

Nesting Pair Density and Abundance of Ferruginous Hawks (*Buteo regalis*) and Golden Eagles (*Aquila chrysaetos*) from Aerial Surveys in Wyoming

Author: Olson, Lucretia E.

Source: Journal of Raptor Research, 49(4) : 400-412

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/rapt-49-04-400-412.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

NESTING PAIR DENSITY AND ABUNDANCE OF FERRUGINOUS HAWKS (*BUTEO REGALIS*) AND GOLDEN EAGLES (*AQUILA CHRYSAETOS*) FROM AERIAL SURVEYS IN WYOMING

LUCRETIA E. OLSON¹

U.S.D.A., Rocky Mountain Research Station, Missoula, MT 59801 U.S.A.

ROBERT J. OAKLEAF

Wyoming Department of Game and Fish, Lander, WY 82520 U.S.A.

JOHN R. SQUIRES

U.S.D.A., Rocky Mountain Research Station, Missoula, MT 59801 U.S.A.

ZACHARY P. WALLACE AND PATRICIA L. KENNEDY

Eastern Oregon Agriculture and Natural Resource Program and Department of Fisheries and Wildlife,
Oregon State University, Union, OR 97331 U.S.A.

ABSTRACT.—Raptors that inhabit sagebrush steppe and grassland ecosystems in the western United States may be threatened by continued loss and modification of their habitat due to energy development, conversion to agriculture, and human encroachment. Actions to protect these species are hampered by a lack of reliable data on such basic information as population size and density. We estimated density and abundance of nesting pairs of Ferruginous Hawks (*Buteo regalis*) and Golden Eagles (*Aquila chrysaetos*) in sagebrush steppe and grassland regions of Wyoming, based on aerial line transect surveys of randomly selected townships. In 2010 and 2011, we surveyed 99 townships and located 62 occupied Ferruginous Hawk nests and 36 occupied Golden Eagle nests. We used distance sampling to estimate a nesting pair density of 94.7 km² per pair (95% CI: 69.9–139.8 km²) for Ferruginous Hawks, and 165.9 km² per pair (95% CI: 126.8–230.8 km²) for Golden Eagles. Our estimates were similar to or lower than those from other studies in similar locations in previous years; thus, we recommend continued monitoring to determine trends in nesting pair density over time. Additionally, we performed double-observer surveys on a subset of transects with a helicopter as the second observation aircraft. We estimated probability of detecting occupied nests from fixed-wing plane versus helicopter, as well as time and expense of each survey mode. Although observers surveying from helicopters were 1.19 and 1.12 times more likely to detect Ferruginous Hawk and Golden Eagle occupied nests, respectively, the helicopter survey was 4.55 times costlier due to longer flight time and the higher hourly costs. Thus, when systematically surveying large areas, we found cost and time of the helicopter surveys outweighed the increase in nest detection.

KEY WORDS: *Ferruginous Hawk*, *Buteo regalis*; *Golden Eagle*, *Aquila chrysaetos*; *distance sampling*; *double-observer sampling*; *grassland ecosystems*; *nesting density*; *sagebrush steppe*; *stratified random sampling*; *survey efficiency*.

DENSIDAD DE PAREJAS NIDIFICANTES Y ABUNDANCIA DE *BUTEO REGALIS* Y *AQUILA CHRYSAETOS* A PARTIR DE CENSOS AÉREOS EN WYOMING

RESUMEN.—Las aves rapaces que habitan la estepa de *Artemisa* y los ecosistemas de pastizales en el oeste de los Estados Unidos pueden estar amenazadas por la continua pérdida y modificación de su hábitat causadas por el desarrollo energético, la conversión de tierras para agricultura y la expansión humana. Las acciones encaminadas a la protección de estas especies se ven obstaculizadas por la falta de información básica como el tamaño poblacional y la densidad. Estimamos la densidad y la abundancia de parejas nidificantes de *Buteo regalis* y *Aquila chrysaetos* en regiones de estepa de *Artemisa* y pastizales en Wyoming, basados en censos aéreos de transectos lineales de municipios elegidos al azar. En 2010 y 2011 censamos 99 municipios y anotamos la

¹ Email address: lucretiaolson@fs.fed.us

ubicación de 62 nidos ocupados por parejas de *B. regalis* y 36 nidos ocupados por parejas de *A. chrysaetos*. Utilizamos la técnica de muestreos por distancia, lo que nos permitió estimar una densidad de parejas nidificantes de *B. regalis* de 94.7 km² por pareja (95% IC: 69.9–139.8 km²) y de 165.9 km² por pareja (95% IC: 126.8–230.8 km²) para *A. chrysaetos*. Nuestras estimaciones fueron similares o menores a las obtenidas en otros estudios en localizaciones similares en años anteriores; por lo tanto, recomendamos un seguimiento continuo para determinar tendencias en el tiempo en la densidad de parejas que nidifican. Además, llevamos a cabo censos de doble observador en un sub-conjunto de transectos con un helicóptero como segunda aeronave de observación. Estimamos la probabilidad de detectar nidos ocupados desde aeroplanos versus helicópteros, así como el tiempo y el coste de cada método de censo. Aunque la probabilidad de detección de nidos ocupados en observaciones desde helicópteros fue 1.19 y 1.12 veces mayor que desde aeroplanos, para *B. regalis* y *A. chrysaetos*, respectivamente, el censo con helicópteros fue 4.55 veces más caro debido a vuelos más largos y mayores costos por hora. Por lo tanto, cuando se censan grandes áreas sistemáticamente, encontramos que el costo y el tiempo de los censos mediante helicóptero no justifican el incremento en la detección de nidos.

[Traducción del equipo editorial]

Ferruginous Hawks (*Buteo regalis*) and, to a lesser extent, Golden Eagles (*Aquila chrysaetos*) rely on grassland and sagebrush steppe ecosystems for foraging and nesting. Large undisturbed areas of these ecosystems are, however, becoming increasingly rare (Noss et al. 1995, Knick et al. 2003, Brennan and Kuvlesky 2005). Anthropogenic activities, altered fire regimes, and invasive species have diminished the sagebrush steppe ecosystem to only 56% of its historic range (Davies et al. 2011), and Wyoming contains one-fourth of the remaining sagebrush steppe habitat in the United States (Knick et al. 2011). Grassland ecosystems are threatened globally, due in part to habitat modification and conversion (Brennan and Kuvlesky 2005, Hoekstra et al. 2005).

Ferruginous Hawks are grassland or desert shrub habitat specialists (Schmutz 1984) and have a distribution centered on Wyoming. Although Golden Eagles are widespread habitat generalists, the grassland and shrubland habitats in which they are sympatric with Ferruginous Hawks in Wyoming have recently experienced elevated disturbance from energy development (Copeland et al. 2011). For example, the number of producing natural gas wells in Wyoming increased from 2600 in 1990 to 22,171 in 2012, a 753% increase (U.S. Energy Information Administration 2014). A decrease in suitable, undisturbed habitat may preclude future nesting efforts by Ferruginous Hawks and Golden Eagles, both of which are sensitive to disturbance while nesting (Suter and Jones 1981, White and Thurow 1985). Both species are also susceptible to mortality from powerlines, nest destruction, and human persecution (Kochert and Steenhof 2002, Lehman et al. 2007, Millsap et al. 2015). Given these concerns, documenting current nesting pair density of these species in Wyoming is central to conservation planning.

Surveys to determine density and abundance of raptors are frequently hampered by imperfect detection or nonrandom sampling methods (Andersen et al. 1985, Andersen 2007). Raptor surveys are often conducted near or along roads due to easy access and ability to cover large areas (Fuller and Mosher 1987). Roadside surveys for raptors may be biased, however, due to influence of roads on probability of detection and/or probability of occurrence (Andersen et al. 1985, Millsap and LeFranc 1988). In contrast, density estimates based on aerial surveys of a randomly sampled population should be more accurate, provided methods are used to account for imperfect detection. Line-transect distance-sampling methods, which control for failure to detect all objects on a transect, produce estimates of true density that can be compared over space and time (Buckland et al. 1993).

A major assumption of distance sampling is that all objects that fall directly on the survey transect are detected; if this assumption is not met, density will be underestimated (Buckland et al. 1993). This assumption is, however, frequently violated when surveying from a fixed-wing plane because visibility directly under the plane is limited. Double-observer methods, in which a second observer independently surveys the same transects as the first observer, can be used to determine the probability of detection directly on the transect (Borchers et al. 1998, Good et al. 2007). The use of a helicopter to obtain a second observation should be particularly effective as the glass cockpit affords a wider range of vision directly on or near the transect. Helicopters cost much more per hour to operate, however, and fly at a slower speed than a fixed-wing plane. A study by Booms et al. (2010) found that estimates of detection probability from a fixed-wing plane were

generally similar or greater than those from a helicopter when searching for nests of cliff-nesting raptors, although their study did not conduct a direct comparison of the two. Fixed-wing planes may be less suitable when counting eggs or young, or surveying rugged terrain (Booms et al. 2010). Thus, the decision to undertake helicopter surveys must consider tradeoffs among objectives of the study, safety, and cost.

Spatial extent and location of a study area can also influence density estimates. For example, small study areas may not adequately capture large-scale spatial heterogeneity, and areas determined solely by proposed development boundaries may be biased by project location. Our study encompasses a large spatial scale, which allows us to estimate density for the majority of shrubland and grassland ecosystems in Wyoming. Previous estimates of nesting pair density for Ferruginous Hawks and Golden Eagles were derived from relatively smaller study areas (Table 3; Kochert et al. 2002). We acknowledge that changes in nesting pair density may misrepresent population trend without additional demographic information (Van Horne 1983). Therefore, our estimate of density represents only an index of population health, given our lack of knowledge of vital population rates such as recruitment or mortality.

For this study, we conducted extensive aerial surveys across sagebrush steppe and grassland habitats in Wyoming for Ferruginous Hawks and Golden Eagles in 2010 and 2011. Our main goal was to provide a current estimate of nesting pair density for these raptors from which to evaluate future trends relative to human disturbance of sagebrush steppe and grassland ecosystems. Specifically, we aimed to: (1) document nesting pair density of Ferruginous Hawks and Golden Eagles using distance sampling and double-observer methods across sagebrush steppe and grassland habitat of Wyoming, and (2) estimate detection probability of nests occupied by Ferruginous Hawks and Golden Eagles from fixed-wing plane versus helicopter. We also determined which aircraft (fixed-wing versus helicopter) was most efficient in terms of survey cost and occupied nest detection.

METHODS

Study Area. Our study area included non-mountainous sagebrush steppe and grassland regions of Wyoming, U.S.A. Because Ferruginous Hawks were the initial primary focus of the study, we further limited our study area to townships within the pre-

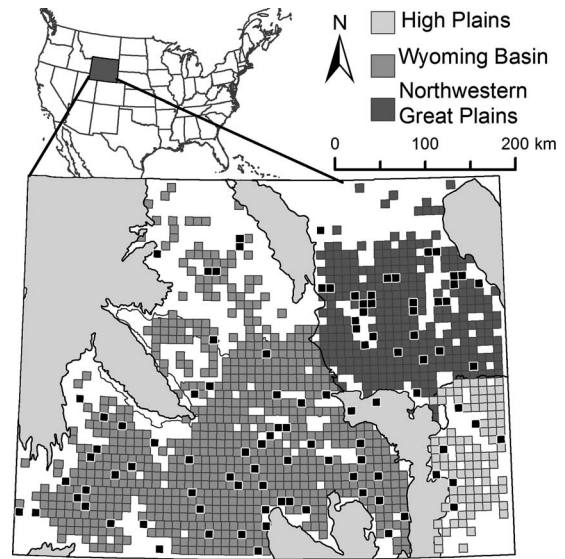


Figure 1. Study area in Wyoming, U.S.A. Detail shows our study area, comprising all townships within the distribution of Ferruginous Hawks in Wyoming, color-coded by ecoregion. Black squares indicate townships randomly selected for sampling, and outlined gray regions are mountainous areas not included in our study.

viously modeled distribution of Ferruginous Hawks in Wyoming (Keinath et al. 2010; total area = 110,112 km²; Fig. 1). We divided our study area based on level III ecoregions of Chapman et al. (2004), which categorize areas based on ecosystem similarity and environmental resources. The eastern portion of our study area, made up of the High Plains (9207 km², 99 townships) and Northwestern Great Plains (29,295 km², 315 townships) ecoregions, is primarily mixed grass prairie; the western and central portion, the Wyoming Basin ecoregion (71,610 km², 770 townships), is primarily Wyoming big sagebrush (*Artemisia tridentata*) or salt desert scrub (*Atriplex* spp.; Chapman et al. 2004). Elevation in our study area ranged from 940 masl to 2200 masl, with a mean of 1780 masl; precipitation averaged 15 cm to 40 cm per year (Knight 1996).

Survey Methods. Our sample unit was a Public Land Survey System "township," a square unit of land with an area approximately 93 km². We chose this unit to maximize our chances of detecting Ferruginous Hawks and Golden Eagles because the area is large enough to potentially incorporate home ranges of several nesting pairs of either species (Dechant et al. 2002, DeLong 2004). Potential sample townships were chosen if their centroid was

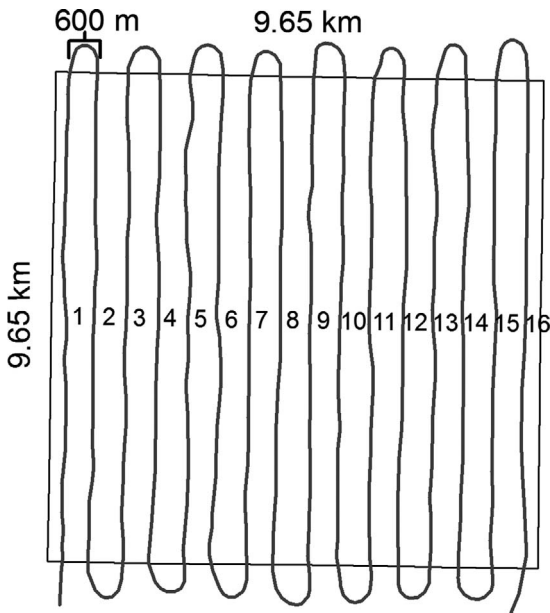


Figure 2. Diagram of the aerial survey flight lines in a survey township in Wyoming. Each transect is 9.65 km long and 600 m apart.

within the previously modeled distribution of Ferruginous Hawks in Wyoming (Keinath et al. 2010) or contained historical records of occupied Ferruginous Hawk nests. We stratified townships by geographical ecoregion (Chapman et al. 2004), with the number of townships selected for survey in each ecoregion proportional to its area. For other study objectives, we selected townships to include three oil and natural gas well densities: none (0 wells/township), low (1–30 wells/township), and high (≥ 31 wells/township), with equal numbers of townships in each stratum.

We used fixed-wing aircraft to search for Ferruginous Hawk and Golden Eagle nests in the townships in our sample between 14 April and 15 May 2010 and 2011. We flew over each township at an altitude of 60 m above ground level and an average approximate speed of 130 km/hr, following 16 parallel north–south transects the length of the township sample unit (9.54 km) with a spacing of 600 m to ensure complete coverage (Fig. 2). To account for possible nonindependence between transects, we treated the 16 north–south transects in each township as a single transect 153.6 km long (16×9.54 km). Surveys were conducted with two fixed-wing planes (Bellanca Scout and Piper PA 18), each

carrying one pilot and one technician, both of whom contributed to nest detection simultaneously; all had previous experience detecting raptors. We used GPS units to record actual flight paths and mark locations of all observed stick nests. We calculated distance to each nest by plotting recorded nest locations in ArcGIS v. 10.0 (ESRI, Redlands, California, U.S.A.) and measuring perpendicular distance from the nest to the transect. We recorded species and status of all stick nests located; we defined an “occupied” Ferruginous Hawk or Golden Eagle nest as one that contained eggs, young, incubating, or defending adults (Steenhof and Newton 2007); we refer to “unoccupied” nests as any nest that does not meet these criteria, including nests that were dilapidated or in disrepair, as long as they could still be distinguished by observers as a stick nest.

On a subset of townships ($n = 57$) in 2010, we resampled approximately 32 km of the transect in a helicopter (Bell 47 Soloy), flying at 80 km/hr and following the same flight path as the fixed-wing plane for three lengths of the township, with start point randomly selected prior to the survey. The helicopter pilot and a single observer acted as a team to record nest status and location using the same methods as the fixed-wing plane; the same pilot and observer performed all helicopter flights. We used GPS flight tracks and nest locations recorded during both fixed-wing and helicopter surveys to determine which nests were detected during one or both surveys. We plotted the location of all nests using ArcGIS, and considered nests to be repeat detections if they were within 100 m of each other and located on the same nest substrate. Helicopter surveys took place an average of 8 d (SD = 9.8 d) before or after the fixed-wing plane survey; given this short lag-time, we expected violations of the assumption of demographic closure between survey occasions to be minimal. Nonetheless, we further accounted for the possibility that nest failure or establishment occurred between survey occasions by considering detections of unoccupied nest structures during one survey as successful repeat detections if the unoccupied nest was located ≤ 100 m from an occupied nest detected during the other survey. We assume independence between the helicopter survey and the fixed-wing because surveys did not take place at the same time and surveyors did not share nest locations.

Nesting Pair Density Estimation. *Distance sampling.* We used distance sampling to estimate nesting pair density for each species over the entire study

area and within each geographic ecoregion (Buckland et al. 1993, Pollock et al. 2002). We binned distance data into 50-m intervals to account for location inaccuracy from GPS points taken while in the air, and truncated the top 5% of distances to avoid a long-tailed distribution (Thomas et al. 2010). To determine whether data between years 2010 and 2011 could be pooled, we performed a separate distance analysis for each year, and compared detection probabilities from the two years using a two-sample *t*-test with the statistical software R (R Core Team 2013).

We used program DISTANCE (Thomas et al. 2010) to calculate separate detection functions for Ferruginous Hawk and Golden Eagle occupied nests detected from the fixed-wing plane. We calculated nesting pair density separately for each ecoregion to investigate regional differences in abundance; however, sample sizes were insufficient to calculate region-specific detection functions. Therefore, we followed Thomas et al. (2010) and used the "Multiple Covariates Distance Sampling" engine in program DISTANCE to estimate a single detection function for the entire study area, and used this detection function to estimate nesting pair density separately for each region. Half-normal and hazard-rate detection functions with cosine and simple polynomial expansions were considered to model the detection function that best fit our data. We ranked models using Akaike's Information Criterion for small sample sizes (AIC_c; Akaike 1973) and chose the model with the lowest value as the best fitting (Burnham and Anderson 2002).

We calculated density using the following equation, based on Buckland et al. (1993):

$$\hat{D} = \frac{n}{\hat{g}(W_1)2L\mu}$$

where n is the number of occupied nests, $\hat{g}(W_1)$ is the probability of detecting an occupied nest on the transect line, L is the length of the surveyed transect, and μ is the effective strip width as determined by distance modeling. This equation compensates for nests missed at the transect line, as well as imperfect detection that increases with distance from the transect line (Good et al. 2007). To determine $\hat{g}(W_1)$, the probability of detecting an occupied nest on the transect line, we used a logistic regression model with data from transects that were surveyed by both fixed-wing plane and helicopter (Good et al. 2007). We treated occupied nests detected

while in the helicopter as random samples of Ferruginous Hawk and Golden Eagle nests available for detection. For each occupied nest detected by helicopter, we determined whether fixed-wing aircraft had detected or missed the nest, and used this binary value as the dependent variable; we used the distance of each occupied nest from the transect as the predictor variable. We then used the resulting equation to predict probability of detection at distance 0 for the fixed-wing plane.

We estimated variance around nesting pair density using a bootstrap procedure. We sampled individual transects within ecoregions with replacement 1000 times and calculated nesting pair density from the resulting number of occupied nests for each iteration. We performed this procedure separately for transects within each ecoregion and then summed occupied nests from all ecoregions for a density estimate over all grassland and shrubland ecosystems in our study area. We then used the middle 95% of the distribution of these values as a 95% confidence interval (Good et al. 2007, Manly 2007). We calculated nesting pair abundance based on this density estimate and total area of each region.

Double-observer sampling. Before beginning our survey, we considered the possibility that we would not locate enough occupied nests using the fixed-wing plane to accurately estimate nesting pair density using distance sampling methods. Therefore, we used a separate approach based on double-observer methods similar to Nichols et al. (2000), but with temporally sequential rather than simultaneous observers (Conway and Simon 2003), to calculate a second set of detection probabilities for each species from the fixed-wing plane. This method estimates probability of detection for primary and secondary observers based on number of occupied nests each detects as well as the number one detects and the other misses. We considered our primary observer to be the team in the fixed-wing plane and our secondary observer to be the team in the helicopter; observers were temporally separated by an average of 8 d, which we assumed to be a sufficient lag-time to ensure independence between observers while maintaining closure in the population. We calculated probability of detection from the plane as the number of occupied nests detected by both survey methods divided by total number of occupied nests detected only by helicopter. We calculated probability of detection from the helicopter as the number of occupied nests detected by both survey methods divided by total number of occupied nests detected

only by plane. We estimated variance following Equation 8 in Nichols et al. (2000). We then used these probabilities of detection to calculate nesting pair density using all occupied nests detected by the fixed-wing plane on all surveyed townships with the following equation:

$$\hat{D} = \frac{n}{LW\hat{P}}$$

where n is the number of occupied nests detected per township, L is township length, W is township width, and $\hat{P}$ is detection probability as estimated by the double-observer method. Variance for this nesting pair density estimate was estimated using the same bootstrap procedure detailed above.

Survey Efficiency. We also used our double-observer data to determine relative ability of observation teams in helicopters versus fixed wing planes to detect occupied nests. Based on double-observer probabilities of detection, we calculated amount of time each survey mode took per occupied nest, cost per occupied nest, and relative efficiency based on their differing probabilities of detecting an occupied nest. We included only occupied nests located on the subset of transects that were surveyed by both fixed-wing plane and helicopter. We summed total distance included in the double-observer survey, and used this to determine how long each survey mode took based on its average speed. We divided this survey time by number of occupied nests detected by each survey mode to determine survey time per occupied nest.

RESULTS

Ferruginous Hawks. We surveyed 60 townships from 15 April to 14 May 2010 and 39 additional townships from 18 April to 7 May 2011. In total, we surveyed approximately 15,206 km of transects and found 62 occupied Ferruginous Hawk nests within the 99 surveyed townships. We located 46 occupied nests in 2010 and 16 occupied nests in 2011 from the fixed-wing plane. Of these, five were in the High Plains, 14 were in the Northwestern Great Plains, and 43 were in the Wyoming Basin (Fig. 3). Occupied Ferruginous Hawk nests were located on a variety of substrates including 17 on artificial nest platforms, 12 ground nests, 13 on rocks or rims, and 20 in trees (13 in narrowleaf cottonwood (*Populus angustifolia*), four in junipers (*Juniperus* spp.), and three in other deciduous trees).

Distance sampling. In 2010, probability of detection as determined by program DISTANCE was 0.66

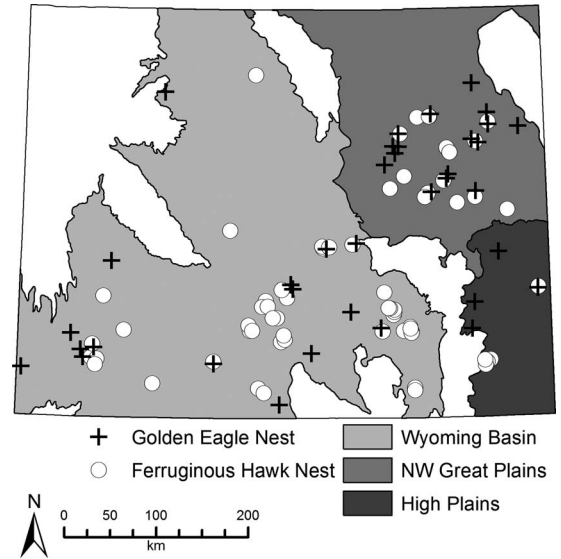


Figure 3. Occupied Ferruginous Hawk and Golden Eagle nests detected during surveys in 2010 and 2011 in shrubland and grassland habitat in Wyoming, U.S.A.

(SE = 0.05), and in 2011 probability of detection was 0.68 (SE = 0.13). We found no difference in detection probability between 2010 and 2011 ($P = 0.83$, $t = 0.215$, $df = 66$); thus, we pooled data over both years for the rest of the analysis.

Detection probability of occupied nests from the fixed-wing plane on the transect line as estimated by logistic regression was 0.71 (95% CI: 0.25–0.95). Based on AIC_c we selected a half-normal key function with a cosine expansion to model the detection function for Ferruginous Hawks. The global detection probability associated with the distance analysis of both years combined was 0.55 (95% CI: 0.45–0.66), and effective strip width on transects was 273.5 m. We estimated a total density of 94.7 km^2 per nesting pair (95% CI: 69.9–139.8 km^2) in our study area. From this density, we calculated a total of 1163 nesting pairs of Ferruginous Hawks (95% CI: 788–1575 pairs) in our study area during the 2010–2011 nesting seasons (Table 1).

Double-observer sampling. On double-observer surveyed transects ($n = 57$), we detected a total of 30 occupied Ferruginous Hawk nests from fixed-wing plane and helicopter combined. Of the 30 occupied nests found, 18 were detected by both plane and helicopter, eight were detected by helicopter but not plane, and four were detected by plane but not helicopter. We estimated a detection probability

Table 1. Nesting pair density and abundance estimates of Ferruginous Hawks in our Wyoming study area by ecoregion, 2010–2011. The upper table provides estimates from distance analysis, lower table is results from the double-observer survey.

ANALYSIS	REGION	NO.	NO. OCCUPIED	NESTING PAIR	NESTING	ABUNDANCE	ABUNDANCE
		TOWNSHIPS SAMPLED	NESTS DETECTED	DENSITY (km ² /PAIR)	PAIR DENSITY 95% CI	OF NESTING PAIRS	OF NESTING PAIRS 95% CI
Distance analysis	High Plains	7	5	83.0	31.9–404.8	110.9	22.8–288.4
	Northwestern	30	14	127.1	84.7–222.4	230.5	131.7–345.8
	Great Plains						
	Wyoming Basin	62	43	85.5	58.4–141.4	837.4	506.3–1226.8
	Total	99	62	94.7	69.9–139.8	1162.8	787.6–1575.3
Double-observer survey	High Plains	7	5	89.0	34.2–404.8	103.4	22.8–268.9
	Northwestern	30	14	131.7	87.8–230.5	222.4	127.1–333.6
	Great Plains						
	Wyoming Basin	62	43	90.2	61.6–149.2	793.8	480.0–1163.1
	Total	99	62	99.5	73.4–146.9	1106.8	749.8–1499.6

of 0.69 (SE = 0.023) from the fixed-wing plane and 0.82 (SE = 0.021) from the helicopter. The joint probability of detection from both survey modes was 0.94 (SE = 0.041). Using the fixed-wing plane probability of detection and occupied nests from all surveyed transects ($n = 62$ nests), we estimated a density of 99.5 km² per nesting pair (95% CI: 73.4–146.9) and an abundance of 1107 (95% CI: 750–1500) nesting pairs of Ferruginous Hawks in the study area (Table 1).

Golden Eagles. For Golden Eagles, we located 36 occupied nests during surveys of all 99 townships; 20 in 2010 and 16 in 2011. We found four occupied nests in the High Plains region, 16 in the Northwestern Great Plains region, and 16 in the Wyoming Basin (Fig. 3). Fourteen of the 36 occupied nests were found on cliffs, 17 in cottonwood trees, one on a man-made structure, and four on rocks or rims.

Distance sampling. Due to small sample sizes, we could not reliably estimate a detection function for each year to determine whether years could be pooled. We decided to proceed on the assumption that detectability of Golden Eagles was constant across years because this was true for Ferruginous Hawks, and the same survey methods and observers were used for both species in both years. Thus, we pooled detection data for Golden Eagles over years.

Detection probability of occupied nests from the fixed-wing plane on the transect line as estimated by logistic regression was 0.74 (95% CI: 0.20–0.97). We selected a half-normal key function with a cosine expansion to model the detection function for Golden Eagles. The global detection probability as-

sociated with the combined distance analysis of both years was 0.59 (95% CI: 0.44–0.78), and effective strip width was 235.3 m. We estimated a mean density of one nesting pair per 165.9 km² (95% CI: 126.8–230.8 km²) across all ecoregions, and a total of 664 nesting pairs of Golden Eagles (95% CI: 477–868 pairs) within our study area during the 2010–2011 nesting seasons (Table 2).

Double-observer sampling. On double-observer surveyed transects, we detected 13 occupied Golden Eagle nests. Of occupied nests, six were detected by both fixed-wing plane and helicopter surveys, four were detected by helicopter but not plane, and three were detected by the plane but missed by the helicopter. Detection probability from the plane was 0.60 (SE = 0.061) and from the helicopter 0.67 (SE = 0.062); combined detection probability was 0.87 (SE = 0.12). Using the fixed-wing plane probability of detection and occupied nests from all surveyed transects ($n = 36$ nests), we estimated a density of 149.0 km² per nesting pair (95% CI: 127.7–233.2 km²) and a nesting pair abundance of 739 (95% CI: 472–862) Golden Eagles in the study area (Table 2).

Survey Efficiency. Our average flight speed during nest surveys was 130 km/hr in the plane and 80 km/hr in the helicopter. The cost per hour for the plane and the helicopter increased annually but the helicopter averaged 2.8 times more expensive per hour than the plane (helicopter: \$650/hr in 2010, \$700/hr in 2011; plane: \$230/hr in 2010, \$250/hr in 2011). Based on a flight distance of 32.3 km per township, after 57 townships surveyed, the helicop-

Table 2. Nesting pair density and abundance estimates of Golden Eagles in our Wyoming study area by ecoregion, 2010–2011.^a The upper table provides estimates from distance analysis, lower table is results from the double-observer survey.

ANALYSIS	REGION	NO. TOWNSHIPS SAMPLED	NO. OCCUPIED NESTS DETECTED	NESTING PAIR DENSITY (km ² /PAIR)	NESTING PAIR DENSITY 95% CI	ABUNDANCE OF NESTING PAIRS	ABUNDANCE OF NESTING PAIRS 95% CI
Distance analysis	High Plains	7	4	93.9	62.6–375.4	98.1	24.5–147.2
	Northwestern	30	16	100.6	70.0–160.9	291.4	182.1–488.7
	Great Plains						
	Wyoming Basin	62	16	277.1	184.7–554.1	258.5	129.2–387.7
	Total ¹	99	36	165.9	126.8–230.8	663.7	477.1–868.3
Double-observer survey	High Plains	7	4	96.8	64.5–387.1	95.1	23.8–142.7
	Northwestern	30	16	100.2	69.7–160.4	292.3	182.7–420.2
	Great Plains						
	Wyoming Basin	62	16	281.1	187.4–562.2	254.8	127.4–382.1
	Total ^a	99	36	149.0	127.7–233.2	739.1	472.2–862.2

^a Nesting pair density and abundance estimates only pertain to Golden Eagles nesting in sagebrush steppe and grassland; pairs nesting in mountainous habitat were not sampled.

ter took 1.63 times as long to complete the survey as the fixed wing plane. Thus, the helicopter cost 4.55 times more than the plane for the same survey, after multiplying survey time by cost. In terms of detection probability, the observers surveying in a helicopter were 1.19 times more likely than those in a survey plane to detect an occupied Ferruginous Hawk nest, and 1.12 times more likely to detect an occupied Golden Eagle nest. During the double-observer survey, the observers surveying by plane detected a total of 22 occupied Ferruginous Hawk nests and nine occupied Golden Eagle nests, whereas those in the helicopter detected 26 occupied Ferruginous Hawk nests and 10 occupied Golden Eagle nests. Based on 2011 rates, cost per occupied Ferruginous Hawk nest for the helicopter survey was 3.85 times greater than for the fixed-wing plane. The cost per occupied nest for Golden Eagles was 4.09 times greater for the helicopter than the survey plane.

DISCUSSION

We used both line-transect distance sampling and double-observer sampling methods to determine nesting pair density of Ferruginous Hawks and Golden Eagles throughout the distribution of Ferruginous Hawks in Wyoming. Because we accounted for probability of detection in our model, our estimates can be used for direct comparison with nesting pair density estimates from other areas. Our stratified random sampling scheme allowed us to make inference to the entire distribution of

Ferruginous Hawks in the state of Wyoming, and provide estimates of nesting pair density for both species that will be useful for assessing current status of nesting pairs and as a baseline for future monitoring.

Our total estimate of 94.7 km² per Ferruginous Hawk nesting pair suggests that density of nesting Ferruginous Hawks in Wyoming is slightly lower than previous nesting pair density estimates across the range of the species (Table 3). Numerous studies have indicated Ferruginous Hawk populations may be in decline (Woffinden and Murphy 1989, Schmutz et al. 1992, Olendorff 1993), with potential causes given as increased disturbance and loss of habitat from energy development and agriculture (Woffinden and Murphy 1977, Houston and Bechard 1984). Energy development is extensive across Wyoming, and is particularly intense within the distribution of Ferruginous Hawks (Keinath et al. 2010, Wyoming Oil and Gas Conservation Commission 2014). Our estimates document abundance of nesting Ferruginous Hawks and Golden Eagles given current levels of energy-related disturbance, and provide a benchmark for comparison as development continues to increase in our study area.

For Golden Eagles, we found one nesting pair per 165.9 km² over our total survey area. Our study area and regional estimates of nesting pair density are generally lower than those from previous studies (Kochert et al. 2002). For instance, Phillips et al. (1984) found an average of one nesting pair per 60 km² over 12 survey areas in Wyoming, with

Table 3. Nesting pair density estimates for Ferruginous Hawks over their distribution in western North America.

STUDY LOCATION	YEAR(s)	STUDY AREA SIZE (km ²)	DENSITY (km ² /PAIR)	RANDOM SAMPLING?	ADJUSTED FOR DETECTION?	SOURCE
North-central Utah ^a	1966–1969	207	20.1	No	No	Smith and Murphy (1973)
Southern Idaho/ northern Utah	1972–1973	2800	33.8–45.8	No	No	Howard and Wolfe (1976)
West-central Utah	1972–1974	238	14.9–34.0	No	No	Woffinden and Murphy (1977)
North-central South Dakota	1973–1974	269	17.4	No	No	Lokemoen and Duebber (1976)
Central North Dakota	1977–1979	16,519	16.7	Yes	No	Gilmer and Stewart (1983)
Western Kansas	1979–1987	31,652	316.5	No	No	Roth and Marzluff (1989)
Western Kansas	1979–1987	6649	71.5	No	No	Roth and Marzluff (1989)
Southeastern Alberta	1982	74,686	66.7	Yes	No	Schmutz (1984)
Southeastern Alberta	1987	74,686	41.4	Yes	No	Schmutz and Hungle (1989)
South-central Wyoming ^a	1993–1994	783	20.1–31.3	No	No	Ayers and Anderson (1999)
Central and east Wyoming	2014	110,112	94.7	Yes	Yes	current study

^a Density estimates from these sources were calculated using counts of occupied nests and study area size given in the paper.

a range of 34–89 km² per survey area, while Camenzind (1969) found 100–119 km² per pair in Utah, and Kochert (1972) found 66 km² per pair in south-west Idaho. This difference may be due in part to the low abundance of leporids, which are the main prey of Golden Eagles (MacLaren et al. 1988), during our study. Abundance of jackrabbits (*Lepus* spp.) and cottontail rabbits (*Sylvilagus* spp.) in Wyoming has been shown to follow an approximate 7- to 8-yr cycle (Gross et al. 1974, Fedy and Doherty 2011), although in recent years the population does not appear to have reached the peak in numbers seen previously (Oakleaf et al. 2014). Based on Fedy and Doherty (2011), the last population peak was in 2006, which indicates a low in population abundance should have occurred during our study period in 2010 or 2011. Additionally, because our survey was limited to the known distribution of Ferruginous Hawks in Wyoming, the density estimate we provide for Golden Eagles includes only those nesting in sagebrush steppe and grassland communities; eagles nesting in mountainous terrain were not included in this population estimate (Kochert et al. 2002).

Our results represent only an index of population health, as actual estimates of population vital rates are not available. Nesting pair density may underestimate the actual population of adults capable of reproduction, as territory availability or breeding opportunity may force some adult raptors into non-

breeding “floater” status (Hunt 1998). Ayers et al. (2009) found several nonbreeding Ferruginous Hawks and 11 breeding pairs in a 783 km² study area near Baggs, Wyoming, whereas Schmutz et al. (2008) found no evidence of a nonbreeding adult population of Ferruginous Hawks in a study in western Canada. Golden Eagles have been generally found to maintain floaters in most populations (Kochert et al. 2002). Anecdotal results from our study agree with these findings: during surveys in 2010 we recorded 101 Golden Eagles and 13 Ferruginous Hawks that were perched or soaring and seemingly not associated with a nest. Thus, our estimate of nesting pair density may be a conservative estimate of the entire adult Ferruginous Hawk or Golden Eagle population, depending on the unknown abundance of nonbreeding adults.

Nesting pair density estimates for Ferruginous Hawks were highest in the Wyoming Basin, while Golden Eagle densities were highest in the North-western Great Plains and High Plains. Estimated densities for the two species were similar in the Northwestern Great Plains and High Plains eco-regions, but Ferruginous Hawks were approximately three times as abundant as Golden Eagles in the Wyoming Basin. The Wyoming Basin is composed largely of sagebrush communities, while the North-western Great Plains is made up of mixed-grass prairie. Both areas have extensive oil and gas development, and are otherwise relatively sparsely

populated by humans. As mitigation for creating habitat disturbance, energy companies and government agencies erect artificial nesting structures within oil and gas fields. The higher densities of Ferruginous Hawks we found in the Wyoming Basin region may therefore be related to an abundance of anthropogenic nesting structures. Identifying causes of regional differences in density for these species, however, was beyond the scope of this study.

Our estimates of occupied nest density for both species may also have been influenced by nest substrate. Ayers and Anderson (1999) found that nest substrate had the greatest effect on detection probability of Ferruginous Hawks from a fixed-wing plane. Differences in detectability due to nest substrate could have produced unmodeled heterogeneity in our sample; however, small sample sizes limited our ability to include nest substrate as a detection covariate. Ferruginous Hawks nest on a variety of substrates, including hill tops, small rock structures, lone trees, and artificial nest platforms (Bechard et al. 1990, Woffinden and Murphy 1983). We found nests on all of these substrates during our study, which may have contributed to uncertainty in our detection estimates.

Within the northern portion of the Wyoming Basin, known as the Bighorn Basin, we found only one occupied Golden Eagle nest and one occupied Ferruginous Hawk nest in seven sampled townships. The Bighorn Basin is composed largely of salt desert shrub, rather than sagebrush steppe (Chapman et al. 2004), and does not support many mammalian prey species common to the southern portion of the Wyoming Basin, including pygmy rabbits (*Brachylagus idahoensis*), and Uinta (*Urocitellus armatus*), Wyoming (*Urocitellus elegans*), golden-mantled (*Callospermophilus lateralis*), and thirteen-lined ground squirrels (*Ictidomys tridecemlineatus*; Knick et al. 2011, Orabona et al. 2012, Thorington et al. 2012). Although white-tailed prairie dogs (*Cynomys leucurus*) occur in the Bighorn Basin, their abundance is much lower than in the southern portion of the Wyoming Basin (Grenier and Filipi 2009). Although we sampled few townships in this area, the lack of occupied nests found may be related to the scarcity of these prey, which make up a large portion of the diets of both Ferruginous Hawks and Golden Eagles (MacLaren et al. 1988).

The use of a helicopter for a second observer on a subset of transects provided a valuable correction to our nesting pair density estimates using distance sampling. Our regression of fixed-wing plane

detections and misses over distance suggested the fixed-wing plane was not adequately detecting all occupied nests directly on the transect, an omission which violates a key assumption of distance modeling. With corrected probability of detection at the transect, however, distance sampling density estimates were very similar to our second set of density estimates using double-observer detection probability. This agreement between results of the two methods provides confidence in our estimates of nesting pair density for both species. Correction for imperfect detection at the transect line can be accomplished with a variety of methods (Alpizar-Jara and Pollock 1996, Quang and Becker 1997, Borchers et al. 1998, Laake et al. 2008). This type of correction is frequently used to improve distance sampling estimates in marine mammal research (Borchers et al. 2006, Pollock et al. 2006) and increasingly in a variety of terrestrial taxa (Kissling and Garton 2006, Buckland et al. 2007, Fewster and Pople 2008). Based on our results, we recommend inclusion of one of these types of correction to model detection at the transect when surveying in fixed-wing planes.

The efficiency of the observers in the helicopter at detecting occupied nests was insufficient to justify the added cost or time of helicopter surveys for estimating density in our study. There was a small difference in detection of occupied Ferruginous Hawk nests between observers in the fixed-wing plane and those in the helicopter, but detection probabilities were almost equal for Golden Eagles. This could be due to the larger size and conspicuousness of Golden Eagles and their occupied nests in the sagebrush steppe and grassland landscape, as both survey modes had a high probability of detecting an occupied Golden Eagle nest. Occupied Ferruginous Hawk nests were more likely to be located by the helicopter, but not enough to make up for the disparity in cost and time between the two modes. Thus, if time to completion or cost are limiting aspects of a survey, a fixed-wing plane will better meet these needs with little loss of detection ability. The results of our comparison, however, are based on linear transects over relatively smooth terrain, which may reduce the relative advantage of using a helicopter. In rugged terrain or with an active search, helicopters may be superior in safety and efficiency due to their greater maneuverability and visibility. Additionally, the efficiency and cost of both survey modes will likely be influenced by several outside factors, including existing occupied nest density, experience of observers, and habitat

type. Thus, the decision to use a fixed-wing plane or helicopter should be determined not only by cost or detection ability, but by considerations of survey objectives, visibility and maneuverability requirements, and safety concerns.

ACKNOWLEDGMENTS

Primary research support was provided by the U.S.D.A. Rocky Mountain Research Station, Bureau of Land Management, and Wyoming Game and Fish Department. Additional funding sources include Wyoming Wildlife Heritage Foundation; PacifiCorp; Pathfinder Renewable Wind Energy, LLC; and the Wyoming Governor's Office. Elizabeth Furtaw provided essential GIS support. Pilots Dave Savage (Savage Air Service, Inc.), Ken Overfield (Sky Aviation, Corp.), Dave Stinson (Sky Aviation, Corp.), and Neil Cadwell (Elkhorn Aviation, LLC) were pivotal in project completion. Bob Oakleaf served as primary observer in the helicopter, Zach Wallace and Matt Wilson as primary observers for fixed-wing aerial surveys of transects and leaders of the field crews, which included Roderick Lawrence, Jon Lipke, and Ray Buchheit.

LITERATURE CITED

- AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 in B.N. Petrov and F. Caski [EDS.], Second international symposium on information theory. Akademiai Kiado, Japan.
- ALPIZAR-JARA, R. AND K.H. POLLOCK. 1996. A combination line transect and capture-recapture sampling model for multiple observers in aerial surveys. *Environmental and Ecological Statistics* 3:311–327.
- ANDERSEN, D.E. 2007. Survey techniques. Pages 89–100 in D. Bird and K. Bildstein [EDS.], Raptor research and management techniques. Hancock House Publishers, Blaine, WA U.S.A.
- , O.J. RONGSTAD, AND W.R. MYTTON. 1985. Line transect analysis of raptor abundance along roads. *Wildlife Society Bulletin* 13:533–539.
- AYERS, L.W. AND S.H. ANDERSON. 1999. An aerial sightability model for estimating Ferruginous Hawk population size. *Journal of Wildlife Management* 63:85–97.
- , R.J. OAKLEAF, AND T. FILIPI. 2009. Distribution and abundance of breeding Ferruginous Hawk pairs in southcentral Wyoming. Completion report. Pages 72–85 in A. Orabona [ED.], Threatened, endangered, and nongame bird and mammal investigations. Wyoming Game and Fish Department, Laramie, WY U.S.A.
- BECARD, M.J., R.L. KNIGHT, D.G. SMITH, AND R.E. FITZNER. 1990. Nest sites and habitats of sympatric hawks (*Buteo* spp.) in Washington. *Journal of Field Ornithology* 61:159–170.
- BOOMS, T.L., P.F. SCHEMPF, B.J. MCCAFFERY, M.S. LINDBERG, AND M.R. FULLER. 2010. Detection probability of cliff-nesting raptors during helicopter and fixed-wing aircraft surveys in western Alaska. *Journal of Raptor Research* 44:175–187.
- BORCHERS, D.L., W. ZUCCHINI, AND R.M. FEWSTER. 1998. Mark-recapture models for line transect surveys. *Biometrics* 54:1207–1220.
- , J.L. LAAKE, C. SOUTHWELL, AND C.G.M. PAXTON. 2006. Accommodating unmodeled heterogeneity in double-observer distance sampling surveys. *Biometrics* 62:372–378.
- BRENNAN, L.A. AND W.P. KUVLESKY. 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69:1–13.
- BUCKLAND, S.T., D.R. ANDERSON, K.P. BURNHAM, AND J.L. LAAKE. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London, U.K.
- , D.L. BORCHERS, A. JOHNSTON, P.A. HENRYS, AND T.A. MARQUES. 2007. Line transect methods for plant surveys. *Biometrics* 63:989–998.
- BURNHAM, K.P. AND D.R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, NY U.S.A.
- CAMENZIND, F.J. 1969. Nesting ecology and behavior of the Golden Eagle *Aquila chrysaetos* L. *Brigham Young University Science Bulletin, Biological Series* 10:4–15.
- CHAPMAN, S.S., S.A. BRYCE, J.M. OMERNIK, D.G. DESPAIN, J. ZUMBERGE, AND M. CONRAD. 2004. Ecoregions of Wyoming (color poster with map, descriptive text, summary tables, and photographs). U.S. Geological Survey, Reston, VA U.S.A.
- CONWAY, C.J. AND J.C. SIMON. 2003. Comparison of detection probability associated with Burrowing Owl survey methods. *Journal of Wildlife Management* 67:501–511.
- COPELAND, H.E., A. POCEWICZ, AND J.M. KIESECKER. 2011. Geography of energy development in western North America: potential impacts on terrestrial ecosystems. Pages 7–22 in D.E. Naugle [ED.], Energy development and wildlife conservation in western North America. Island Press/Center for Resource Economics, Washington, DC U.S.A.
- DAVIES, K.W., C.S. BOYD, J.L. BECK, J.D. BATES, T.J. SVEJCAR, AND M.A. GREGG. 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573–2584.
- DECHANT, J.A., M.L. SONDRAL, D.H. JOHNSON, L.D. IGL, C.M. GOLDADE, A.L. ZIMMERMAN, AND B.R. EULISS. 2002. Effects of management practices on grassland birds: Ferruginous Hawk. Northern Prairie Wildlife Research Center, Jamestown, ND U.S.A.
- DELONG, J.P. 2004. Effects of management practices on grassland birds: Golden Eagle. Northern Prairie Wildlife Research Center, Jamestown, ND U.S.A.
- FEDY, B.C. AND K.E. DOHERTY. 2011. Population cycles are highly correlated over long time series and large spatial scales in two unrelated species: Greater Sage-Grouse and cottontail rabbits. *Oecologia* 165:915–924.

- FEWSTER, R.M. AND A.R. POPE. 2008. A comparison of mark-recapture distance-sampling methods applied to aerial surveys of eastern grey kangaroos. *Wildlife Research* 35:320–330.
- FULLER, M.R. AND J.A. MOSHER. 1987. Raptor survey techniques. Pages 37–65 in B.A. Giron Pendleton, B.A. Millspaugh, K.W. Cline, and D.M. Bird [Eds.], *Raptor management techniques manual*. National Wildlife Federation, Washington, DC U.S.A.
- GILMER, D.S. AND R.E. STEWART. 1983. Ferruginous Hawk populations and habitat use in North Dakota. *Journal of Wildlife Management* 47:146–157.
- GOOD, R.E., R.M. NIELSON, H.H. SAWYER, AND L.L. McDONALD. 2007. A population estimate for Golden Eagles in the western United States. *Journal of Wildlife Management* 71:395–402.
- GRENIER, M. AND T. FILIPI. 2009. Estimate of abundance for the white-tailed prairie dog in Wyoming. Pages 149–172 in A. Orabona [Ed.], *Threatened, endangered, and nongame bird and mammal investigations*. Wyoming Game and Fish Department, Lander, WY U.S.A.
- GROSS, J.E., L.C. STODDART, AND F.H. WAGNER. 1974. Demographic analysis of a northern Utah jackrabbit population. *Wildlife Society Monographs* 40:3–68.
- HOEKSTRA, J.M., T.M. BOUCHER, T.H. RICKETTS, AND C. ROBERTS. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8:23–29.
- HOUSTON, C.S. AND M.J. BECHARD. 1984. Decline of the Ferruginous Hawk in Saskatchewan. *American Birds* 38:166–170.
- HOWARD, R.P. AND M.L. WOLFE. 1976. Range improvement practices and Ferruginous Hawks. *Journal of Range Management* 29:33–37.
- HUNT, W.G. 1998. Raptor floaters at Moffat's equilibrium. *Oikos* 82:191–197.
- KEINATH, D.A., M.D. ANDERSEN, AND G.P. BEAUVAIS. 2010. Range and modeled distribution of Wyoming's species of greatest conservation need. Report prepared by the Wyoming Natural Diversity Database, Laramie, WY, for the Wyoming Game and Fish Department, Cheyenne, WY and the U.S. Geological Survey, Fort Collins, CO U.S.A.
- KISSLING, M.L. AND E.O. GARTON. 2006. Estimating detection probability and density from point-count surveys: a combination of distance and double-observer sampling. *Auk* 123:735–752.
- KNICK, S.T., D.S. DOBKIN, J.T. ROTENBERRY, M.A. SCHROEDER, W.M. VANDER HAEGEN, AND C. VAN RIPER, III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634.
- , S.E. HANSER, M. LEU, C.L. ALDRIDGE, AND M.J. WISDOM. 2011. Introduction: an ecoregional assessment of the Wyoming Basins. Pages 1–9 in S.E. Hanser, M. Leu, S.T. Knick, and C.L. Aldridge [Eds.], *Sagebrush ecosystem conservation and management: ecoregional assessment tools and models for the Wyoming Basin*. Allen Press, Lawrence, KS U.S.A.
- KNIGHT, D.H. 1996. *Mountains and plains: the ecology of Wyoming landscapes*. Yale Univ. Press, New Haven, CT U.S.A.
- KOCHERT, M.N. 1972. Population status and chemical contamination in Golden Eagles in southwestern Idaho. M.S. thesis, Univ. Idaho, Moscow, ID U.S.A.
- AND K. STEENHOF. 2002. Golden Eagles in the US and Canada: status, trends, and conservation challenges. *Journal of Raptor Research* 36:32–40.
- , C.L. MCINTYRE, AND E.H. CRAIG. 2002. Golden Eagle (*Aquila chrysaetos*). In A. Poole [Ed.], *The birds of North America online*, No. 684. Cornell Lab of Ornithology, Ithaca, NY U.S.A. <http://bna.birds.cornell.edu/bna/species/684> (last accessed 22 May 2014).
- LAAKE, J., M.J. DAWSON, AND J. HONE. 2008. Visibility bias in aerial survey: mark-recapture, line-transect or both? *Wildlife Research* 35:299–309.
- LEHMAN, R.N., P.L. KENNEDY, AND J.A. SAVIDGE. 2007. The state of the art in raptor electrocution research: a global review. *Biological Conservation* 136:159–174.
- LOKEMOEN, J.T. AND H.F. DUEBBERT. 1976. Ferruginous Hawk nesting ecology and raptor populations in northern South Dakota. *Condor* 78:464–470.
- MACLAREN, P.A., S.H. ANDERSON, AND D.E. RUNDE. 1988. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. *Western North American Naturalist* 48:548–553.
- MANLY, B.F. 2007. Randomization, bootstrap and Monte Carlo methods in biology, Third Ed. Chapman and Hall, Boca Raton, FL U.S.A.
- MILLSAP, B.A., T.G. GRUBB, R.K. MURPHY, T. SWEM, AND J.W. WATSON. 2015. Conservation significance of alternative nests of Golden Eagles. *Global Ecology and Conservation* 3:234–241.
- , AND M.N. LEFRANC, JR. 1988. Road transect counts for raptors: how reliable are they? *Journal of Raptor Research* 22:8–16.
- NICHOLS, J.D., J.E. HINES, J.R. SAUER, F.W. FALLON, J.E. FALLON, AND P.J. HEGLUND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117:393–408.
- NOSS, R.F., E.T. LAROE, III, AND J.M. SCOTT. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28. U.S.D.I. National Biological Service, Washington, DC U.S.A.
- OAKLEAF, R.J., L.E. OLSON, J.R. SQUIRES, AND Z.P. WALLACE. 2014. The status of Golden Eagles (*Aquila chrysaetos*) in Wyoming: a preliminary review. Pages 357–396 in A.C. Orabona and N. Cudworth [Eds.], *Threatened, endangered, and nongame bird and mammal investigations*. Annual completion report. Wyoming Game and Fish Department, Lander, WY U.S.A.

- OLENDORFF, R.R. 1993. Status, biology, and management of Ferruginous Hawks: a review. Raptor Research and Technical Assistance Center, Spec. Rep. U.S.D.I. Bureau of Land Management, Boise, ID U.S.A.
- ORABONA, A.C., C. RUDD, M. GRENIER, Z. WALKER, S. PATLA, AND R. OAKLEAF. 2012. Atlas of birds, mammals, amphibians, and reptiles in Wyoming. Wyoming Game and Fish Department, Nongame Program, Lander, WY U.S.A.
- PHILLIPS, R.L., T.P. MCNEANEY, AND A.E. BESKE. 1984. Population densities of breeding Golden Eagles in Wyoming. *Wildlife Society Bulletin* 12:269–273.
- POLLOCK, K.H., H.D. MARSH, I.R. LAWLER, AND M.W. ALLDREDGE. 2006. Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. *Journal of Wildlife Management* 70:255–262.
- , J.D. NICHOLS, T.R. SIMONS, G.L. FARNSWORTH, L.L. BAILEY, AND J.R. SAUER. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13:105–119.
- QUANG, P.X. AND E.F. BECKER. 1997. Combining line transect and double count sampling techniques for aerial surveys. *Journal of Agricultural, Biological, and Environmental Statistics* 2:230–242.
- R CORE TEAM. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (last accessed 20 May 2013).
- ROTH, S.D., JR. AND J.M. MARZLUFF. 1989. Nest placement and productivity of Ferruginous Hawks in western Kansas. *Transactions of the Kansas Academy of Science* 92:132–148.
- SCHMUTZ, J.K. 1984. Ferruginous and Swainson's Hawk abundance and distribution in relation to land use in southeastern Alberta. *Journal of Wildlife Management* 48:1180–1187.
- , S.H. BRECHTEL, K.D. DESMET, D.G. HJERTAAS, G.L. HOLROYD, C.S. HOUSTON, AND R.W. NERO. 1992. Recovery plan for the Ferruginous Hawk in Canada. Recovery of National Endangered Wildlife (RENEW). Ottawa, Canada.
- , D.T.T. FLOCKHART, C.S. HOUSTON, AND P.D. MCLOUGHLIN. 2008. Demography of Ferruginous Hawks breeding in western Canada. *Journal of Wildlife Management* 72:1352–1360.
- AND D.J. HUNGLE. 1989. Populations of Ferruginous and Swainson's Hawks increase in synchrony with ground squirrels. *Canadian Journal of Zoology* 67:2596–2601.
- SMITH, D.G. AND J.R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. *Brigham Young University Science Bulletin-Biological Series* 18:1–76.
- STEENHOF, K. AND I. NEWTON. 2007. Assessing nesting success and productivity. Pages 181–190 in D.M. Bird and K.L. Bildstein [Eds.], *Raptor research and management techniques*. Raptor Research Foundation, Hancock House Publishers, Blaine, WA U.S.A.
- SUTER, G.W. AND J.L. JONES. 1981. Criteria for Golden Eagle, Ferruginous Hawk, and Prairie Falcon nest site protection. *Raptor Research* 15:12–18.
- THOMAS, L., S.T. BUCKLAND, E.A. REXSTAD, J.L. LAAKE, S. STRINDBERG, S.L. HEDLEY, J.R.B. BISHOP, T.A. MARQUES, AND K.P. BURNHAM. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology* 47:5–14.
- THORINGTON, R.W., J.L. KOPROWSKI, M.A. STEELE, AND J.F. WHATTON. 2012. *Squirrels of the world*. The Johns Hopkins Univ. Press, Baltimore, MD U.S.A.
- UNITED STATES ENERGY INFORMATION ADMINISTRATION. 2014. Number of producing gas wells. U.S. Department of Energy, Washington, DC U.S.A. <http://www.eia.gov> (last accessed March 2014)
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- WHITE, C.M. AND T.L. THUROW. 1985. Reproduction of Ferruginous Hawks exposed to controlled disturbance. *Condor* 87:14–22.
- WYOMING OIL AND GAS CONSERVATION COMMISSION. 2014. Well header data 052013 DB5. <http://wogcc.state.wy.us/> (last accessed 30 May 2013).
- WOFFINDEN, N.D. AND J.R. MURPHY. 1977. Population dynamics of the Ferruginous Hawk during a prey decline. *Western North American Naturalist* 37:411–425.
- AND ———. 1983. Ferruginous Hawk nest site selection. *Journal of Wildlife Management* 47:216–219.
- AND ———. 1989. Decline of a Ferruginous Hawk population: a 20-year summary. *Journal of Wildlife Management* 53:1127–1132.

Received 18 June 2014; accepted 24 February 2015
Associate Editor: Chris W. Briggs