al. 2020), so we included herbaceous grassland, shrub-scrub mix, mixed forest, and cottonwood land cover in our Ferruginous Hawk model. Breeding Golden Eagles occupy open and forested landscapes and usually nest on cliffs or

Table 1. Variable categories considered for inclusion in analysis of nest sites of four raptor species in Colorado, USA, during 2010–2020. In each column, X indicates the variable was included in models for the species.

	SPECIES			
VARIABLE	BALD EAGLE	FERRUGINOUS HAWK	GOLDEN EAGLE	PRAIRIE FALCON
Biological[a]				
Prairie dog colony (distance)	X	X	X	X
Prairie dog range (distance)	X	X	X	X
Land cover[b]				
Cliffs (distance)			X	X
Herbaceous grassland		X	X	X
Shrub-scrub mix		X	X	X
Forest (mixed)	X	X	X	
Cottonwood	X	X	X	
Riparian-riverine	X			
Cultivated areas	X	X	X	X
Developed areas	X	X	X	X
Water (distance)	X			
Topography				
Local elevation difference[c]		X	X	X
Elevation	X	X	X	X
Roads (interstates, highways, county routes)	X	X	X	X
Topographic ruggedness index (TRI)[d]	X	X	X	X
Climate				
Temperature (mean annual days > 5°C)	X	X	X	X
Ecoregions				
BCR[e]	X	X	X	X

[a] Prairie dog colony (distance) represents the distance to the nearest prairie dog colony (potential occurrence based on imagery analysis), whereas range (distance) represents the distance to the nearest pixel that is classified as being within known prairie dog range.
[b] Units are in percent cover of the variable.
[c] Degree of elevational variation within a 27-cell radius moving window, relative to the local minimum.
[d] From Riley et al. (1999), the standard deviation of elevation within a 9-cell square moving window.
[e] Bird Conservation Regions (Bird Studies Canada and NABCI 2014).

in trees (Steenhof et al. 1983, López-López et al. 2007, Watson et al. 2014, Dunk et al. 2019, Katzner et al. 2020), so we included herbaceous grassland, shrub-scrub mix, mixed forest, cottonwood, and linear distance to cliffs/bluffs/rocky outcrops in our Golden Eagle distribution model. Prairie Falcons primarily occupy open grassland and shrubland, and usually nest on cliffs (Squires et al. 1993, Steenhof 2020), so we included herbaceous grassland and shrub-scrub mix, and linear distance to cliffs/bluffs/rocky outcrops in our Prairie Falcon distribution model. For all four species, we included developed (urban/suburban) land cover, cultivated agriculture, and linear distance to roads in our models, to examine the potential effects of human-altered and disturbed cover types on nest distribution (Schmutz 1984, McGarigal et al. 1991, Stangl 1994, Wallace et al. 2016). In addition, because prairie dogs (*Cynomys* spp.) are an important prey species for Ferruginous Hawks (Cook et al. 2003), and either prairie dogs or birds and mammals associated with prairie dog colonies are prey species for our other target raptor species (Smith and Lomolino 2004, Goguen 2012), we included layers that mapped black-tailed (*C. ludovicianus*), Gunnison's (*C. gunnisoni*), and white-tailed (*C. leucurus*) prairie dog colonies and ranges in our models. We also included elevation, topography variables (local elevation variation, topographic ruggedness index [TRI; Riley et al. 1999]), and temperature (mean degree-days above 5°C) in our models for all species, as these variables may influence macro- and micro-environmental conditions at nest sites and in surrounding foraging areas. Finally, we considered Bird Conservation Regions (Shortgrass Prairie, Northern Rockies, Southern Rockies/Colorado Plateau; Bird Studies Canada and NABCI 2014) as categorical variables in models for all species to account for spatial heterogeneity across the landscape. Root sources, associated dates, and resolution (used and of the root source) of covariate layers are available in Supplemental Material File 1.

Model Development. *Covariate spatial scale.* Nest-site selection may occur at different spatial scales for different variables. For example, a nest may be placed according to the percent cover of cottonwood at one scale (within 1 km) and a certain TRI at another scale (within 5 km). Our modeling framework allowed for this possibility by testing multiple spatial buffers (summarized as means, as in Johnson et al. 2004) of 3-, 5-, and 10-km radii around nest locations (which were within 1 km^2 cells, "pixel level"), as these values had support in the literature for being relevant to raptor nesting decisions (e.g., McGarigal et al. 1991, Gerrard et al. 1992, Garrett et al. 1993, Squires et al. 1993, Stangl 1994, Plumpton and Andersen 1997, Dechant et al. 2002, Paton 2002, Watson 2002, Sandgren et al. 2014). We did not apply buffers to variables related to linear distance to a certain land cover feature.

Available locations. To determine the number of available locations to sample from the background study area (Colorado), we performed univariate logistic regression with a subset of covariates that were being tested in the model set for all four target species (following Northrup et al. 2013): developed areas, distance to roads, TRI, elevation, and temperature. We iterated the model over increasingly large numbers of available locations, such that the response variable initially composed all used locations (i.e., occupied nest locations), *n*, and 10 locations at which no observation had been recorded (randomly selected background locations, *b*) across the state. At each iteration, *i*, we increased the number of available locations a set amount, up to 20 times the number of used locations:

$$\left(b_{i+1} = b_i + \frac{n}{20}\right)$$

We monitored the mean value of the coefficients for developed areas, distance to roads, TRI, elevation, and temperature for each *i*. We interpreted the point at which the coefficient value stabilized as the sample of available locations that adequately represented the landscape available to the species (Northrup et al. 2013). In all cases, the simulations demonstrated stability with <10,000 available locations. Therefore, we used 10,000 available locations for each species, as this ensured a representative sample of the landscape.

We selected available locations using each of the four different selection frames described above: (1) We first sampled from the past decade of unique occupied nests in the raptor nesting database (3195 records for all species), excluding occupied nests for each of our four target species (e.g., available locations for Bald Eagles could be drawn from all non-Bald Eagle nests, including nests of any of the other target species). This target-group approach limits inference to the relatively narrow range of conditions within which raptor nests have been documented, but it helps ensure that the used and available samples are subject to the same observation bias and allows for analysis of the way each species differs in its habitat use from other species (as in Phillips et al. 2009). (2) We also sampled from within a 20-km buffer around all known nest locations, ensuring that the available sample would be drawn from the same general area as the used locations. This within-buffer selection frame approach is the same as that used by Dunk et al. (2019) to model nest-site selection for Golden Eagles and serves as a useful comparative tool. (3) In contrast to the within-buffer selection frame, we included an available sample that might better represent true absences (i.e., areas where no other nests for a given species have been observed; as in Olivier and Wotherspoon 2006). This outside-buffer selection suffers from observation bias and nonrandom sampling, but it may generate a more representative sample of the spatial heterogeneity present in the landscape for more narrowly distributed species like Ferruginous Hawks. (4) Finally, we sampled completely randomly from across the entire extent of the state without respect to used nest locations. This commonly used background selection approach (Manly et al. 2002, Lele 2009, Northrup et al. 2013) neither accounts for observation bias in used locations, nor maximizes the likelihood that available locations represent true absences, but serves as a useful baseline for comparison with other models.

Variable selection. To select which variables from our global set to apply to each species, we performed a two-step process. First, we checked for multicollinearity (correlation among variables), which can lead to redundant information, lack of parsimony, and skewed regression results. We assessed multicollinearity using generalized variance-inflation factors (VIF; Fox and Monette 1992, Fox and Weisberg 2018; implemented in R using the *stepVIF* function from the *pedometrics* package, Samuel-Rosa 2020) with a threshold of 5 (Kline 1998). We removed covariates with VIFs greater than this threshold (5) from consideration in models. If multiple covariates had VIFs > 5, we retained the covariate with the greatest R^2 and reran the model. We adopted a conservative VIF threshold, relative to recommendations of 10 (as in Hair et al. 2009), because we sought to minimize the number of parameters in models, thereby generating more parsimonious models. Our threshold definition meets the strictures of how strong collinearity must be before estimation precision suffers (Fox 2016).

Second, we used the *dredge* function in R (from the MuMIn package, Barton 2018) with our reduced set of variables (from step one above) to identify the best-performing model assembled from the variable list (excluding correlated variables) for each species. We used logistic regression, with Bayesian Information Criterion (BIC) for model selection. In cases where multiple models had adequate support (ΔBIC ≤ 2), we implemented model-averaging to derive a predictive model (Brewer et al. 2016). Each species' "final" model was either the best-performing or averaged model from this process.

Additionally, we sought to determine the covariate space in which each species' nesting locations occurred, and compare this to the covariate space available in the landscape as a whole. For example, elevation across Colorado ranges from 867 to 4397 masl, with most areas falling between 1200 and 3000 masl. Thus, if most observed locations of nests of a particular raptor species occur at elevations above 3500 masl, for example, that would provide evidence that it is using higher elevation habitat disproportionately, relative to how much is available in the landscape. We generated kernel-density plots of the distribution of covariate values for each species for both used and available locations, and used these as a comparison tool to distinguish qualitatively among candidate covariates. This was not used as a formal model-selection tool to exclude or include variables, but rather to visualize the degree of difference between used and available locations for each covariate, and for each species and selection frame.

Sampling. We transformed nest locations and variables to the Albers equal-area conic projection. We selected values from the land cover layers (as identified in the variable selection step) extracted at the used and available locations within the state as covariates in a generalized linear model (GLM) with a binomial link to evaluate the differential use of habitats across the landscape. We applied the GLM via JAGS in R using the *R2jags* package (Su and Yajima 2015). We iterated the models 10,000 times across three chains with a burn-in of 5000. All covariates demonstrated convergence (R-hat $< \sim 1.1$; Gelman and Rubin 1992). The model had the following form:

$$Y \sim dbern\Big(P(Y)\Big)$$

$$logit\Big(P(Y)\Big) = \beta_0 + \beta_1 \times X_1 + \ldots + \beta_n \times X_n$$

We evaluated the estimated values for each β (coefficient) to determine the effect of each particular covariate. When calculated in a Bayesian framework, the estimated values are referred to as posterior coefficient estimates.

Validation. To validate models, we applied a repeated ($n = 5$) k-fold cross validation ($k = 10$) with training and testing datasets (Johnson et al. 2006). Briefly, this involved calculating frequencies of cross-validation points (divided by the area of the landscape composed of a given range of relative probability of use values (i.e., area-adjusted frequencies) in each partitioned bin of area-adjusted frequencies, with bin ranks calculated for each cross-validated model (Boyce et al. 2002). We used 10 bins of approximately equal sample size to partition the predicted relative probability of use values (from 0 to 1 in increments of 0.1, as in Boyce et al. 2002). As is recommended for presence-availability data, we relied on the Spearman rank correlation (r_s) to evaluate the degree of correlation between area-adjusted frequencies and the predicted relative probability of use values (with higher correlation values indicating better performing models; Boyce et al. 2002).

RESULTS

Model performance (quantified as Spearman rank correlation, r_s) was strong for all species across the four selection frames for available locations (all $r_s > 0.53$; top model per species $r_s \geq 0.81$; Table 2). There was not one selection frame that performed best for all four target species; each species had a different selection frame perform best (Table 2), contrary to our expectation that models accounting for bias would always produce the best predictions. The target-group selection frame recommended by Phillips et al. (2009) outperformed the others for Ferruginous Hawks, whereas the background selection frame performed best for Bald Eagles, the within-buffer selection frame performed best for Golden Eagles, and the outside-buffer selection frame performed best for Prairie Falcons (though,

Table 2. Model performance metrics for models of distribution for four raptor species in Colorado, USA, and each selection frame for available locations (r_s = Spearman rank correlation). Selection frames are samples of available locations taken completely at random (background), from outside a buffer around used locations (outside), from a subset of locations from the raptor dataset for nontarget species (target group), or from within a buffer around used locations (within).

SPECIES	SELECTION FRAME	r_s
Bald Eagle	Background	0.81
	Outside	0.74
	Target group	0.72
	Within	0.71
Ferruginous Hawk	Background	0.72
	Outside	0.80
	Target group	0.82
	Within	0.79
Golden Eagle	Background	0.94
	Outside	0.62
	Target group	0.89
	Within	0.99
Prairie Falcon	Background	0.67
	Outside	0.89
	Target group	0.57
	Within	0.53

again, the differences in Spearman rank correlation coefficients were small; Fig. 1, Table 2).

The distributions of covariate values were similar among the four selection frames for available locations (Supplemental Material Files 2, 3). Therefore, the differences apparent in the prediction surfaces for each species (Fig. S2.9–S2.12) most likely arise not from dissimilar distributions of covariate values among the available samples, as we hypothesized, but rather from divergent covariate sets selected for inclusion in final models (whether averaged or not; Fig. 2). In instances where covariates were included in the top model for multiple selection frames, there was evidence of concordance in spatial scales and posterior coefficient estimates (e.g., cottonwood cover, riparian-riverine cover, and distance to water for Bald Eagles; forest cover and herbaceous grassland cover for Ferruginous Hawks; cliffs, herbaceous grassland cover, prairie dog range distance, shrub-scrub cover, and TRI for Golden Eagles; and prairie dog range distance and shrub-scrub cover for Prairie Falcons; Fig. 2). Bird Conservation Region was not included in any best-performing model.

Ferruginous Hawk, Golden Eagle, and Prairie Falcon nest sites had the greatest degree of overlap among covariates, as herbaceous grassland and shrub-scrub were included in the final models for all three species for at least two selection frames (Fig. 2). Golden Eagle and Prairie Falcon nest sites were both correlated with distance to prairie dog range in models across multiple selection frames. Models of Prairie Falcon nest sites additionally included temperature (degree-days $> 5°C$, nonlinearly) across selection frames (Fig. 2), whereas cliffs, cultivated areas, distance to roads, and terrain ruggedness were all included in top models across multiple selection frames for Golden Eagles. Bald Eagle nest sites exhibited relationships with cottonwood cover, distance to prairie dog colonies, riparian-riverine cover, distance to roads, and distance to water across all selection frames (Fig. 2). Land cover covariates across all species were supported mainly at the 1-km buffer scale, occasionally at the 10-km buffer scale, and seldom (5-km) to not at all (3-km) at intermediate buffer scales (Fig. 2). These covariate-response relationships are illustrated in Supplemental Material File 2 (Fig. S2.1–S2.4).

The prediction surfaces of nest-site distribution produced by the best-performing models for each species (Fig. 3) revealed some commonalities, with the most distinct result occurring for Ferruginous Hawks. The distribution maps for Bald and Golden Eagles showed similarities along Colorado's northern Front Range (Fig. 3), a rapidly developing area that is an interface between mountains and plains. Most observations of Bald Eagle nests occurred along the South Platte, Colorado, and Arkansas Rivers, with smaller numbers of observations (and corresponding probability of predicted use) along other rivers and reservoirs (e.g., Blue, Cache la Poudre, Dolores). The nest dataset during 2010–2020 contained few occupied Ferruginous Hawk nests in western Colorado (although many were occupied in previous decades); therefore, predicted distribution was more widespread on the eastern plains (Fig. 3). Prairie Falcons and, to a lesser extent, Golden Eagles, which often nest on cliffs or bluffs in open terrain, both had greater probabilities of use in the higher elevation intermountain areas of central Colorado (Fig. 3). GeoTIFF files are provided for georeferencing and high resolution evaluation in Supplemental Material File 3.

Bald Eagles demonstrated a moderate divergence between used and available locations for cottonwood land cover and riparian-riverine land cover (Fig.

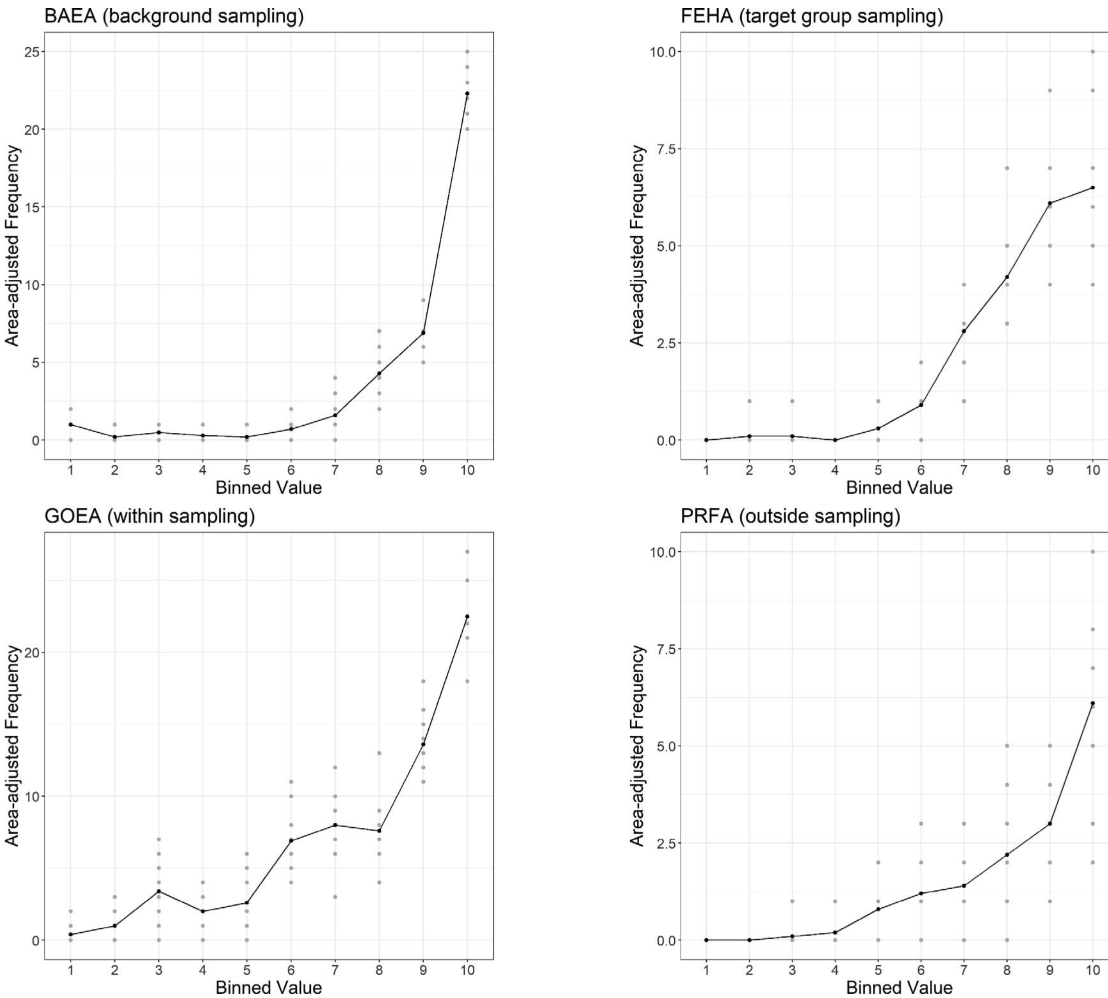

Figure 1. Area-adjusted frequency of classified relative probability of use values for withheld raptor nesting locations in Colorado, USA. Gray dots represent area-adjusted frequencies for each individual cross-validation set for each bin; the black dots and line represent the mean area-adjusted frequencies. Spearman rank correlation scores are presented in Table 2. BAEA = Bald Eagle; FEHA = Ferruginous Hawk; GOEA = Golden Eagle; PRFA = Prairie Falcon.

S2.5), consistent with covariate selection results for this species. Similarly, the strongest land cover covariates in our models of Ferruginous Hawk nest distribution exhibited some divergence between used and available locations (herbaceous grassland and shrub-scrub cover; Fig. S2.6). Golden Eagles showed some evidence of use of higher levels of terrain ruggedness, shrub-scrub cover, and cliffs (Fig. S2.7). Prairie Falcons exhibited divergence between used and available distributions for temperature (degree-days > 5°C) and shrub-scrub cover (Fig. S2.8).

DISCUSSION

We quantified the relationship of environmental predictors to nest distribution and produced predictive maps of the relative probability of use across Colorado for four raptor species of conservation concern. We also identified the degree of similarity (and dissimilarity) among different approaches for selecting available locations used to model probability of use. Importantly, we did not find that models accounting for observation bias always outperformed those that did not. These species

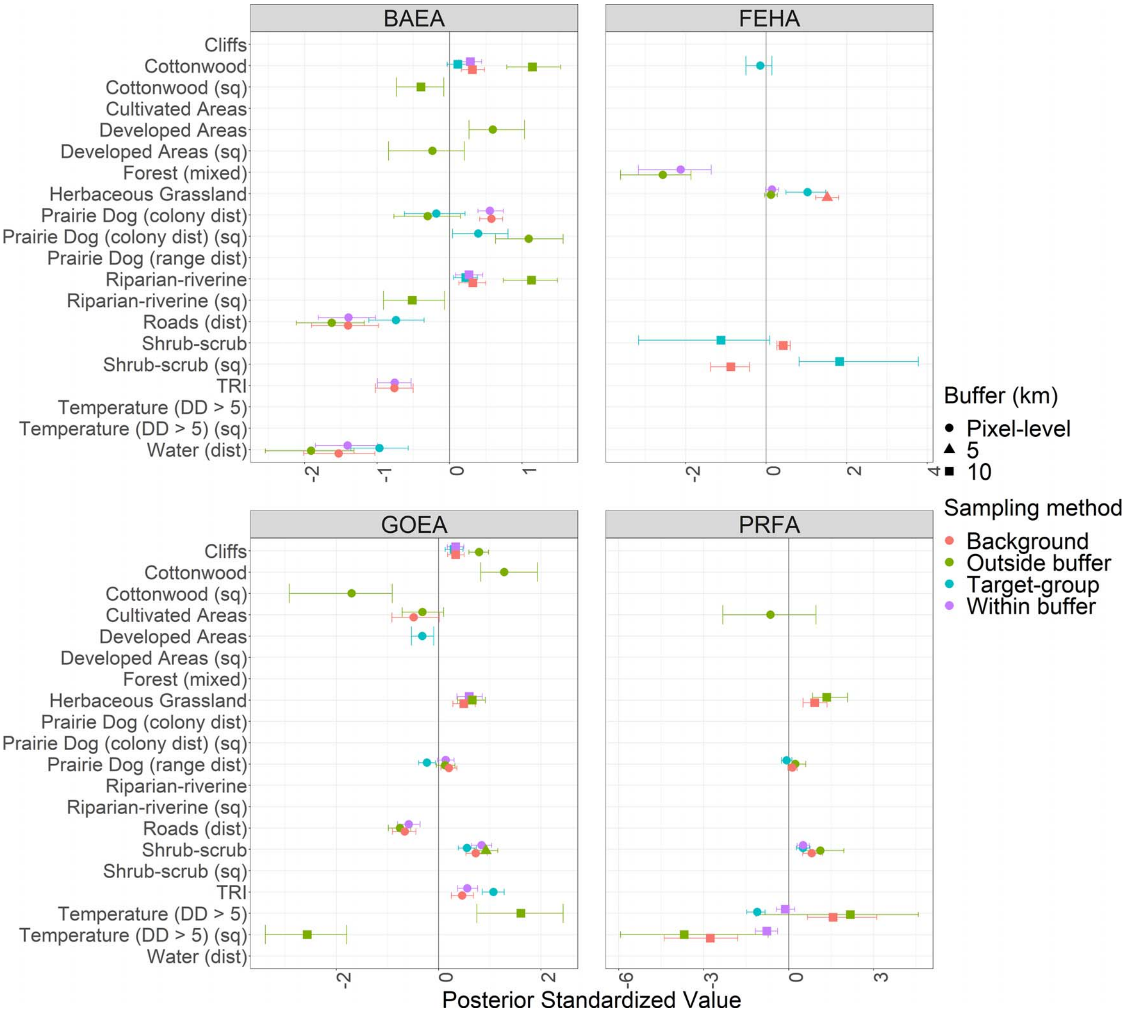

Figure 2. Standardized (mean-centered and standard deviation-scaled) posterior coefficient estimates (shapes) and 95% confidence intervals (bars) for best-supported covariates used in species distribution models of nest sites of four raptor species in Colorado, USA. The shape (circle, square, or diamond) of each mean value corresponds to the scale of the spatial buffer applied to each covariate (if any; distance covariates have a buffer of 0, "Pixel-level" is 1-km). Whiskers represent 95% confidence intervals and demonstrate significance if not overlapping 0. Colors represent the four sampling methods used to select available locations (target group, within-buffer, outside-buffer, background). Covariates included in a quadratic form are noted with (sq). "TRI" represents the terrain ruggedness index; "dist" indicates that the covariate was a point estimate of distance. Note that the scale of the x-axis differs with raptor species. BAEA = Bald Eagle; FEHA = Ferruginous Hawk; GOEA = Golden Eagle; PRFA = Prairie Falcon.

distribution models can be used to help guide conservation and management for these four raptor species of conservation concern across Colorado and likely in similar landscapes in western North America.

There was overlap among the covariates selected as useful predictors across multiple species (cottonwood cover, grassland cover, shrub-scrub cover, distance to roads, TRI). However, in most cases the covariates and their effects were not similar among species (and some varied across selection frames), as most covariates appeared to be useful predictors for only one or two raptor species. This suggests that an individualized approach to identify factors to target

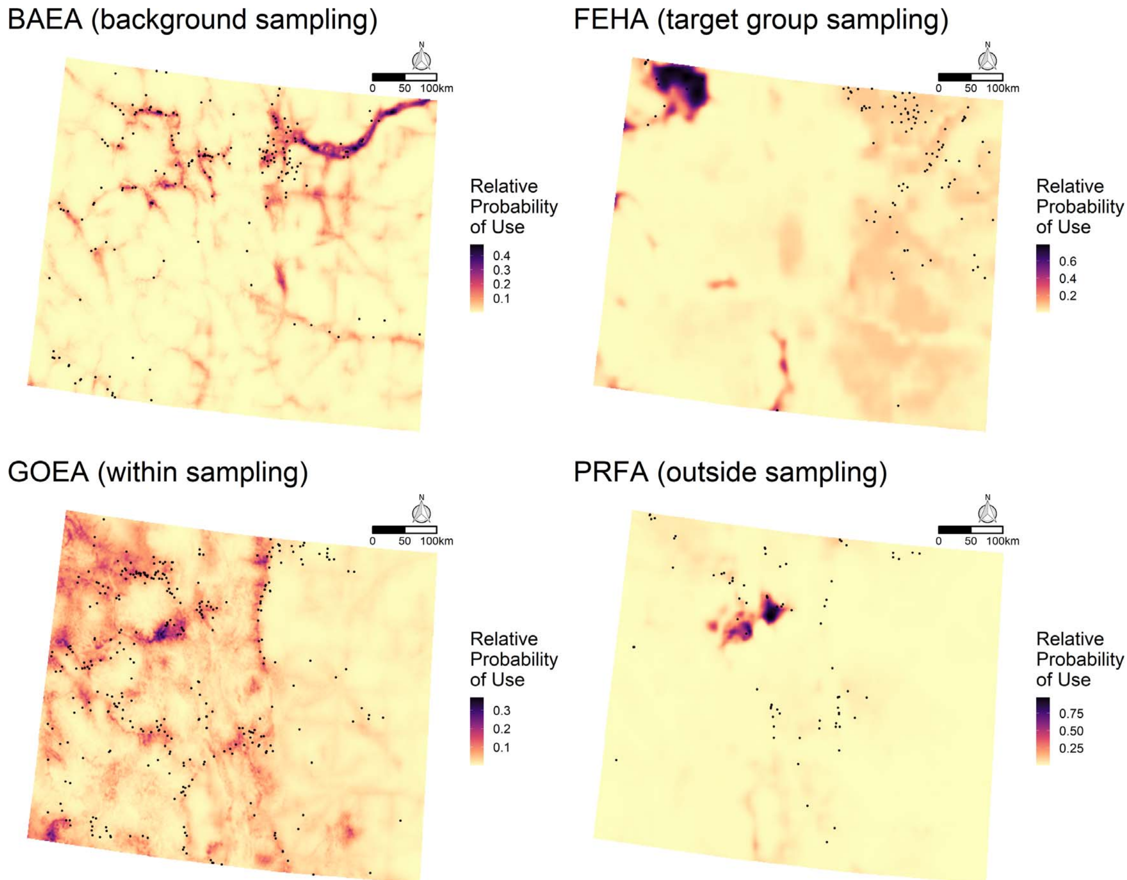

Figure 3. Predicted relative probability of use surfaces for four raptor species in the state of Colorado, USA, based on nest locations from 2010–2020, using the best-supported selection frame (target group, within-buffer, outside-buffer, background). Light areas indicate lower probability of use and dark areas indicate higher probability of use. Black dots are observed nest locations. BAEA = Bald Eagle; FEHA = Ferruginous Hawk; GOEA = Golden Eagle; PRFA = Prairie Falcon.

for management efforts would be more effective than broad application across species.

Our findings were consistent with generally understood habitat associations of these raptor species. Bald Eagle nests were located in areas with more cottonwood and riparian-riverine cover in less rugged terrain and closer to roads and water features. Ferruginous Hawk nests were located within herbaceous grassland and shrub-scrub cover. Many Ferruginous Hawks in Colorado nest in isolated cottonwood trees in these land cover types, but are rarely found in areas where land cover is dominated by cottonwoods or other forest types. Golden Eagle nests were located in shrub-scrub cover in rugged terrain and closer to roads in areas containing cliff and grassland cover. Prairie Falcon nests were located in shrub-scrub cover in areas containing more grassland cover, with a weak tendency to be located in areas with cooler mean temperatures and less cultivation. Distance to prairie dog colonies and/or range was a covariate included in the best-performing model for several of our target species; however, the 95% confidence intervals on the coefficients generally overlapped zero, and these layers may have inaccuracies due to rapid population change caused by sylvatic plague and issues with imagery (e.g., mistaking anthills for prairie dog mounds, etc.). CPW data (R. Conrey unpubl. data) suggest that raptors forage over active prairie dog colonies at a higher rate than post-plague colonies; it is possible that prairie dog layers would be more useful predictors of raptor nest distribution if more accurate layers were available that reflected true occurrence of live prairie dogs.

Our results for Golden Eagles in Colorado are in line with the ecoregional results presented by Dunk et al. (2019): our maps tended to predict similar areas of higher relative probability of use as their areas of higher relative nest-site density. Like Dunk et al. (2019), we found higher probability of use associated with shrub land cover and rough terrain, although we also found a positive association with grassland and roads. The best-performing selection frame for the available locations was the within-buffer approach also used by Dunk et al. (2019). This was not the case for the other raptor species we considered, and this method identified less area with moderate-to-high probability of use than the other methods for acquiring the available sample.

We compared model fit among different samples of available locations in terms of their predictive abilities. All models demonstrated strong predictive performance across selection frames. This highlights to us the caution necessary when designing sampling protocols and generating samples of available locations in presence-only studies: models created without respect to sampling bias may produce strong performance metrics but suffer from inherent, and unaccounted for, biases. Future survey data collected within a structured framework will allow further testing and refinement of our models.

We suggest that sample size and dispersion of nests influenced which selection frame yielded the best-performing model of raptor nest sites. For example, Prairie Falcon nest sites were the most spatially restricted and there were fewer of them than any other species, so selecting available locations from >20 km from used locations may more adequately represent spatial heterogeneity across the landscape. The effect of this potentially more representative sample cannot have been great, however, given the overlap in covariate distributions across selection frames noted earlier. In contrast, Bald Eagle nest sites had the largest sample size and were widely dispersed across the state, and likely captured most of the nests on the landscape in some areas (e.g., there are likely few Bald Eagle nests along the Front Range not included in our database). It is possible that the nearly complete census of Bald Eagle nest sites mitigated potential bias arising from selecting available locations completely at random from the background landscape. For this reason, we advocate for a careful consideration of which selection frame to use when generating predictions of species distribution, perhaps even including explicit comparison of alternative options for selecting available locations.

Our models can inform future monitoring efforts for raptors in Colorado. Weighting survey locations by predicted relative probability of use can more efficiently identify areas to target in future surveys. The implicit observation bias and the broad spatio-temporal extent of the CPW raptor database demonstrate advantages and limitations: it is useful for identifying areas where we can reasonably expect to discover new nests, but areas with low relative probability of use may represent true absence or conversely, insufficient survey effort. Both convenience (surveys near roads) and prior expectations about areas likely to support raptor nests guided the opportunistic sampling represented in the CPW database, and so there is some justification for future surveys in areas that we predicted would have low relative probability of use; documenting true absences will be valuable. Some locations have historically supported raptor nests that are no longer monitored due to logistical or organizational constraints, and low relative probabilities of use in these areas may indicate a lack of information about the status of historical nests, rather than changes in distribution over time. To address this issue, CPW has begun to prioritize surveys of historical nest sites. These limitations also illustrate the value of monitoring methods that use a standardized, stratified sampling design and target areas predicted to have a low probability of use to confirm absence or reveal unexpected nesting locations. We have begun testing aerial survey methods similar to those used by Olson et al. (2015), which will increase our ability to monitor re-occupancy of known sites (Wallace et al. 2016) and add new sites to the observed sample, as recommended by Johnson et al. (2019).

Our models provide support for maintaining and improving (in terms of resolution) several landscape data layers that were useful predictors for each species, and suggest alternative data layers that may improve prediction of raptor nest distribution. For instance, identifying data layers for temporal variation in wetlands and waterways may be useful in predicting Bald Eagle nest distribution, which showed clear relationships with riparian-riverine covariates. Additionally, evaluating intermediate spatial buffer scales other than 3- and 5-km may illuminate the proper resolution at which to consider each covariate (only 1-km and 10-km scales were included in our best-performing models), including using a wider range of species-specific, home-range size estimates (Kocina and Aagaard 2021).

We have identified landscape characteristics that are important in managing and conserving four raptor species of conservation concern and our models indicate where in Colorado mitigation efforts might be targeted. Numerous threats to raptor populations have been identified in management documents such as State Wildlife Action Plans. Our distribution models point toward actions such as preserving or enhancing cottonwood galleries, native grasslands, and grass-shrub communities in areas with a high probability of use by each raptor species, based on other landscape characteristics such as proximity to water or cliffs and bluffs. Our results also suggest where to focus standardized surveys and where to be especially judicious in future land use consultations, particularly where our nest distribution models predict high probability of nests but no nests have been documented. Our models and modeling approach illustrate how a presence-only database (albeit a large one) based on opportunistic sampling can be appropriately used in broad-scale assessments. Such location datasets are frequently maintained by land management agencies and can be important resources in conservation planning.

Supplemental Material (available online). File 1: Table S1: Covariate layers, dates, and the aggregation resolution used in raptor distribution models for Colorado, USA.

File 2: Figures S2.1–S2.4: Partial residual plots for each covariate in the final model (best-supported or averaged, for any models with ΔBIC scores ≤ 2). Figures S2.5–S2.8: Distributions of used and available locations in Colorado, USA, for each target raptor species for the covariates selected in the final species distribution models. Figures S2.9–S2.12: Predicted relative probability of use surfaces from models of nest site locations of Bald Eagles, Ferruginous Hawks, Golden Eagles, and Prairie Falcons in Colorado, USA, for the four selection frames we considered. Figure S2.13: Covariate kernel density plots for Bald Eagles, Ferruginous Hawks, Golden Eagles, and Prairie Falcons in Colorado, USA, across all selection frames for all covariates included in any species' final model.

File 3 (S3_rsf_surfaces.zip): GeoTIFF formatted rasters of resource selection function surfaces for each raptor species and each selection frame.

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