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WINTER DISTRIBUTIONS AND HABITAT ASSOCIATIONS OF RAPTORS ACROSS NEVADA

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ABSTRACT: Raptors wintering in Nevada comprise both local breeders and migrants from long distances, making winter surveys valuable for evaluating trends within multiple regional populations. We evaluated data on Nevada's wintering raptors recorded over six years from two programs—the statewide road-based surveys coordinated by the Nevada Department of Wildlife and the boat-based surveys of Lake Mead and Lake Mohave led by the National Park Service. Observations were sufficient for us to develop well-performing predictive models of the distribution and habitat use of seven species plus all species of *Accipiter* pooled. The distribution of the Bald Eagle (*Haliaeetus leucocephalus*) was stable over the six years, while the density of the Golden Eagle (*Aquila chrysaetos*) increased in 2018. Numbers of some of the other species may vary cyclically, possibly over a period three to six years, as expected for species that feed on small mammals. Patterns of the American Kestrel (*Falco sparverius*), Prairie Falcon (*F. mexicanus*), and *Accipiter* hawks were similar, possibly the result of these species focusing on the same prey in winter. Among the species whose models performed well, a positive correlation with pasture and fallow cropland was the most frequent habitat association, ranking high for all. *Accipiter* hawks and the American Kestrel were associated positively with a moderate degree of human modifications of the habitat other than agriculture, but the Northern Harrier (*Circus hudsonius*), Rough-legged Hawk (*Buteo lagopus*), Ferruginous Hawk (*B. regalis*), and Prairie Falcon showed a strong negative association with all levels of such development.

Raptors have long been used as indicators of habitat structure, quality, and health (Sergio and Newton 2003, Sergio et al. 2006, Caro and Girling 2010). The use of a species as an umbrella for ecosystem management,

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however, requires a thorough analysis of its ecology and its interaction with other species (Seddon and Leech 2008, Branton and Richardson 2011). Cabeza et al. (2008) cautioned against the use of indicator species without a systematic case study of the species involved and the environment being managed, yet Sergio et al. (2008) suggested that the data available could support the umbrella-species concept at a general level, although more analyses may be required to meet specific management objectives.

Raptors are often surveyed in winter (e.g., Eakle et al. 1996, Meunier et al. 2000, Andersen 2007), yet the winter season is generally underrepresented in the literature by comparison with studies in the breeding season. Winter represents almost half of a raptor's annual life cycle, and winter mortality rates are often similar to those at other seasons (Klaassen et al. 2014). Data from winter raptor surveys can be used to quantify the birds' land use at multiple scales (Newton 1995, Meunier et al. 2000, Williams et al. 2000, Pandolfino et al. 2011b) and can be useful for assessing habitat degradation (Berry et al. 1998, Rodríguez-Estrella et al. 1998). They may serve in assessing biological attributes such as age and sex differences that differ from those on the breeding grounds (Olson and Arsenault 2000, Pandolfino et al. 2011a), and identifying shifts in winter distributions in response to weather and climate change (Kim et al. 2008, Pandolfino and Wells 2009, Paprocki et al. 2014, 2015).

Raptors are often surveyed from the ground, from a vehicle along roads, or from a boat (see summary by Andersen 2007). Road surveys are a common tool for monitoring winter raptor populations (e.g., Eakle et al. 1996, Rodríguez-Estrella et al. 1998, Meunier et al. 2000). Because roads are not distributed randomly, however, inferences from the results may be limited to the areas actually surveyed (Andersen 2007).

Eight species of raptors (excluding nocturnal owls) have been classified as "species of conservation priority" in the Nevada Wildlife Action Plan: the Bald Eagle (*Haliaeetus leucocephalus*), Northern Goshawk (*Accipiter gentilis*), Ferruginous Hawk (*Buteo regalis*), Golden Eagle (*Aquila chrysaetos*), Burrowing Owl (*Athene cunicularia*), Short-eared Owl (*Asio flammeus*), Peregrine Falcon (*Falco peregrinus*), and Prairie Falcon (*Falco mexicanus*; Wildlife Action Plan Team 2012). Regarding these priority species, the plan has set the objectives to "maintain statewide wintering populations of priority raptors at stable or increasing trend within natural range of annual fluctuation." To assist with these objectives, and to gather information on the more common species, we undertook standardized road and boat surveys for wintering raptors across the state of Nevada with the hope of clarifying species' distribution, status, and habitat associations.

METHODS

Study Area

Participants in the program surveyed raptors by motor vehicle across the broad road network of Nevada and by boat along the shorelines of Lake Mead and Lake Mohave in southern Nevada (Figure 1).

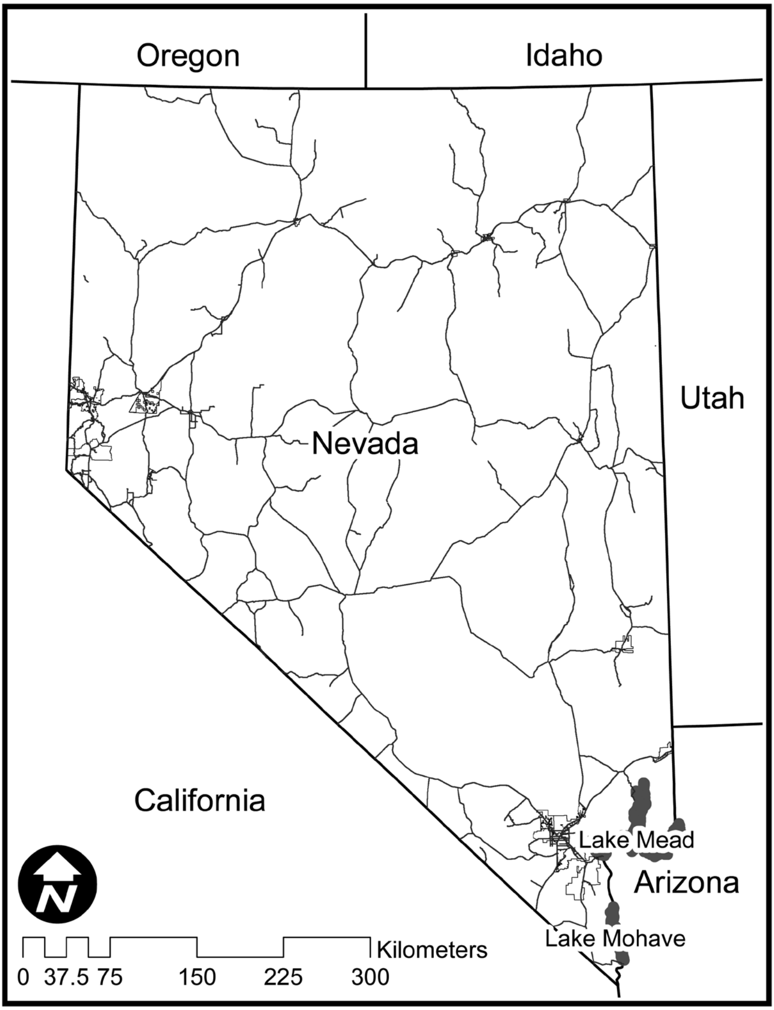

Figure 1. Most recent set of road-survey routes (narrow, gray lines) and the three bodies of water surveyed for wintering raptors in Nevada.

Field Methods

The surveys' protocols were designed initially to maintain compatibility with the National Midwinter Bald Eagle Survey coordinated by the U.S. Army Corps of Engineers but subsequently evolved to cover all raptor species.

Boat Surveys. Boat surveys took place in January of each year. Although annual midwinter Bald Eagle surveys along the shorelines of Lake Mead and Lake Mohave began in the early 1980s, the route lengths and survey protocol were not standardized until 2009. Each boat survey involved at least three participants: a boat operator, a lead observer, and a data recorder. Nine crews survey predefined routes concurrently, ensuring full coverage of the shorelines of each lake. The boats travel approximately 50–200 m offshore and at a speed not exceeding 24 km/hr.

For each survey, participants recorded the date, time, starting and ending locations, temperature, sky conditions, and wind conditions at the start and end of the survey. They noted the location on a map and recorded the time, age, and activity of each raptor observed. We later georeferenced the locations. Only three years of boat survey data have been fully georeferenced (2015–2017), so we limited our analyses to these years.

Road Surveys. The road surveys were originally developed in 1994 to complement the midwinter Bald Eagle boat surveys by adding routes in areas of high Bald Eagle concentrations. These routes were covered once every three years, and while observations of some other raptors were recorded in the earlier years, most surveyors limited their recorded observations to eagles. Over time, routes and protocols were added, modified, or reduced to address all raptors, and the surveys now cover most of Nevada's road network (Figure 1). The surveys have been annual since 2013 with an emphasis on recording observations of all raptors, so we limited our analyses of road-survey data to the years 2013–2018.

We asked road-survey participants to complete each survey route at least once between December and February each year, with a preference for January if surveying only once. Participants worked solo or in pairs (preferred), driving each route at a safe speed, slow enough to detect raptors, yet not so slow as to be a hazard on the road (55–85 km/hr, and slower if possible). We attempted to keep routes consistent from year to year, but mud or deep and drifting snow compelled some variation.

For each survey, we asked participants to record the date, time, and coordinates of the starting location, and the time, coordinates, and distance traveled at the conclusion of the survey. Participants recorded temperature, sky conditions, and wind conditions at the start and end of each survey. Participants submitted Global Positioning System track logs that were converted into Geographical Information System (GIS) shapefiles for data analyses.

For each raptor detected, participants recorded the coordinates of their location, the distance and direction to the bird, the time of observation, species, activity at first observation, and age and sex (if known). If a positive identification could not be made we categorized it as unknown (e.g., unknown falcon, unknown *Accipiter*, unknown raptor).

Statistical Analysis

Reflecting the standardization of protocols over time, we confined our analyses to the most recent six years (2013–2018). For each type of analysis, we restricted the data used to only those portions of the dataset accompanied by appropriate and consistently collected metadata, while remaining cognizant of possible biases in data completeness. Furthermore, we restricted the data used in the analyses to only the first survey completed during January of a given year, as we assume that raptors' use of space varies through the winter. Our intent was that the abundance estimates, habitat associations, and distributions represent the situation in January.

Distance Sampling. For the road-survey data, we used distance sampling to generate an estimate of population density (Buckland et al. 2001, 2004). Distance sampling accounts for a rate of detection less than 100% by modeling the probability of detection as a function of the distance to each bird observed. We chose to analyze only those species with more than 100 detections from 2013 to 2018 to ensure that the size of the sample was adequate for analysis. Once we established a detection curve for each species by pooling all observations, we used the detection curve to generate estimates of each species' density by year (Buckland et al. 2004).

Some key data were still missing even from the 2013–2018 surveys, hindering analyses. In some cases, we made assumptions enabling us to complete necessary data when we had enough information to do so. For example, if a survey's distance was not indicated but the start and end coordinates and the survey's duration were roughly consistent with those in other years, we took the distance from those other years. When data on distance traveled were missing, we estimated it on the basis of the survey's duration in previous years. These prorated estimates could introduce additional variance in the analysis, yet we believe any bias introduced via this method was overcome by the increase in sample size. If we could not estimate the necessary missing data, we eliminated that survey from the analyses.

For all analyses, we investigated each species independently, except for the hawks of the genus *Accipiter*. Because of the challenge of identifying them properly, we combined counts of reported Sharp-shinned Hawks (*A. striatus*), Cooper's Hawks (*A. cooperii*), Northern Goshawks (*A. gentilis*), and "unknown *Accipiters*" into one category of *Accipiter* hawks.

For each species, we defined a maximum possible distance of observation through a combination of methods, starting with a visual inspection of the histogram of observation distances, looking for a logical break point, as the curve representing detections as a function of distance approaches zero asymptotically; Buckland et al. 2001). We then evaluated these subjectively selected break points and shorter distances by a goodness-of-fit analysis. For example, if visual inspection suggested that detections were truncated at a distance beyond 500 m, then we tested 500 m, 400 m, and 300 m, selecting the greatest distance that did not result in a fit significantly greater than at the next lower distance. We did not always choose the best fit, as very small truncation distances (e.g., < 100 m) may fit the best, leaving very few observations remaining for analysis (Buckland et al. 2001, 2004).

For each species, we fit both half-normal and hazard-rate detection curves of all observations, with polynomial and cosine adjustment terms (Miller and Thomas 2015). We selected the best model for each species by Akaike's information criterion (AIC; Burnham and Anderson 2002). We present density estimates along the road network for each year with 80% confidence intervals, along with the average density for all years to help identify years with significant deviations in density numbers. We have not measured linear trends in density over time, as to do so reliably requires data beyond at least one prey cycle (Johnson et al. 2013).

Maximum-Entropy Modeling. For the 2013–2018 road-survey data and the 2015–2017 boat-survey data combined, we used maximum-entropy modeling (the program MaxEnt; Phillips et al. 2006, 2017) to assess the influences of climate and habitat. We included all recorded observations of each species as positive presence points. For integration as pseudo-absence points in the analysis, we generated 5000 random points within 1 km of established road routes. Then to distinguish presence from pseudo-absence more clearly, we eliminated all pseudo-absence points located within 1 km of recorded observations, resulting in a minimum of 4074 pseudo-absence points for the Red-tailed Hawk (*Buteo jamaicensis*) and a maximum of 4909 pseudo-absence points for *Accipiter* hawks.

For predictor variables within the MaxEnt analyses, we used a digital elevation model (for elevation), the U.S. Geological Survey's 2012 Landfire data (for coarse habitat types; www.landfire.gov/viewer), and the 19 WorldClim variables (quantifying climate; Fick and Hijmans 2017; Table 1). We grouped similar Landfire land-cover classifications together into broad categories (e.g., all development grouped into a single variable, all grassland types grouped together, all sagebrush types grouped together). The resulting Landfire classifications were not mutually exclusive. For example, the

Table 1 Climate, Geographic, and Habitat Variables Analyzed with MaxEnt to Characterize Habitat Use of Raptors in Nevada

Variable	Source
Annual mean temperature (°C)	worldclim.org bio_1
Mean of monthly averages of daily temperature range (max temp – min temp) (°C)	worldclim.org bio_2
Isothermality (BIO2/BIO7) (×100)	worldclim.org bio_3
Temperature seasonality (standard deviation ×100)	worldclim.org bio_4
Maximum temperature of warmest month (°C)	worldclim.org bio_5
Minimum temperature of coldest month	worldclim.org bio_6
Annual range of temperature	worldclim.org bio_7
Mean temperature of wettest quarter	worldclim.org bio_8
Mean temperature of driest quarter	worldclim.org bio_9
Mean temperature of warmest quarter	worldclim.org bio_10
Mean temperature of coldest quarter	worldclim.org bio_11
Annual precipitation (mm)	worldclim.org bio_12
Precipitation of wettest month (mm)	worldclim.org bio_13
Precipitation of driest month (mm)	worldclim.org bio_14
Precipitation seasonality (coefficient of variation)	worldclim.org bio_15
Precipitation of wettest quarter	worldclim.org bio_16
Precipitation of driest quarter	worldclim.org bio_17
Precipitation of warmest quarter	worldclim.org bio_18
Precipitation of coldest quarter	worldclim.org bio_19
Elevation (m)	U.S. Geological Survey digital elevation model
Proportion row and close crops within 150 m	Landfire
Proportion pasture, hay, and fallow cropland within 150 m	Landfire
Proportion marshland within 150 m	Landfire
Proportion grassland within 150 m	Landfire
Proportion shrubland within 150 m	Landfire
Proportion sagebrush within 150 m	Landfire
Proportion development within 150 m	Landfire

shrubland category includes all sagebrush and non-sagebrush shrublands, whereas the sagebrush category includes sagebrush only. We excluded roadways from the category of development as our road-based survey would naturally bias conclusions toward roadways. We excluded cropland from the development category as we expected species' responses to cropland and other types of development to differ. For croplands, we grouped Landfire classes for row and close crops into one category ("row and close cropland"), pasture, hay, and fallow fields into a second category ("pasture/hay/fallow cropland"), and orchards, vineyards, and berry crops into a third category. We later dropped this last category as the extent of this type of agriculture in Nevada is insufficient for analysis.

We included elevation data in the analysis but acknowledge that most raptor species are not likely sensitive to elevation per se, but they may respond to conditions favored at certain elevations such as the presence or absence of snow cover, certain habitat elements, or prey. The WorldClim data are based on records from 1970 to 2000 (Fick and Hijmans 2017). We used them to represent subtle habitat differences influenced by climate, not to measure the year-to-year variation in raptor density. The evaluation of the effect of year-to-year weather variation is beyond the scope of our analyses.

From the Landfire data, we produced raster maps of our study area showing the proportion of each cover type (e.g., shrubs, sagebrush, grass) within 150 m of each 30 m × 30 m pixel. Similarly, we created study-wide maps of elevation and the 19 WorldClim variables. All values were then resampled down to 30-second blocks (~1 km; resolution of the climate data) by means of bilinear interpolation.

We used all presence and pseudo-absence points for each species in the analyses. We evaluated the feature classes in the MaxEnt model (linear, linear-quadratic, and linear-quadratic-hinge) with Akaike's information criterion adjusted for small sample size (AIC_c; Shcheglovitova and Anderson 2013). We considered relationships of predictors to detected presence more complex than a simple linear one. The use of AIC_c as the criterion for selection of a model helps balance the goals of better fit to the data and less complexity. In assessing the fit of the resulting models, we used the area under the curve (AUC) of the receiver operating characteristic plot (ROC). The ROC represents the proportion of observed presences correctly predicted plotted against the proportion of observed absences incorrectly predicted (Pearson 2010). A perfect model has an AUC of 1.0; a random model has an AUC of 0.5. We consider any values of AUC less than 0.75 to be marginally predictive, values between 0.75 and 0.80 to be moderately predictive, and values greater than 0.80 to be strongly predictive. For all species with an AUC value of 0.75 or higher, we report the top influential variables for the species across Nevada. We selected and report the top influential variables by the "gain" or "predictive power" of the variable in a model by itself and the decrease in "gain" or "predictive power" when the variable is removed from the global model (which incorporates all variables), suggesting that the variable in question includes the most information not included in other variables. Marginally predictive models are those in which our predictor variables do not include the characteristics relevant to the birds. We present the best statewide prediction map for each species regardless of the model's fit.

RESULTS

In our analyses, we used a total of 346 road surveys spread across 66 separate routes spanning six years (2013–2018) and 26 boat surveys across nine survey routes spanning three years (2015–2017). They yielded observations of 3281 Red-tailed Hawks, 1080 Golden Eagles, 1014 Rough-legged Hawks (*Buteo lagopus*), 731 Bald Eagles, 699 Northern Harriers (*Circus hudsonius*), 428 American Kestrels (*Falco sparverius*), 379 Prairie Falcons, 325 Ferruginous Hawks, 131 *Accipiter* hawks, 46 Peregrine Falcons, 32 Great Horned Owls (*Bubo virginianus*), 13 Swainson's Hawks (*Buteo swainsoni*), 11 Merlins (*Falco columbarius*), eight Red-shouldered Hawks (*Buteo lineatus*), four Barn Owls (*Tyto alba*), four Ospreys (*Pandion haliaetus*), three Short-eared Owls, two Turkey Vultures (*Cathartes aura*), one Burrowing Owl, one Northern Pygmy-Owl (*Glaucidium gnoma*), and 451 other raptors that could not be identified to species.

Over the six-year period, we found no significant deviations in Bald Eagle density along the road network from the average density (Figure 2). For the Northern Harrier, we found density along the road network to be significantly below the six-year average in 2013 and 2014, and significantly above the six-year average in 2016 and 2017 (Figure 2). For *Accipiter* hawks, 2013 and 2015 were the only years with a significant deviation from the six-year average, although numbers in the later three years were significantly higher than in the earlier three (Figure 2).

For the Red-tailed Hawk, we found its density in 2013 and 2014 to be significantly below the six-year average and in 2016 to be above the six-year average (Figure 3). We found Rough-legged Hawk density along the road network to be below the six-year average in 2015 and above the six-year average in 2017 (Figure 3). For the Ferruginous Hawk, only in 2015 was density significantly below the six-year average (Figure 3).

For the Golden Eagle, we found its density in 2013 and 2014 to be significantly below and in 2018 to be significantly above the six-year average (Figure 4). We found the American Kestrel's density to be below the six-year average in 2013 and above it in 2016 and 2018 (Figure 4). Last, the Prairie Falcon's density was significantly below the six-year average in 2013 and significantly above it in 2016 (Figure 4). In general, 2013 and 2014 were poor for most species in comparison with later years.

For the habitat and distribution analyses (MaxEnt; based on both road- and boat-survey data), associations varied in direction of influence and by species (Table 2). The most broadly influential habitat variables were cropland (primarily pasture/hay/fallow, row and close croplands to a lesser degree) and development (Table 2). The top model for the Bald Eagle included linear and quadratic feature classes. The AUC for the model based on 239 presence and 4890 pseudo-absence records was 0.88, suggesting the model is strongly predictive (Figure 5). From the jackknife test for importance of variables, the single most important predictor variable, in terms of the gain produced by a one-variable model, was elevation (density decreasing with increasing elevation), followed by most of the temperature variables (density increasing with increases in all temperature variables). The Bald Eagle's association with the Landfire variable representing the extent of sagebrush

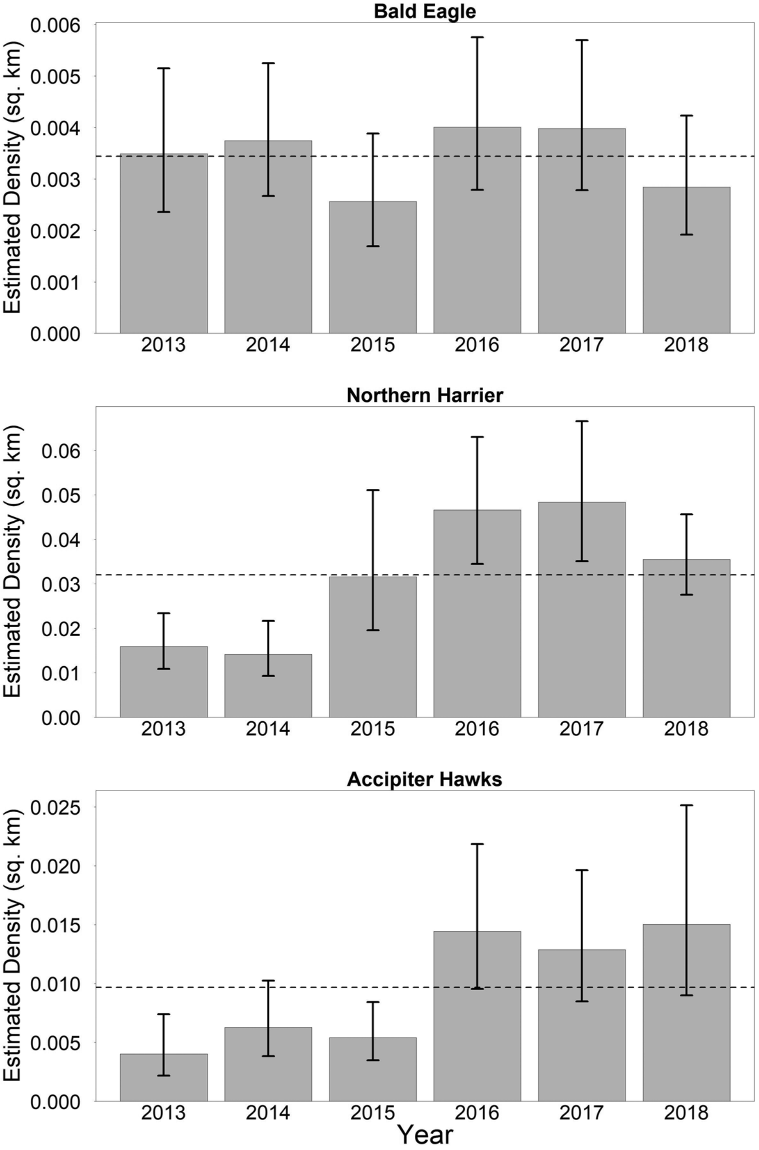

Figure 2. Estimated winter density across the road network of Nevada of the Bald Eagle, Northern Harrier, and *Accipiter* hawks per square kilometer, with 80% confidence intervals and the mean over all six years.

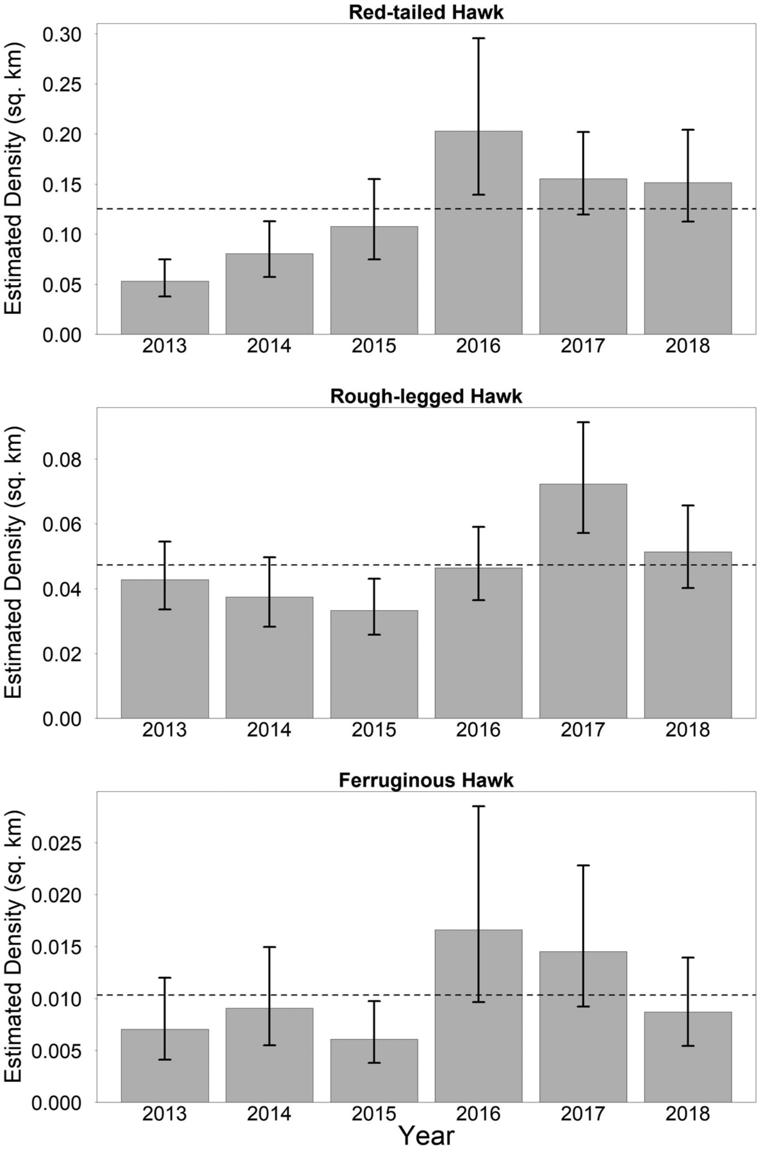

Figure 3. Estimated winter density across the road network of Nevada of the Red-tailed Hawk, Rough-legged Hawk, and Ferruginous Hawk per square kilometer, with 80% confidence intervals and the mean over all six years.

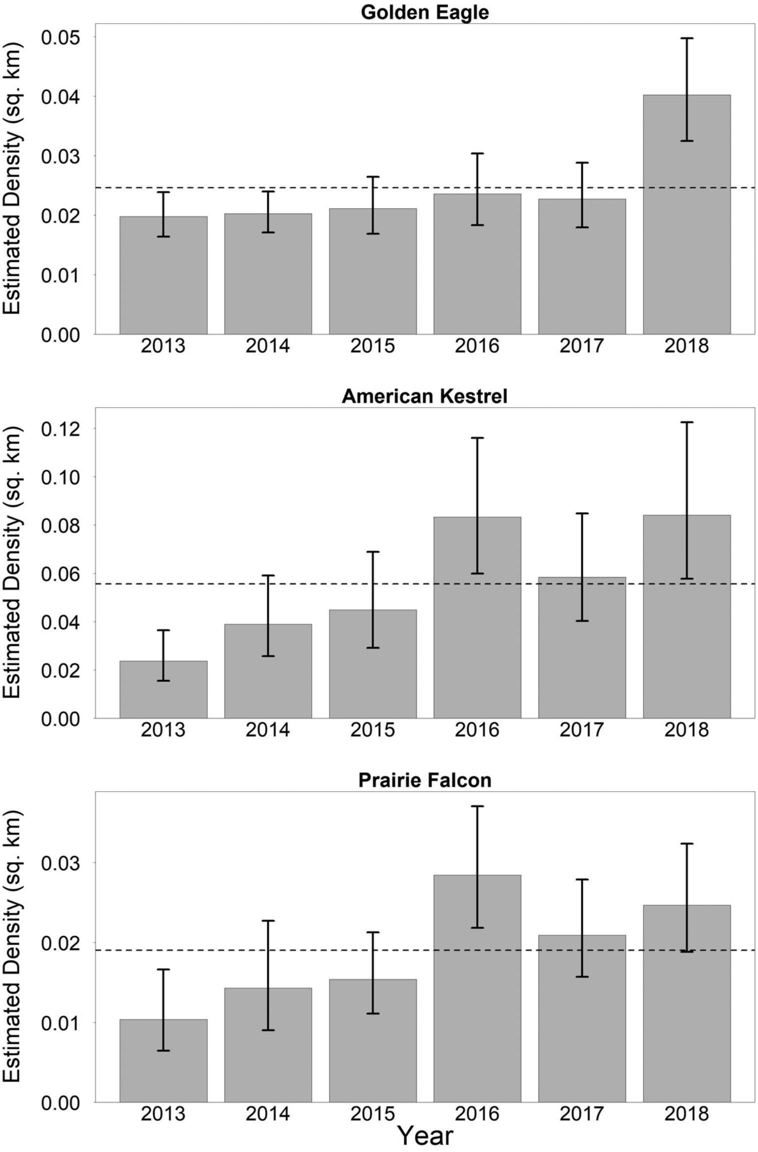

Figure 4. Estimated winter density across the road network of Nevada of the Golden Eagle, American Kestrel, and Prairie Falcon per square kilometer, with 80% confidence intervals and the mean over all six years.

Table 2 Trends of Predictor Variables Constituting MaxEnt Models of Winter Habitat Use of Raptors in Nevada[a]

Variable	Bald Eagle	Northern Harrier	Accip-iters	Red-tailed Hawk	Rough-legged Hawk	Ferru-ginous Hawk	Amer-ican Kestrel	Prairie Falcon
Annual temperature			+	+				
Mean diurnal temp. range		+	++	+		++	+	
Isothermality			—		—			
Temperature seasonality	+	+				+	+	
Max temp. warmest month								–
Min temp. coldest month	—	–	–					
Annual temp. range					++			
Temp. wettest quarter		+						++
Temp. driest quarter	++	+	+			—	+	—
Temp. warmest quarter	++			+				
Temp. coldest quarter		–			—		–	
Annual precip.		–					–	
Precip. wettest month								–
Precip. driest month	+/–		+	–	+/–	–	+	++
Precip. seasonality	+	+	+	–		–	+	+
Precip. wettest quarter								
Precip. driest quarter		+			+	+		+
Precip. warmest quarter		–	–	—		–		—
Precip. coldest quarter				+				
Elevation (m)	—	—	+	–	–	–	–	–
Row and close crops		++	++			++	++	++
Pasture/hay/fallow	++	++	++	++	++	++	++	++
Marshland						–		
Grassland	–		+/–					
Shrubland		++		–			+/–	
Sagebrush	—	—		–	–	—	+	—
Development	–	—	++/—	++/—	—	—	++/—	—

[a]Restricted to species for which the model was moderately or strongly predictive (AUC ≥ 0.75). +, trend positive and the variable increases the probability of the species' presence by a factor >0.25 over the range of the variable; –,trend negative and the variable increases the probability of the species' absence by a factor >0.25; +/–,response greater than a factor 0.25 at intermediate values, lower at low or high values of the variable. The most influential variables for each species are emphasized by "++", "—", or "++/—."

was negative, and omission of this variable from the full model decreased the gain, which suggests that it contained the most predictive information not present in the other variables. In summary, our model shows that Bald Eagles were more common at lower elevations, where temperatures are warmer, and where the proportion of sagebrush in the landscape is lower.

For the Northern Harrier, the top model included linear and quadratic feature classes. The AUC for the model based on 531 presence and 4654 pseudo-absence records was 0.78, suggesting the model is moderately predictive (Figure 6). The single most important predictor variable was the habitat category pasture/hay/fallow cropland (strong positive association), followed by row and close cropland (positive, but not as strong). Omission from the full model of the variable representing pasture/hay/fallow cropland

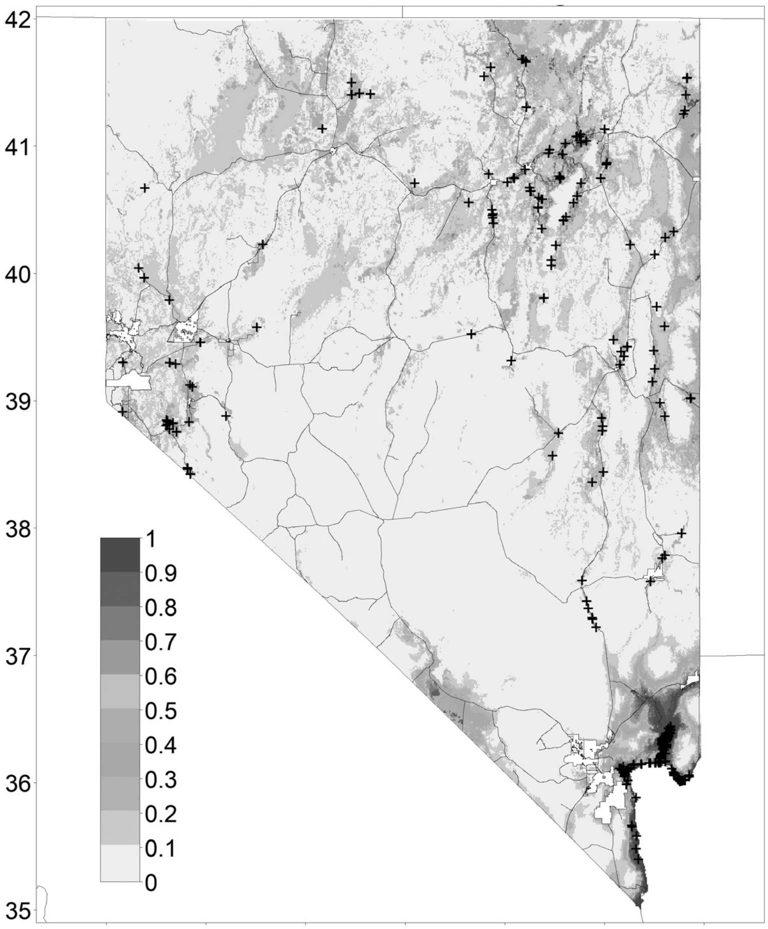

Figure 5. Predicted distribution of wintering Bald Eagles in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys (2015–2017), shown with the road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in shading graduated from a probability of 0 (white) to 1 (dark gray; scale at left).

also decreased the gain more than did omission of any other variable. Other variables with moderate influence include sagebrush (negative association), shrubland (positive association), elevation (negative association), and development (negative association). Thus Northern Harriers were more often found near lower-elevation cropland, in shrublands other than sagebrush, and in areas with low levels of development.

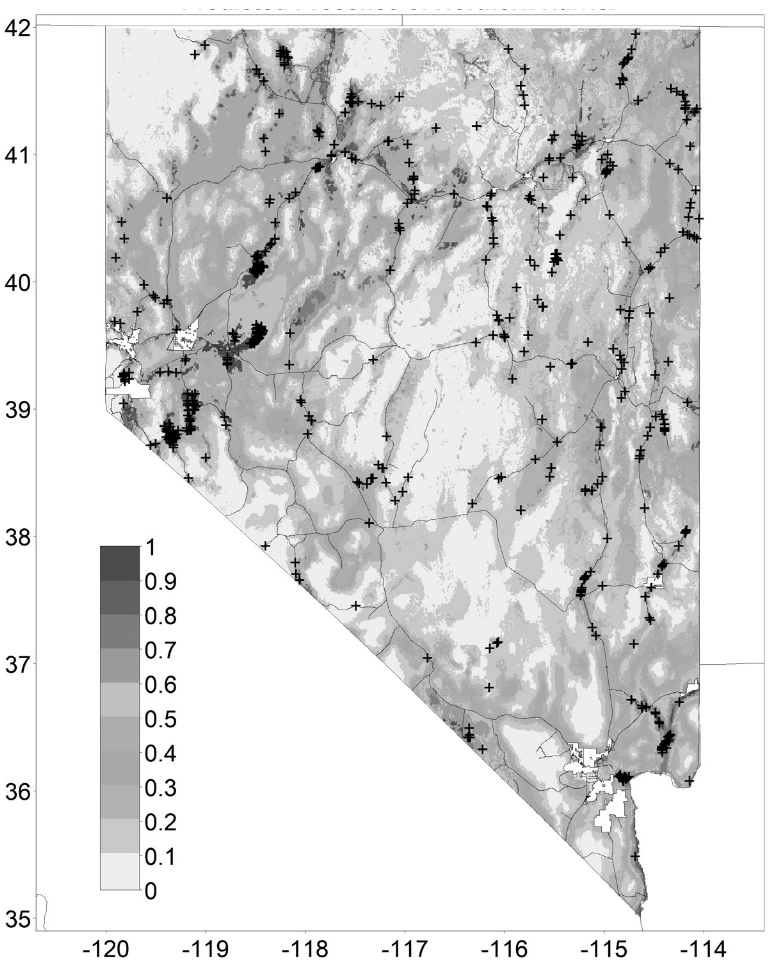

Figure 6. Predicted distribution of wintering Northern Harriers in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys data (2015–2017), shown the with road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in shading graduated from a probability of 0 (white) to 1 (dark gray; scale at left).

For *Accipiter* hawks, the top model included linear and quadratic feature classes. The AUC for the model based on 120 presence and 4909 pseudo-absence records was 0.89, suggesting a strongly predictive model (Figure 7). The single most important predictor variables were the habitat categories for development (positive association with intermediate levels of development), pasture/hay/fallow cropland, and row and close cropland. The variables

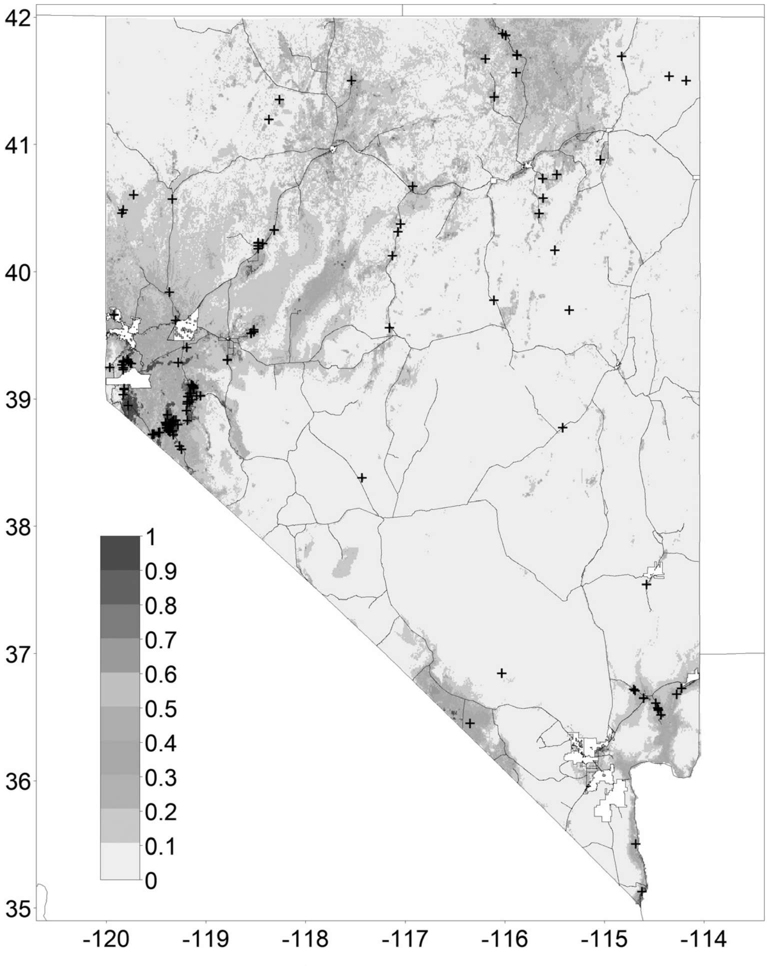

Figure 7. Predicted distribution of wintering *Accipiter* hawks in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys (2015–2017), shown with the road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in shading graduated from a probability of 0 (white) to 1 (dark gray; scale at left).

representing development and pasture/hay/fallow cropland decreased the gain the most when they were omitted from the full model. Other influential variables represented a positive association with wider temperature ranges (higher mean diurnal temperature range and lower isothermality). Thus *Accipiter* hawks were more often found in areas of intermediate levels of development that include pasture/hay/fallow cropland.

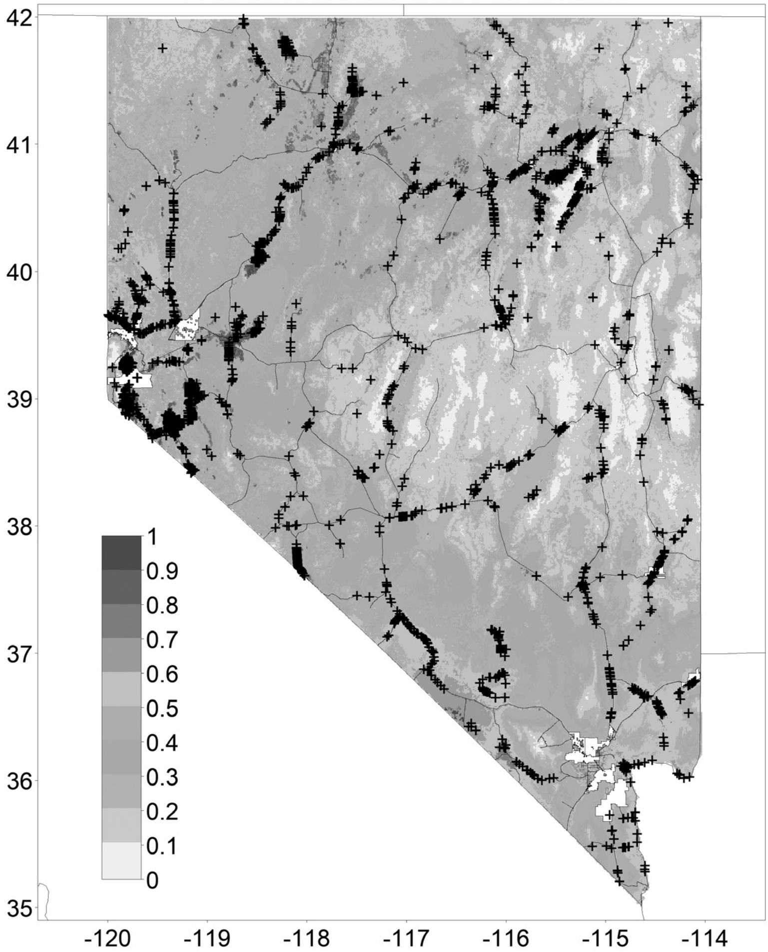

Figure 8. Predicted distribution of wintering Red-tailed Hawks in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys (2015–2017), shown with the road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in shading graduated from a probability of 0 (white) to 1 (dark gray; scale at left).

For the Red-tailed Hawk, the top model included linear, quadratic, and hinge feature classes. The AUC for the model based on 2373 presence and 4074 pseudo-absence records was 0.77, suggesting the model is moderately predictive (Figure 8). The single most important predictor variable was the habitat category of development (positive association at intermediate levels). Omission from the full model of the development variable decreased the gain more than did omission of any other variable. The next most important variable for the Red-tailed Hawk was the presence of pasture/hay/fallow cropland. Other influential variables were associations with lower elevations and areas with less precipitation in the warmest quarter. Thus Red-tailed Hawks were more often found in moderately developed areas that include pasture/hay/fallow cropland and have summers drier than in the rest of Nevada.

For the Rough-legged Hawk, the top model included linear and quadratic feature classes. The AUC for the model built with 785 presence and 4481 pseudo-absence records was 0.76, suggesting a moderately predictive model (Figure 9). The most important predictor variable was the presence of pasture/hay/fallow cropland (positive association). This was followed by three climate variables, minimum temperature in coldest month (negative), mean temperature in coldest quarter (negative), and annual range of temperature (positive), and by the habitat variable for development (negative association). The variable for pasture/hay/fallow cropland (positive association), followed by that for development (negative association), decreased the gain the most when omitted from the full model. In summary, Rough-legged Hawks were found more often in pasture/hay/fallow cropland, in the colder areas of Nevada with a wide annual range in temperature, and away from development.

The top model for Ferruginous Hawk included linear and quadratic feature classes. The AUC for the model based on 216 presence and 4865 pseudo-absence records was 0.85, suggesting the model is strongly predictive (Figure 10). The most important predictor variables were two representing habitat, first the one for cropland (positive association), followed by the one for development (positive at very low levels, but mostly negative association). The variable representing pasture/hay/fallow cropland (positive association) decreased the gain the most when it was omitted from the full model. The most important climate variable was a positive association with mean diurnal temperature range. Thus we found Ferruginous Hawks in areas with low levels of development, cropland nearby, and broad daily temperature ranges.

The top model for the Golden Eagle included linear and quadratic feature classes. The AUC for the model based on 829 presence and 4502 pseudo-absence records was only 0.71, suggesting the model is marginally predictive, so we do not discuss the results for this species (Figure 11).

For the American Kestrel, the top model included linear and quadratic feature classes. The AUC for the model based on 336 presence and 4780 pseudo-absence records was 0.83, suggesting a strongly predictive model (Figure 12). The most important predictor variables were the two Landfire classes for cropland (positive associations), followed by that for development (positive association only with intermediate levels of development). The variable for pasture/hay/fallow cropland (positive association) decreased the gain the most when it was omitted from the full model. Omission of the variable for development had the second greatest effect. Thus, overall, American Kestrels were most often found in areas of cropland and medium levels of development.

The top model for the Prairie Falcon included linear and quadratic feature classes. The AUC for the model based on 329 presence and 4737 pseudo-absence records was 0.75, suggesting a moderately predictive model (Figure

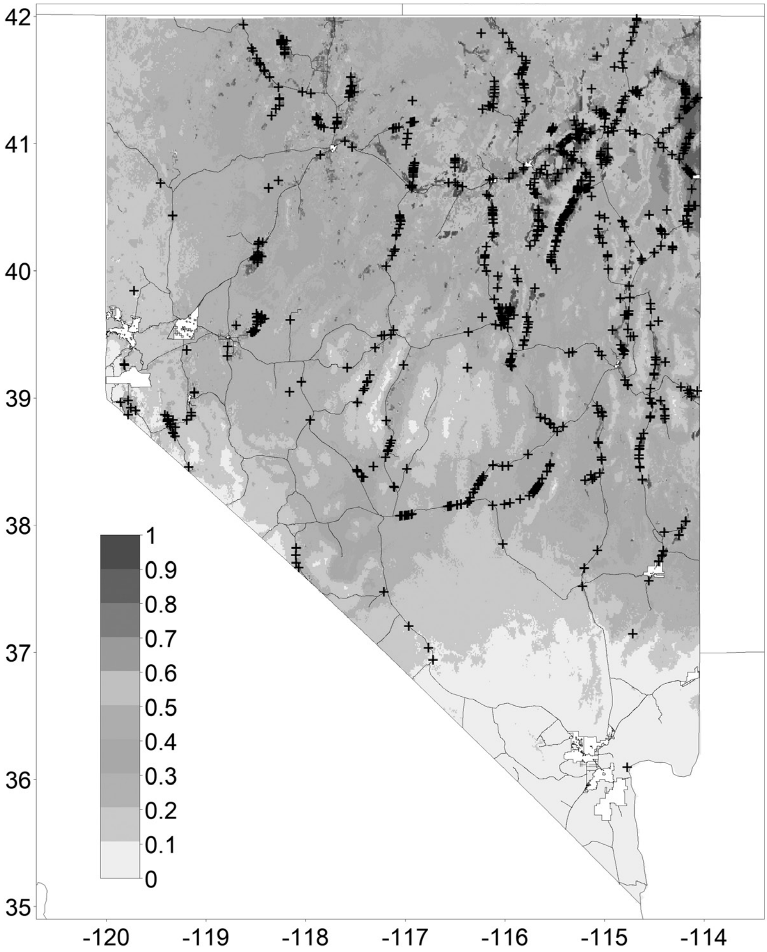

Figure 9. Predicted distribution of wintering Rough-legged Hawks in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys (2015–2017), shown with the road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in shading graduated from a probability of 0 (white) to 1 (dark gray; scale at left).

13). The most important predictor variables were the two representing cropland (positive associations), followed by those for sagebrush (negative association) and development (association positive with low to intermediate levels of development but negative with higher levels of development). The variable for pasture/hay/fallow cropland decreased the gain the most when

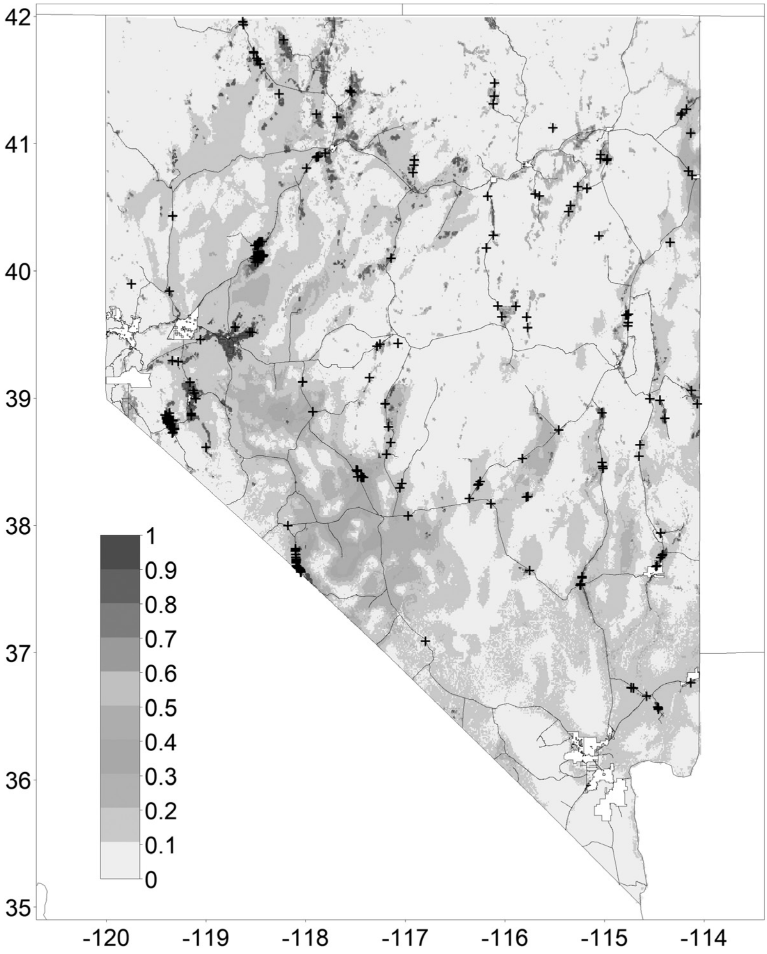

Figure 10. Predicted distribution of wintering Ferruginous Hawks in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys (2015–2017), shown with the road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in shading graduated from a probability of 0 (white) to 1 (dark gray; scale at left).

it was omitted from the full model, followed by the variable for development. Thus Prairie Falcons were most often found in areas of cropland with low to medium levels of development.

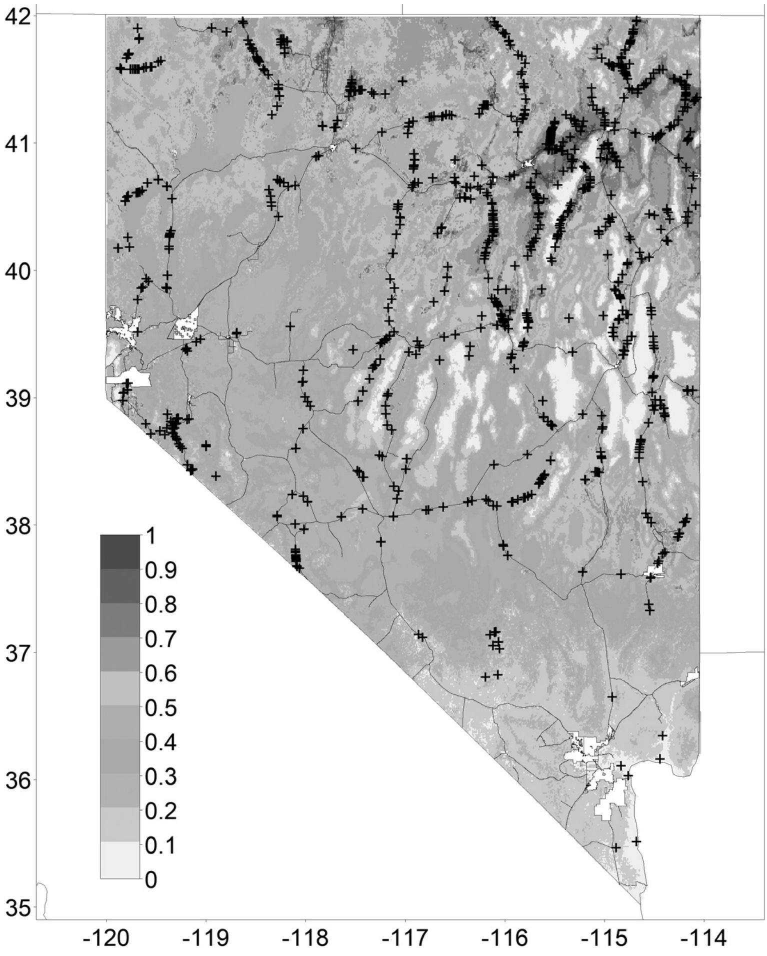

Figure 11. Predicted distribution of wintering Golden Eagles in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys (2015–2017), shown with the road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in shading graduated from a probability of 0 (white) to 1 (dark gray; scale at left).

DISCUSSION

Nevada's annual winter raptor surveys are the result of a large investment by many individuals and organizations. The project has yielded useful information on long-term trends that has improved in resolution, confidence, and application as the protocol and coordination have been refined. The result of our work is the first statewide estimate of the density of wintering

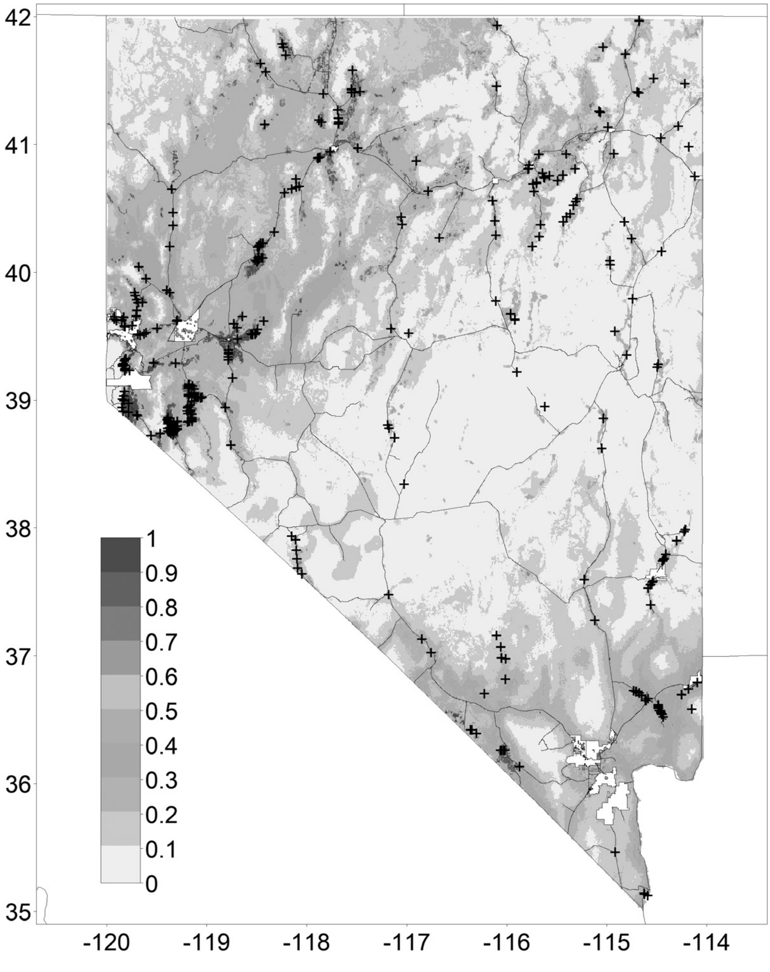

Figure 12. Predicted distribution of wintering American Kestrels in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys (2015–2017), shown with the road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in shading graduated from a probability of 0 (white) to 1 (dark gray; scale at left).

raptors in Nevada and the state's most comprehensive assessment of winter habitat associations by species. While the inference from these surveys may technically be limited to the areas surrounding the routes (road and boat), the vast coverage of the survey suggests that the density estimates we generated should be valid throughout Nevada's lower elevations, which are the areas we expect to be occupied by the majority of wintering raptors.

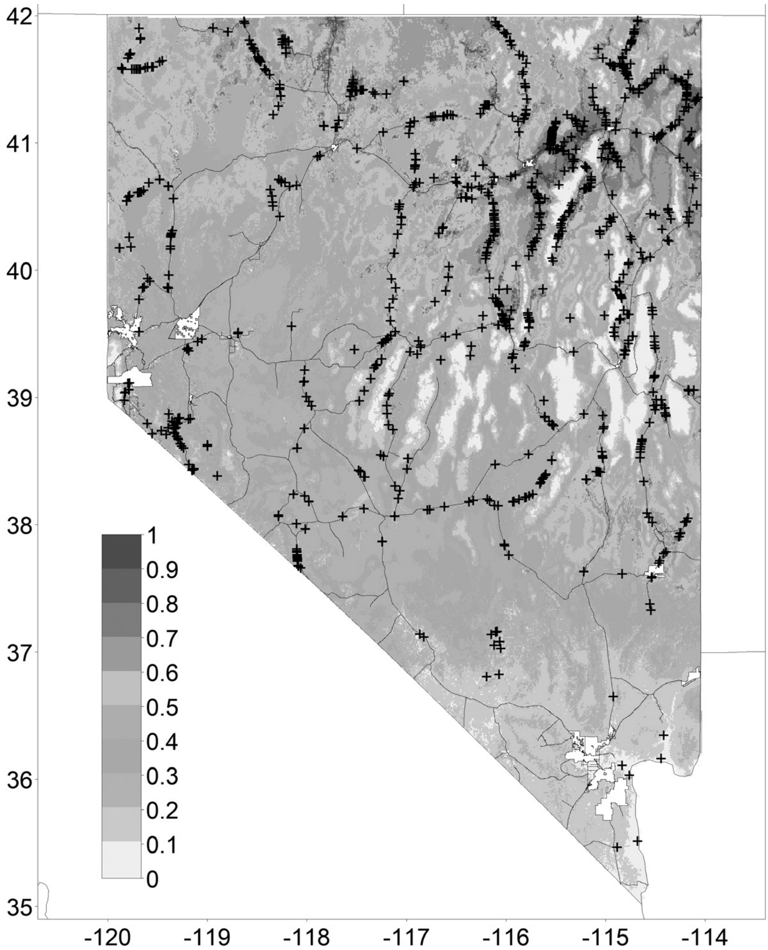

Figure 13. Predicted distribution of wintering Prairie Falcons in Nevada based upon six years of road surveys (2013–2018) and three years of boat surveys (2015–2017), shown with the road network, major cities, and survey observations (+). Predicted probability of occurrence is indicated in graduated shading from a probability of 0 (white) to 1 (dark gray; scale at left).

As with all population estimates, the interpretation of the results of winter raptor surveys is complicated by many factors including prey abundance and availability, snow cover, migration, and the annual life cycle of the species being studied. One of the more specific complicating factors is the mixing of different breeding populations into a more general wintering population. Most of the raptors that winter in Nevada are considered incomplete migrants, suggesting that the birds being counted are a mix of resident and nomadic local birds with an influx of migrants from the north. Of the species encountered most frequently, only the Rough-legged Hawk is a complete migrant, not breeding in Nevada. In spite of this, surveying winter raptor distributions may be the most efficient way to track raptor populations of multiple species over time, which may be informative over a wide geographic region. It is possible that genetic and stable-isotope analyses of feathers sampled from raptors in their winter range may point toward the birds' location of breeding or hatching (Rundel et al. 2013), which in turn may help clarify the value Nevada offers during the winter months to raptors breeding across western North America.

As each species occupies its own niche with respect to habitat and prey, broad generalizations about species' abundances are difficult to make. However, we do see some patterns that appear to be shared, most notably apparent cycles in the densities of some species. The most convincing example is the Northern Harrier, a species with close relatives that are known to respond both numerically and functionally to cyclic prey species such as voles (Salamolard et al. 2000). Our results suggest that a cycle may be six years in length, whereas longer-term data have shown variations ranging over periods of from three to six years (Hoffman and Smith 2003, Lambin et al. 2006). Since we have included only six years of data in these analyses, additional years of surveys are required to confirm a six-year cycle in the Northern Harrier. Similarly, but to a slightly lesser degree, the same six-year cycle may apply to the Rough-legged Hawk and Red-tailed Hawk, though the data are less conclusive. The Ferruginous Hawk's density may or may not be following a three-year cycle or the same six-year cycle as the other species.

The density of wintering Bald Eagles appears reasonably stable over the past six years, with no year significantly above or below the others. The wintering population of the Golden Eagle was even more stable, with the exception of 2018 being a very good year. This large increase in Golden Eagle numbers mirrors record observations of Golden Eagles on a number of winter raptor-survey routes in northwestern Utah (N. Paprocki pers. comm.). Recent increases in Black-tailed Jackrabbit (*Lepus californicus*) numbers in northeastern Nevada and northwestern Utah may be responsible for the robust numbers of Golden Eagles in 2018 (N. Paprocki and J. Barnes pers. comm.). An increase in jackrabbit numbers should influence Ferruginous Hawks positively (Smith et al. 1981), but that is not represented in our results. In Nevada, however, Ferruginous Hawks depend heavily upon ground squirrels when available (J. Barnes pers. obs.), so variation in ground squirrel abundance may have dampened the positive effect of a surge of jackrabbit populations on Ferruginous Hawk numbers. An examination of the numbers of the various prey species over time might help clarify these results.

The surprising result with the falcons is that the pattern of density variation from year to year in the Prairie Falcon and American Kestrel was nearly identical. Even densities of *Accipiter* hawks were highly correlated with the densities we detected in the Prairie Falcon and American Kestrel. We generally assume little overlap among the primary prey of these species. While the Prairie Falcon may specialize on ground squirrels during the breeding season (Steenhof et al. 1999), it may be forced into taking other prey in the winter

(White and Roseneau 1970). Speculatively, a change in the availability of prey in winter may push both the American Kestrel and Prairie Falcon into a dietary niche more similar to that of the *Accipiter* hawks.

The MaxEnt habitat models performed well for most species. The models were strongly predictive for four of the species, moderately predictive for four, and marginally predictive for only one species, the Golden Eagle. The most notable habitat variable reflected in the results was the strong positive association of all eight species with pasture/hay/fallow cropland. Furthermore, half of the species had a positive association with row or close crops, but never was this association stronger than with the pasture/hay/fallow cropland. The associations with cropland are likely the result of prey availability, as the abundance of small mammals has been shown to be greater in cropland than in surrounding shrublands (Moulton et al. 2006). Our findings are consistent with other studies that have found a strong association of many raptor species with pastures and hay (e.g., Berry et al. 1998, Pandolfino et al. 2011b), but we also found a stronger signal for half of our species with row crops. We suspect that this may have arisen because of incorrect classification in the Landfire data, and further investigation is warranted.

Many species appear to respond to development other than that related to agriculture. The *Accipiter* hawks, Red-tailed Hawk, and American Kestrel were more often found in areas with some low levels of development but were less likely in heavily developed areas. This intermediate response was also a top predictor, suggesting these species may not just tolerate development, it may be an important winter niche for them. The Northern Harrier, Rough-legged Hawk, Ferruginous Hawk, and Prairie Falcon all had strong negative associations with development. This finding is consistent with Berry et al. (1998), who also found negative associations with development in the Rough-legged Hawk, Ferruginous Hawk, and Prairie Falcon.

We had a number of observations sufficient to analyze four species classified as species of conservation priority by the state of Nevada: the Bald Eagle, Ferruginous Hawk, Golden Eagle, and Prairie Falcon. Our density estimates for these species provide some insight into the factors that may influence their densities (e.g., jackrabbits in the case of the Golden Eagle). Furthermore, we have established habitat associations for three of these species that can be used in the prioritization of conservation actions. Most notable is the dichotomous response of the Ferruginous Hawk and Prairie Falcon to human activity—positive for cropland (both types analyzed), and negative for development.

This study has a number of limitations and potential sources of bias. The most significant bias in the program is that road-survey routes are limited to roads accessible in winter and were originally developed to survey locations of known raptor aggregations. If the routes were still so constrained, this limitation would significantly bias the results of both density and habitat associations. However, the program has evolved over time to cover more routes and more habitats. The result is that much of the road network within Nevada is now covered by road-survey routes, and we limited our analysis to those later years with more complete survey coverage. Furthermore, the road network represents most of the landscape available for raptors to occupy in the winter.

The distance-sampling approach we employed assumes that the survey path (i.e., road) should be randomly placed with respect to available habitat. We failed to meet this assumption fully, as powerlines, development, and cropland are all associated with the road network. The effect of this bias is that density estimates cannot be extrapolated to absolute numbers on a statewide basis. However, they can still be used for comparisons among years and among species. The habitat associations are valid for all habitats represented adjacent to the road network.

As noted under Methods, we did our best to fill in missing information within the dataset. We believe that this approach, while introducing bias, introduces less biased than omitting the surveys that were missing key data. However, whether the data are omitted or extrapolated, the result is sure to be of lower quality than if the data are complete. Some of the missing data could not be filled in (e.g., distance to bird). In this case, the data were dropped from the distance-sampling analyses. If this happened more often along certain routes or in certain habitats, then a bias would be injected. As with many broad-scale projects that rely on various organizations, and a large number of community-science volunteers, it is critical to ensure protocols are standardized and followed closely and that appropriate quality-control measures be taken before analysis, as we have done. Though we acknowledge these limitations, our project illustrates the value the participation of a broad front of constituents can add to an broad-scale project otherwise not possible.

The last major source of bias comes from the observers. Different levels of observer skill can have a large effect on the results (Kamp et al. 2016). Some observers work in teams (suggested but not required), but some do not. We expect a wide degree of variation in observers' driving speed, which can affect detection rates, especially for distant or smaller birds. This is a bias that affects both professional surveyors and community-scientist volunteers. As have other successful community-science-based programs (e.g., Ries and Oberhauser 2015, Miller et al. 2016), we have structured this program to minimize, but not fully eliminate, these effects.

In conclusion, the winter raptor-survey programs within the state of Nevada provide valuable resources for evaluating raptor populations, habitat associations, and eventually trends. We were able to provide high-quality analyses of four of the eight raptors classified in Nevada as species of conservation priority. This analysis helped identify methods needing revision and refining, but even with the challenges of inconsistent or missing data, our results are informative. The long-term nature of these monitoring programs greatly enhances their value, and they should be continued. Furthermore, there is an opportunity to expand and collaborate over a larger area and across state boundaries, which would provide even further insight into the larger-scale distribution, trends, and habitat associations of the numerous raptor species wintering in North America.

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